Avian diversity in Southern Africa: patterns, processes and conservation

by

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"If we give our very best to all the children of today, and if we pass on our planet in the fullness of her beauty and natural richness, we will be serving the children of the future."

Nelson R. Mandela (2001)

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Abstract

Understanding the mechanisms, both biological and anthropogenic, that account for changes in environmental variables and that translate into altered species richness and species turnover (β-diversity) patterns is an important component of efficient conservation planning. However, several issues need to be addressed to understand these mechanisms. First, at which scale(s) should species richness and turnover patterns be examined? These patterns, as well as the role of variables explaining them, may differ across scales. Second, what influences do landscape transformation and human population size have on species biogeographic patterns? These factors pose the single most important threat to biodiversity, and are often overlooked. If anthropogenic land transformation plays a dominant role in determining species richness and turnover patterns, then using present patterns to understand biological processes could provide erroneous answers. Third, despite the dynamic nature of the environment, studies that take the manner in which humans may affect biodiversity patterns into account are often based on static perspectives. Environmental change could therefore also precipitate changes in the relationships between species richness, environmental variables and human densities. Consequently, it is crucial for land-use decision makers to incorporate such changes into conservation strategies to achieve effective long-term conservation. Fourth, spatial autocorrelation in ecological data results in lack of data independence and, consequently, may lead to spurious results in statistical analyses. Finally, are ecological transition zones spatially congruent and are these adequate conservation areas? This thesis addresses these issues by combining South African avifaunal, environmental, human population and land use data in a GIS and statistically analysing the emergent patterns. The potential effects of climate change on these species and human patterns and their conservation implications are also investigated. The results indicate that: (i) bird richness is correlated with, and hence likely a function of several environmental variables including primary productivity, precipitation, absolute minimum temperature, and, at coarser resolutions, habitat heterogeneity; (ii) spatial resolution and extent must be considered during investigations of these relationships; (iii) species richness and human density are positively correlated, apparently because both respond positively to increased levels of primary productivity; and (iv) conservation area selection procedures tend to identify high ecological transition areas as important for biodiversity conservation. Elevated β-diversity in the avifauna is found in biome transition areas but not in land transformation transition areas, suggesting that the latter has little influence on the avifauna. Finally, although current human demands on natural resources are high in and around most conservation areas, there are some areas important for biodiversity conservation outside formal protected areas with lower than expected human population densities both prior to and after considering climate change. These latter areas could minimize potential future conflict between human resource and conservation needs.

Keywords: biological mechanisms, anthropogenic mechanisms, species richness, species turnover, β-diversity, conservation, scale, human population, biogeography, spatial autocorrelation, ecological transition zones

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Disclaimer

This thesis consists of a series of chapters that have been prepared for submission to, or publication in, a range of scientific journals. As a result styles may very between chapters in the thesis and overlap may occur to secure publication entities.

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CHAPTER 1

General Introduction

Broad-scale patterns of spatial variation in biotic diversity have received the attention of ecologists and biogeographers for almost two centuries (Gotelli & Graves 1996). Recently, with the increasing need to understand human impacts on biodiversity, there has been renewed interest in examining patterns of species richness through space and time, and the mechanisms underlying these patterns (see e.g. Rohde 1992, Rosenzweig 1995, Rahbek 1997, Brown & Lomolino 1998, Roy et al. 1998, 2000a, b, Gaston & Blackburn 2000, Rahbek & Graves 2000, 2001, see also the review by Gaston 2000 and references therein). This increasing interest has also been precipitated partially by the increasing availability of broad-scale data on biotic diversity and climatic variables, and the analytical tools required for testing the competing hypotheses proposed to explain these patterns. Indeed, it has been argued that the lack of modern data sets was one of the main factors that previously prevented rigorous hypothesis testing (Rahbek & Graves 2000, see also Blackburn & Gaston 2002 for why deficiencies often exist in data sets capturing information at large spatial extents). Several significant themes have emerged from this recent work.

Mechanisms underlying species richness gradients

From a multitude of hypotheses proposed to explain latitudinal gradients in species richness, four are gaining increasing currency. These are the area hypothesis (Rosenzweig 1992, 1995, Rosenzweig & Sandlin 1997, Chown & Gaston 2000a, b), the species-energy hypothesis (Currie 1991, Wright et al. 1993, Gaston & Blackburn 1995, Blackburn & Gaston 1996a, Kerr & Packer 1997, O'Brien 1998, Lennon et al. 2000), the evolutionary rates hypothesis (Pianka 1966, Rohde 1998, Ricklefs et al. 1999, Qian & Ricklefs 2000, Willis & Whittaker 2000), and the Rapoport's rule hypothesis (Stevens 1989, Rahbek 1997, Gaston et al. 1998, Rohde 1999, Ashton 2001). A fifth hypothesis, namely null models which assume that a random latitudinal relationship between the size and placement (based on the midpoint) of the geographical ranges of species alone (i.e. in the absence of any environmental gradients) explains latitudinal gradients in richness has also been proposed (Colwell & Hurtt 1994, Colwell & Lees 2000, Jetz & Rahbek 2001). However, generally this hypothesis is only weakly supported (notably the shortcoming to explain the mid-domain effect in two-dimensional models – see Bokma et al. 2001). Of these different hypotheses, the species-energy hypothesis, is thought to be a prime contender for explaining variation in richness across latitude, although there are still significant problems associated with this idea (notably the small proportion of incoming energy that is converted to biomass – see Gaston 2000).

Furthermore, although it has long been recognized that spatial scale (i.e. resolution and/or extent) affects the outcomes of studies seeking to identify correlates of, or causal mechanisms underlying, the variation in species richness patterns (see e.g. Whitehead & Jones 1969, Whittaker 1977, Ricklefs 1987, Wiens 1989), the effects of spatial scale are only now being investigated adequately (e.g. Taylor & Gaines 1999). Although there is clearly no correct spatial scale at which ecological patterns and processes should be studied

(Kendal & Aschan 1993, Blackburn & Gaston 1996b, Böhning-Gaese 1997, Rahbek 1997, Kaspari et al. 2000a, b, Rahbek & Graves 2000, Blackburn & Gaston 2002), it is clear that the scale at which a study is undertaken can have profound effects on its conclusions (Ricklefs 1987, Økland et al. 1996, Rahbek & Graves 2000, Whittaker et al. 2001). This is because the importance of one set of explanatory variables may vary across scales (Rosenzweig 1995, Böhning-Gaese 1997, Chown & Gaston 1999, Scheiner et al. 2000, Whittaker et al. 2001). For example, in the context of the species-energy theory, Fraser (1998) suggested that the extent to which habitat heterogeneity serves as a correlate of species richness increases in importance with a decline in spatial resolution. There are many other examples of how spatial resolution or extent of a study can affect perceived ecological patterns. Indeed, in a recent review, Waide et al. (1999) examined *c.* 200 relationships between productivity and species richness and found a complex variety of forms of the relationships and potential mechanisms explaining them. Based on both theoretical considerations and empirical analyses Waide et al. (1999) concluded that the relationship between productivity and species richness is highly scale dependent (both extent and resolution) (see also Mittelbach et al. 2001). Consequently, there is a considerable need to understand scaling effects when studying ecological patterns and processes.

The importance of beta-diversity

A second significant theme emerging from recent work seeking to understand the fundamental mechanisms underlying patterns in biotic diversity is the recognition that understanding spatial turnover patterns in species richness and species identity forms an essential part of such investigations (Williamson 1988, Williams 1996, Lennon et al. 2001, Whittaker et al. 2001). Despite a long history of interest in species turnover (Whittaker 1960, 1977, Cody 1975, Wilson & Shmida 1984, Ryti & Gilpin 1987, Brown 1995, Hanski & Gyllenberg 1997, Desrochers & Fortin 2000, Rahbek & Graves 2001), the concept has remained reasonably poorly understood until quite recently (see e.g. Lennon et al. 2001). This is mainly true because of a poor understanding of what precisely is being measured when examining spatial turnover in species richness (see Lennon et al. 2001). Nonetheless, testing predictions concerning patterns of species turnover may be one means of independently testing several key hypotheses proposed for explaining spatial patterns in species richness. For example, Koleff & Gaston (2001) showed that examination of beta diversity patterns might provide an independent means of assessing the extent to which mid-domain models can account for latitudinal patterns in species richness. Moreover, identifying the location of considerable species turnover and environmental transition zones (i.e. areas with major changes in climate, topography and vegetation), may provide insight into the extent to which faunal changes in diversity might be driven by changes in environmental variables. This is because sharp transition areas in the environmental variables explaining species turnover patterns should be reflected in areas with uneven species turnover patterns (see e.g. Gosz 1993, Krasnov & Shenbrot 1998, Bestelmeyer & Wiens 2001). Furthermore, identifying areas showing considerable species turnover may also be crucial from a conservation perspective when using area selection techniques. For example, if algorithms used to identify minimal area networks for conservation have a tendency to select areas with considerable species turnover, then most species will be protected at the edge of their distribution ranges, and this might not always result in the long-term persistence of a given assemblage (Araújo & Williams 2001, Reyers et al. 2002).

Spatial autocorrelation

There has been an explosion of interest in the effects of spatial autocorrelation on the outcomes of investigations of large-scale patterns (Borcard et al. 1992, Smith 1994, Legendre & Legendre 1998, Boone & Krohn 2000, Lennon et al. 2001). Spatial autocorrelation is the lack of statistical independence of data points that are closely associated in space, essentially because the same entities are being measured more than once. Consequently, autocorrelation leads to an overestimation of the number of degrees of freedom, which in turn leads to spurious significance levels in statistical tests (Clark 1982, Clifford et al. 1989, Legendre & Legendre 1998, Boone & Krohn 2000, Lennon 2000). Moreover, variation in a given variable, such as species richness, may result from spatial autocorrelation of the variable itself, from relationships between the variable of interest and another variable that is spatially structured, or from relationships between the two variables that are independent of space (Legendre & Legendre 1998). However, because many studies examining large-scale patterns in species richness across space have been confounded by the problems associated with spatial structuring of the data, this problem has generally been downplayed or glossed over (see e.g. Currie 1991, O'Brien 1993, Kerr & Packer 1997, Jetz & Rahbek 2001). This might lead to the support of hypotheses, proposed to explain species richness patterns, that are at best only partially correct or, at worst, incorrect (Lennon 2000). Therefore it is critical to understand the form of spatial autocorrelation in the data sets used for examining spatial patterns.

There are several ways to minimize the problems for statistical inference caused by spatial autocorrelation. First, Clifford et al.'s (1989) modified correlation test can be implemented. This corrects the significance of the standard product-moment correlation coefficient for the spatial dependency within and between two patterns (see Lennon et al. 2001). Second, the spatial structure in data sets can be examined using partial regression analyses to partition variation in the dependent variable of interest into its non-environmental spatial, spatially structured environmental, non-spatial environmental and residual variation (see Legendre & Legendre 1998). Third, spatial autocorrelation analysis (Moran's I; see Legendre & Legendre 1998) can also be used to further understand the form of spatial autocorrelation in data sets by examining the spatial patterns in the dependent and independent variables. Fourth, a randomization test for the association of two spatial patterns has been proposed by Lennon (2000) to deal with spatial autocorrelation problems (see Lennon 2000 for discussion on this method).

Human impacts on biodiversity

Finally, the influence of human activities on large-scale patterns in biodiversity has grown at an unprecedented rate. The major impacts on biodiversity include those of habitat destruction (Tilman et al. 1994, 1997, 2001, Stone 1995, Bawa & Dayanandan 1997, Laurance et al. 1999, 2001), climate change (Parmesan 1996, Dunn & Winkler 1999, Parmesan et al. 1999, Pounds et al. 1999, Thomas & Lennon 1999, Sillett et al. 2000, Shannon 2000, Pennisi 2001, van Jaarsveld & Chown 2001, Warren et al. 2001, Erasmus et al. 2002, Hannah et al.

2002, McLaughlin et al. 2002, Walther et al. 2002) and biological invasions (Lodge 1993, Mack & Dantonio 1998, Everett 2000, Levine 2000). One consequence of increasing impacts is that the ways in which humans and other species might be in conflict owing to similar responses to environmental variables has become a major cause of concern. Recent studies have shown that areas of high human activity and therefore significant human land transformation (Easterling et al. 2001, Harcourt et al. 2001) are spatially congruent with areas of high species richness (Balmford & Long 1994, Fjeldså & Rahbek 1998). This is true apparently because both variables respond positively to increasing levels of primary productivity (Balmford et al. 2001a, but see also Huston 1993), and this overlap has several profound negative consequences for biodiversity (see e.g. Bibby 1995, Lombard 1995a, Freitag et al. 1998, Brooks et al. 1999, Ceballos & Ehrlich 2002, Fairbanks et al. 2002). One way to mitigate these negative impacts on biodiversity of human activities is to undertake well-informed conservation and land-use planning. It is therefore important to understand and to take into account the extent to which conservation planning may be influenced by unexpected outcomes of the methods often used for conservation. For example, recent studies have shown that there is a tendency for human population densities to be higher than expected by chance in areas surrounding currently designated reserves (Terborgh 1999, Harcourt et al. 2001, Parks & Harcourt 2002). This result indicates that formal reserve areas, which serve as one of the most commonly used and often most effective conservation methods (Bruner et al. 2001), are under increasing external pressure. Moreover, because the environment is not static, i.e. both biological and anthropogenic processes influencing the distribution of biodiversity are dynamic, a change over time will also bring about a change in the form of the relationships between species richness, environmental variables, and human densities. Consequently, it is important that land-use decision-makers consider ways of incorporating these changes into their conservation strategies if they are to succeed in their goal of long-term conservation (see Rodrigues et al. 2000a, b, Fairbanks et al. 2001, Hannah et al. 2002 for discussion).

In this thesis, these four major concerns are explored explicitly using data from the Southern African Bird Atlas Project (SABAP; Harrison et al. 1997).

Objectives

The initial objective of this study was to develop a better understanding of species richness patterns for all birds across South Africa and Lesotho (see Chapter 2). The study therefore complements existing investigations of plants and mammals (e.g. O'Brien 1993, 1998, O'Brien et al. 1998, 2000, Andrews & O'Brien 2000) by examining which environmental variable or combination of variables best explains gradients in avian species richness across South Africa. Specifically, the spatial structure in the avian data is examined using partial regression analyses (see Legendre & Legendre 1998).

Previous studies have shown that there are gentle richness gradients across the region, with subtraction in the eastern forests as one moves south, and a decline in species richness associated with a decline in productivity levels to the west (O'Brien 1993, 1998, O'Brien et al. 1998, Andrews & O'Brien 2000, see also Chapter 2). To further understand bird species richness patterns in South Africa and Lesotho, the relationship between avian transition and sharp climatic transition zones, sharp vegetation transition zones or some combination of the two variables are therefore examined (see Chapter 3).

After gaining a better understanding of avian transition areas in South Africa (see Chapter 3), the bird distribution data are then used to determine whether an approach based on the complementarity principle, which is often used as a starting point for selecting priority conservation areas (Nicholls & Margules 1993, Margules et al. 1994, Cabeza & Moilanen 2001), tends to select sites in areas of ecological transition (see Chapter 4). The outcome of this study provides a useful contribution to the debate on potential drawbacks of such approaches, (e.g. the minimum set approach) when used to assist effective species conservation over the long-term.

Finally, the relationships between current and future human activity, species richness and conservation requirements are examined by comparing the bird data with South African population census data (Statistics South Africa 1996) using the data resolution employed for local conservation in South Africa, namely a quarter-degree resolution (see Lombard 1995a, Lombard et al. 1995, Anonymous 1997, SA-ISIS 2001). These results are consistent with previous results for the rest of Africa (see Balmford et al. 2001a, b, Harcourt et al. 2001), and contribute to the debate on how best to integrate human development and conservation needs for the region (see Chapters 5, 6, see also Lombard 1995a, Freitag et al. 1998, Erasmus & van Jaarsveld 2002). The importance of taking the dynamics of the environment into account when planning species conservation strategies is crucial if conservation efforts are to succeed in real world scenarios (McNeely 1994, Soulé & Sanjayan 1998, Faith 2001, Huston 2001, James et al. 2001, see also Rodrigues et al. 2000a, b).

Data and the rationale underlying its use

South Africa and data on birds were chosen for several reasons.

Data availability and reliability

Birds have regularly been used for delineation of biogeographic regions and for transitions among them (see Williams et al. 1999 for partial review), and the SABAP constitutes the most comprehensive database available on a southern African animal group (Harrison et al. 1997). Moreover, the SABAP represents one of the most detailed datasets on birds at a national-level in Africa (Brooks & Thompson 2001). It is the product of the combined efforts of a large body of professional and amateur ornithologists who worked for twelve years on the production of this database. The data provide information on the distribution and relative abundance of 900 bird species in southern Africa (here considered a reasonable surrogate for biodiversity – see Gaston 2000). In addition, analyses of species representation in major biomes and of seasonality are available. Data were collected mainly between 1987 and 1992, at a spatial resolution of a quarter-degree grid (15' x 15' ≈ 676 km^2) for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid (30' x 30' ≈ 2500 km^2) for Botswana (for a detailed description of methods see Harrison et al. 1997). Areas that received relatively few visits were specifically targeted for additional fieldwork, resulting in a thorough coverage of all but approximately 5% of the grid cells. As such, the atlas represents one of the most powerful tools available for investigating patterns of diversity in southern Africa. Several works addressing conservation planning issues have already emerged from analyses of the SABAP data, and these include Harrison & Martinez (1995), Lombard (1995a), Allan et al. (1997), Fairbanks et al. (2001, 2002), Rodrigues & Gaston (2002), Gaston & Rodrigues (in press). For the purpose of this study the analyses were restricted to South Africa and Lesotho ($N = 1858$ quarter-degree grid cells – Fig. 1) because of the availability of appropriate environmental and human population density data. Marine, vagrant, marginal and escaped bird species were excluded from the analysis (651 species were analysed).

Marked abiotic variation in the region

Southern Africa is characterized by marked spatial variations in the abiotic environment (i.e. has a broad range of energy availabilities). Specifically it is characterized by a marked east-west (longitudinal) aridity gradient that is thought to have a significant effect on vegetation heterogeneity in South Africa (O'Brien 1993, Schulze 1997a, b, O'Brien 1998, O'Brien et al. 1998, Andrews & O'Brien 2000, Woodward et al. 2001). This considerable gradient is responsible for considerable transitions in vegetation and climate, and therefore if there is spatial congruence in transition zones between environmental variables and avian species turnover these should be readily identifiable. This longitudinal gradient also provides a useful test of the species-energy hypothesis that is not confounded by changes in other latitudinal variables (e.g. season length). Marked transition zones are also characteristic of South Africa's seven major biomes (Rutherford & Westfall 1994, Low & Rebelo 1996) (Fig. 2). These biomes are defined based on five explicit criteria (i) they are the largest land community unit recognized at a continental or subcontinental level; (ii) they are units mappable at a scale of no larger than about 1:10 million; (iii) they are distinguished from other biomes primarily on the basis of dominant plant life form(s) in climax systems; (iv) they are distinguishable from other biomes secondarily on the basis of those major climatic features that most affect the vegetation; and (v) they are not unnatural or major anthropogenic systems (see Rutherford & Westfall 1994 for further discussion). This study included the forest, thicket, savanna, grassland, Nama karoo, succulent karoo, and fynbos biomes. Each of these biomes is characterised by several vegetation types, giving a total of 68 different vegetation types for the study area (see Low & Rebelo 1996 for further information).

Human population density and conservation area data availability

There are modern data available on the region's human population density (Statistics South Africa 1996), and extent and nature of anthropogenic activities (Fairbanks et al. 2000). In addition, the size of protected areas, their spatial location, and year of proclamation are well known (WCMC 1997, see http://www.wcmc.org.ukindexshock.html/). In conjunction with the avian data, this information can be used to examine the relationships between bird species richness, human population density, landscape transformation, and conservation areas in South Africa. Moreover, although South Africa is considered a developing country (O'Riordan 1998), these relationships can be examined in a country characteristic of a well-developed, mechanized agricultural infrastructure, which means both local food security and substantial export-based agricultural contributions to its GDP (World Development Report 2000/2001).

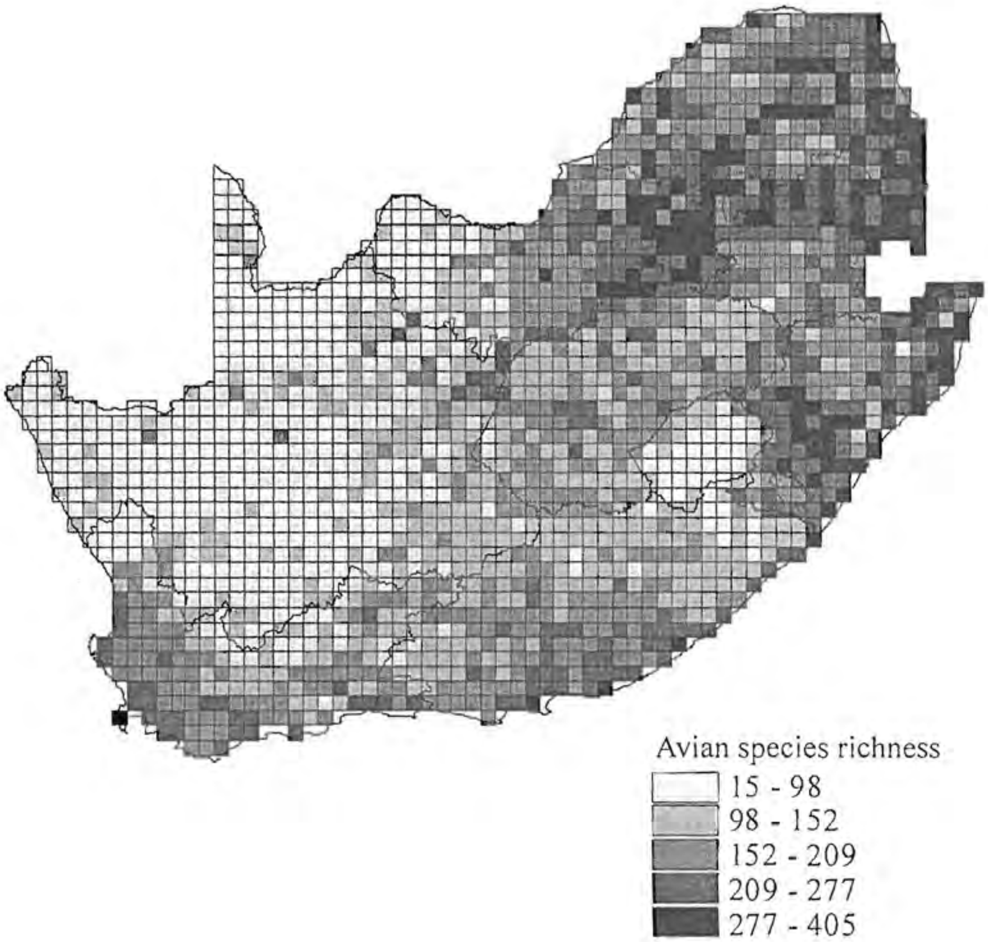

Figure 1 Avian species richness variation across South Africa.

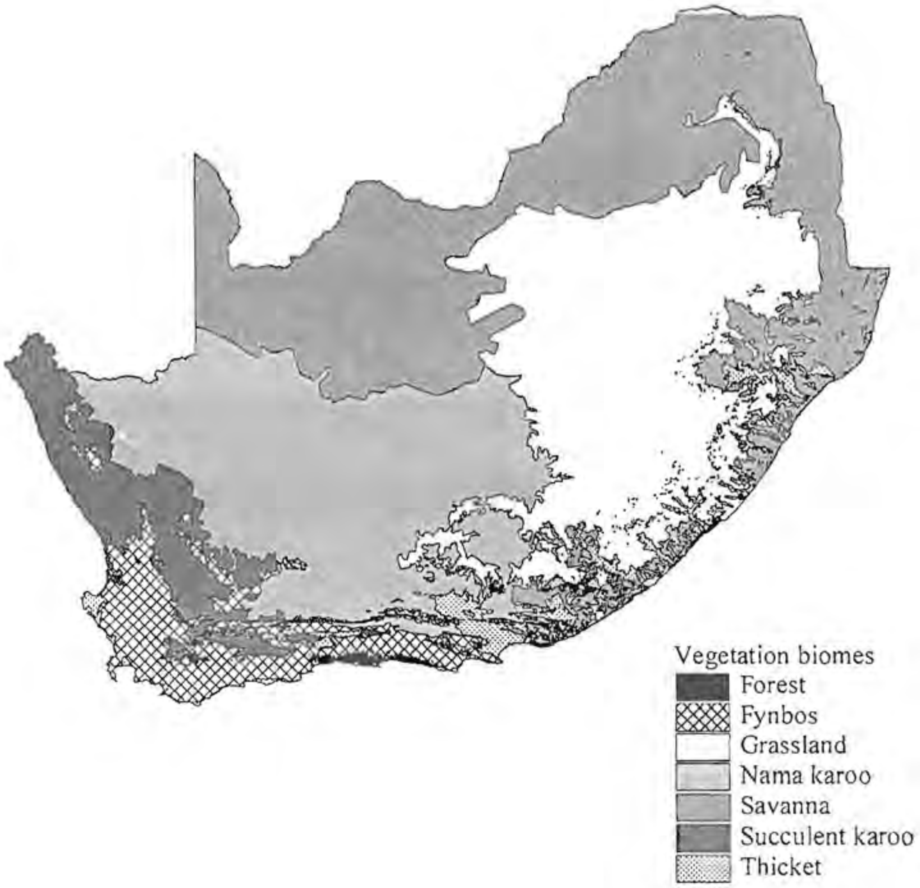

Figure 2 The vegetation biomes of South Africa and Lesotho based on Low & Rebelo (1996).

This well-developed agricultural infrastructure is useful to further evaluate Huston's (2001) argument that such an infrastructure is likely to reduce the correlation between human population density and net primary productivity that is apparently a characteristic of developing nations.

The availability of highly transformed areas

Although some areas in South Africa remain relatively untransformed by humans, there are some large parts which have been transformed by extensive human land use over the past several hundred years (Macdonald 1989, Scholtz & Chown 1993). Indeed, the south-western region of the country has been farmed for the past 350 years, leading to massive landscape transformation over much of the region (e.g. Richardson et al. 1996). Thus, if anthropogenic landscape transformation has an influence on broader scale species richness patterns it should be detectable, at least in the heavily transformed south-western parts of South Africa. If this transformation has an overt effect on avian richness patterns, it will further stress the influence of human activities on large scale patterns in biodiversity.

A scale relevant to conservation planning in times of change

The spatial scale (resolution and extent) at which this study is conducted is also useful to test conservation planning ideas because it is that at which conservation planning often takes place. That is, within countries, and using data that are at the finest resolution available for the region (e.g. Lombard 1995a, b, van Jaarsveld et al. 1998). Indeed, data at a quarter-degree resolution, which represents the finest resolution for national data sets in South Africa, are generally used for conservation planning in South Africa (Lombard 1995a, Lombard et al. 1995, Anonymous 1997, SA-ISIS 2001). Consequently, the results obtained from this study, and discussions leading from these results are therefore potentially applicable for landscape planning in South Africa.

Furthermore, in South Africa, a great deal of emphasis has been placed on predictions of the effects of climate change on the biota and on development options for the region (see Rutherford et al. 1999, Erasmus et al. 2002, Erasmus and van Jaarsveld 2002). This has considerable significance for conservation planning because conservation planning strategies need to be dynamic to achieve sustainable land use planning over the long term (Rodrigues et al. 2000a, b, Fairbanks et al. 2001, Hannah et al. 2002). To investigate climate change effects on the region, a South African country study was conducted, focusing on assessing, predicting and quantifying climate change impacts on the environment at a national level (Kiker 2000). This study not only provided impetus for a number of related studies but also continued work on existing themes of climate change predictions and sustainable land use planning. Collating data from Kiker (2000), van Jaarsveld & Chown (2001) assessed the degree of changing conflict between conservation and human development needs in South Africa with climate change being highly likely to occur. Expanding on the South African country study with specific reference to biodiversity impacts, Erasmus et al. (2002) modelled and discussed the conservation consequences of distribution range shifts for several bird species across South Africa after taking the effects of a doubling in pre-industrial CO_2 levels using the HadCM2 (no sulphates) model (Shannon 2000) into account.

This information is particularly useful in a conservation planning context and has been partially incorporated into development scenarios for South Africa (see Erasmus & van Jaarsveld 2002).

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CHAPTER 2

Species richness, environmental correlates, and spatial scale: a test using South African birds

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ABSTRACT: Energy and habitat heterogeneity are important correlates of spatial variation in species richness, though few investigations have sought to determine simultaneously their relative influences. Here, we use the South African avifauna to examine the extent to which species richness is related to these variables, and how these relationships depend on spatial grain. Taking spatial autocorrelation and area effects into account, we find that primary productivity, precipitation, absolute minimum temperature, and, at coarser resolutions, habitat heterogeneity account for most of the variation in species richness. Species richness and productivity are positively related, whereas the relationship between potential evapotranspiration (PET) and richness is unimodal. This is largely because of the constraining effects of low rainfall on productivity in high-PET areas. The increase in the importance of vegetation heterogeneity as an explanatory variable is caused largely by an increase in the range of vegetation heterogeneity included at coarse resolutions and is probably also a result of the positive effects of environmental heterogeneity on species richness. Our findings indicate that species richness is correlated with, and hence likely a function of several variables, that spatial resolution and extent must be taken into account during investigations of these relationships, and that surrogate measures for productivity should be interpreted cautiously.

A recurrent theme emerging from recent studies is that energy either has a primary role in generating spatial variation in species richness or is an important modulating factor (Currie 1991; O'Brien 1998; Chown and Gaston 1999; Gaston 2000; Morin 2000). Studies have shown not only that energy is strongly correlated with species richness (Currie 1991; O'Brien 1998) but also that there is a clear set of mechanisms that can account for the way in which changes in energy availability translate to alterations in numbers of individuals and the way these, in turn, are partitioned between species (O'Brien 1998; Kerr et al. 1998; Chown and Gaston 1999; Kerr and Currie 1999; Currie et al. 1999; Kaspari et al. 2000*a*, 2000*b*). However, many scientists believe that several other factors may be responsible for some component – and perhaps in a large way - of spatial variation in species richness (Rosenzweig 1995). Of particular interest is the idea that at the highest energy levels energy loses its grip on species richness and other factors become more significant (Kerr and Packer 1997; Chown and Gaston 1999). At least in some terrestrial systems, habitat heterogeneity is thought to account for the remaining variation (Kerr and Packer 1997).

That habitat heterogeneity is likely to explain some proportion of the variance in species richness is not surprising. The literature is replete with studies showing that species richness is correlated with habitat heterogeneity and complexity at local, regional and continental scales (e.g., MacArthur 1964; Verner and Larson 1989; O'Connor et al. 1996; Wiebe and Martin 1998; Ricklefs and Lovette 1999; Boone and Krohn 2000*b*). Moreover, many studies have provided insight into the way heterogeneity might cause changes in species richness by influencing the presence or abundance (Verboom et al. 1991; Villard et al. 1995), movements (Wegner and Merriam 1979; Machtans et al. 1996), and persistence (Hanski et al. 1994) of species.

Nonetheless, few investigations have sought to determine simultaneously the relative influences of energy availability and habitat heterogeneity on species richness. This is particularly important because energy availability is thought to have a direct effect on habitat heterogeneity (Wylie and Currie 1993; Waide et al. 1999; Morin 2000), which in turn has an effect on species richness that increases in importance from the local to regional scales (Wright et al. 1993). At least one regional-scale study has suggested that the extent to which habitat heterogeneity serves as a correlate of species richness is also dependent on the spatial grain of the study, increasing in importance with a decline in spatial resolution (Fraser 1998). This may occur for both statistical and biological reasons. A decline in spatial resolution means larger sampling units, which in turn incorporate greater climatic, and hence habitat variability. Thus, fewer sampling units cover a wider range of vegetation types. In consequence, the strength of the relationship between vegetation heterogeneity and species richness is likely to increase as spatial resolution declines (see Currie 1993 for discussion of this effect in another context). At the same time, a change in spatial resolution may result in a difference in the importance of habitat heterogeneity as a correlate of species richness because of an increase in the heterogeneity of resource production characteristics, which in turn has an influence on species richness (Wright et al. 1993).

The aim of this article is, therefore, to examine the extent to which species richness is related to abiotic variables (some of which provide measures or reasonable surrogates of ecosystem productivity and others of environmental energy) and habitat heterogeneity at a regional scale, and how these relationships depend on the resolution (spatial grain) of the study when the spatial extent is kept constant. For this purpose we use the South African avifauna as a test case. We do this because there are marked spatial variations in the abiotic environment across South Africa, specifically a marked east-west aridity gradient (Schulze 1997*a*; see also O'Brien 1993, 1998; O'Brien et al. 1998), and because it has long been maintained that vegetation complexity accounts for most variation in bird species richness in the region (Winterbottom 1978; Osborne and Tigar 1992; Allan et al. 1997).

Methods

Data

The Southern African Bird Atlas Project (SABAP; Harrison et al. 1997) provides the most comprehensive information available on the distribution of birds in southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid (15 min x 15 min ≈ 676 km^2) for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid (30 min x 30 min ≈ 2500 km^2) for Botswana (for a detailed description of methods see Harrison et al. 1997). For the purpose of this study the analyses were restricted to South Africa and Lesotho because of the availability of appropriate environmental data.

To determine the effect of variation in spatial resolution on the relationship between species richness and environmental variables, we divided South Africa into three different geographical quadrant resolution systems consisting of 1,858 quarter-degree grid cells (approximately equal area, but varying from 635 km^2 in the north to 712 km^2 in the south), 458 half-degree grid cells, and 102 one-degree grid cells (~100 km x 100 km). Grid cells including both land and ocean surfaces simultaneously were excluded from the analysis. The number of bird species occurring in each quarter-degree cell was determined using the SABAP data. Bird species richness within the section of a grid cell extending outside the study area (e.g., into Botswana) was assumed to be equivalent to the species richness inside the study area (although the overall proportion of such grid cells in the study was low at 4%, 3% and 3% of the total number of grid cells for each resolution, respectively). Marine, vagrant, marginal and escaped bird species were excluded from the analysis (651 species were analyzed).

For each quarter-degree cell, values were calculated for each of seven abiotic environmental variables (some acting as surrogates for energy availability) that were selected *a priori*, based on an assessment of which of these were biologically most meaningful in the context of our investigation (see also Currie 1991; Kerr and Packer 1997; O'Brien et al. 1998; Andrews and O'Brien 2000). These variables were mean absolute monthly minimum (MIN) and mean absolute monthly maximum (MAX) temperatures (^{0}C) averaged over the year; mean monthly minimum (MINMO) and mean monthly maximum (MAXMO) temperatures (^{0}C) of the coldest and hottest months, respectively; mean annual precipitation (PPT; mm yr^{-1}); mean annual solar radiation (SRAD; MJ m^{-2} yr^{-1}); and mean annual potential evapotranspiration (PET; an unscreened A-Pan equivalent; mm yr^{-1}). These values were calculated using monthly data based on interpolated climate surfaces for the past 30 – 50 yr; these data were supplied to us by the South African Computing Center for Water Research (see Schulze 1997*b*). In the central and western parts of the study area these surfaces may be subject to greater error given a paucity of meteorological stations from which data for the interpolations could be gathered.

Abiotic and richness data at the quarter degree resolution were rescaled to half-degree and one-degree grid cell sizes. For the richness data, duplicate species were removed and for the abiotic data the mean value of participating quarter-degree grid cells was assigned to the appropriate half- or one-degree grid cell. For measuring productivity, we obtained data on mean annual net primary productivity (NPP; g C m^{-2} yr^{-1}) and leaf area index (LAI; the total one-sided leaf area over a unit area of ground, i.e., area of leaf divided by area of ground) based on model simulation outputs only at the half-degree resolution (see Woodward et al. 2001 for information on the SDGVM model used to generate these simulated data sets). The data were then similarly rescaled to a one-degree grid cell size.

For measuring habitat heterogeneity, we enumerated the number of vegetation types (VEG) occurring in each quarter-degree cell based on Low and Rebelo (1996). These authors define "vegetation type" as a coherent array of communities that share common species (or abundances of species), have similar vegetation structure, and share the same set of ecological processes. Number of vegetation types is commonly employed as a measure of habitat heterogeneity or habitat complexity (Reed 1981; Kohn and Walsh 1994); VEG was also rescaled for half- and one-degree grid cell sizes, which provided one way of measuring habitat heterogeneity within a grid cell. A second method used evenness of vegetation-type cover. Low and Rebelo's (1996) map of 68 vegetation types across South Africa was digitized and replotted in ArcInfo. This software was used to calculate the percentage of vegetation-type coverage of each cell at each resolution (Albers equal area projection). As in the case of bird species richness, vegetation-type cover within the section of a grid cell extending outside the study area was assumed to be equivalent to that of the grid cell section inside the study area. From these vegetation type proportion values in each cell, the Shannon-Wiener function was used as a measure of vegetation type evenness (*E*) for each cell at each resolution (Krebs 1999). Evenness values vary between 0 and 1, with higher values indicating more evenly distributed vegetation types and therefore greater heterogeneity within a cell.

Regression analysis

For each resolution, we used linear and curvilinear regressions to investigate relationships between all pairs of environmental variables and between avian species richness and each independent environmental variable (bivariate relationships). Tabulated regression results were subject to sequential Bonferroni corrections (Rice 1989). We subsequently explored the data in greater depth using models that included all combinations of two explanatory variables, but only those providing the best significant fits after sequential Bonferroni correction are reported. Stepwise variable selection procedures were not used because of significant collinearity and because of the problems associated with interpretation of model outputs (James and McCulloch 1990). Because O'Brien et al. (1998) found that a combination of PPT and minimum monthly PET (PEMIN) explained a considerable portion of the variation of woody plant richness in southern Africa, we also assessed the ability of their multivariate model to explain avian species richness.

Spatial data analysis

The presence of spatial autocorrelation within ecological data results in a lack of independence of data points and, consequently, an overestimation of the number of degrees of freedom in an analysis (Clark 1982; Legendre and Legendre 1998; Boone and Krohn 2000*a*). Moreover, variation in a given variable, such as species richness, may result from spatial autocorrelation of the variable itself, from relationships between the variable of interest and another variable that is spatially structured, or from relationships between the two variables that are independent of space (Legendre and Legendre 1998). Unlike many previous analyses that have generally downplayed or glossed over the problems associated with spatial structuring of the data, here we employed partial regression analyses to address both issues. Variation in avian species richness was partitioned into four components: (*a*) non-environmental spatial – that component of the spatial variation in species richness that is not shared with the environmental variables; (*b*) spatially structured environmental – spatial structuring in the species richness data that is shared with the environmental variable data; (*c*) non-spatial environmental – that component of the spatial variation in species richness that can be explained by the environmental variables independent of any spatial structure; and (*d*) unexplained (residual) variation (Legendre and Legendre 1998).

The spatial component of avian species richness for each resolution was modeled using a third-order polynomial of the form

$$f(x,y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3, \qquad (1)$$

where x and y represent longitude and latitude respectively. This expression is sufficient to extract any linear gradients from the data as well as more complex features such as patches or gaps (Legendre 1990; Borcard et al. 1992). The coefficient of determination (r^2) for this relationship was used as a measure of that component of the variation in bird species richness that is explained by a combination of the non-environmental spatial component (component *a*) and the spatially structured environmental component (component *b*). The r^2 values of the bivariate or multivariate relationships between species richness and environmental variables, obtained from the previous analyses, were used as a measure of the variation explained by a combination of the spatially structured environmental component (component *b*) and the non-spatial environmental component (component *c*). The variation in species richness explained by components $a + b + c$ was determined from a model incorporating both the environmental and spatial variables. Tabulated partial regression model results were subject to sequential Bonferroni corrections. By subtraction we estimated the amount of variation accounted for by each of the components separately.

To understand further the form of the spatial autocorrelation in the data, we investigated spatial patterns in avian species richness and the most significant environmental correlates of this variation at the one-degree grid square resolution. To do this, we used spatial autocorrelation analysis (Moran's I; see Legendre and Legendre 1998) and, specifically SAAP-PC Version 4.3 (Exeter Software; Wartenberg 1989; program limitations precluded analysis at the other scales). Correlograms based on fifteen equal distance classes (123 km) (covering the full spatial extent of the data) were used to graphically represent the changes in the autocorrelation coefficients with physical distance between pairs of grid cells (Legendre and Legendre 1998). Distance classes with less than 1% of the total number of point pairs (the two largest distance classes) were considered unreliable and were not interpreted (Legendre and Fortin 1989). We used Bonferroni approximation (correcting for multiple comparisons) to evaluate the overall significance of each correlogram (Legendre and Fortin 1989). All correlograms proved significant at the Bonferroni corrected level $\acute{\alpha} = 0.001$.

Results

Bird species richness at each resolution generally exhibited highly significant linear relationships with the environmental variables (table 1). Weak curvilinear relationships were found in only a few instances and generally did not greatly improve the fit of the models (e.g., for species richness and PET at the half-degree resolution, r increased from 0.59 to 0.64). Species richness was most strongly correlated with PPT at both the quarter- and one-degree resolutions, and with NPP or LAI at the half-degree resolution (table 1; fig. 1). Strong relationships were also found between PET and species richness at each resolution (table 1; fig. 2). Correlations between species richness and the environmental variables increased with a decline in the spatial resolution of the data in six (PET, MAX, PPT, MAXMO, SRAD and VEG) of the eight variables that were available for all three resolutions. This was true especially of both measures of habitat heterogeneity (table 1).

Five successive jackknife analyses were conducted for each environmental variable to investigate the robustness of these bivariate correlations (see Krebs 1999, 336-338). At each step, a random sample of 10% of the grid cells was excluded. Thus in the final step 50% of the grid squares had been excluded. The jackknife values for each of the comparisons were robust, leading to small standard deviations of the r values, which varied between 0 and 0.019 for all resolutions. Consequently, the correlation coefficients between species richness and each of the environmental variables were considered robust.

A combination of PPT and MIN or PPT and MINMO explained most variation in species richness at the quarter-degree resolution. At the half-degree resolution a combination of PPT and MIN, NPP and MIN, or NPP and MINMO accounted for most variation in species richness, whereas combinations of PPT and habitat heterogeneity (VEG), or VEG and NPP or LAI accounted for most of the variation in richness at the one-degree resolution (table 2).

Table 1: Pearson's correlation coefficients between avian species richness and environmental variables at each resolution before taking spatial autocorrelation into account

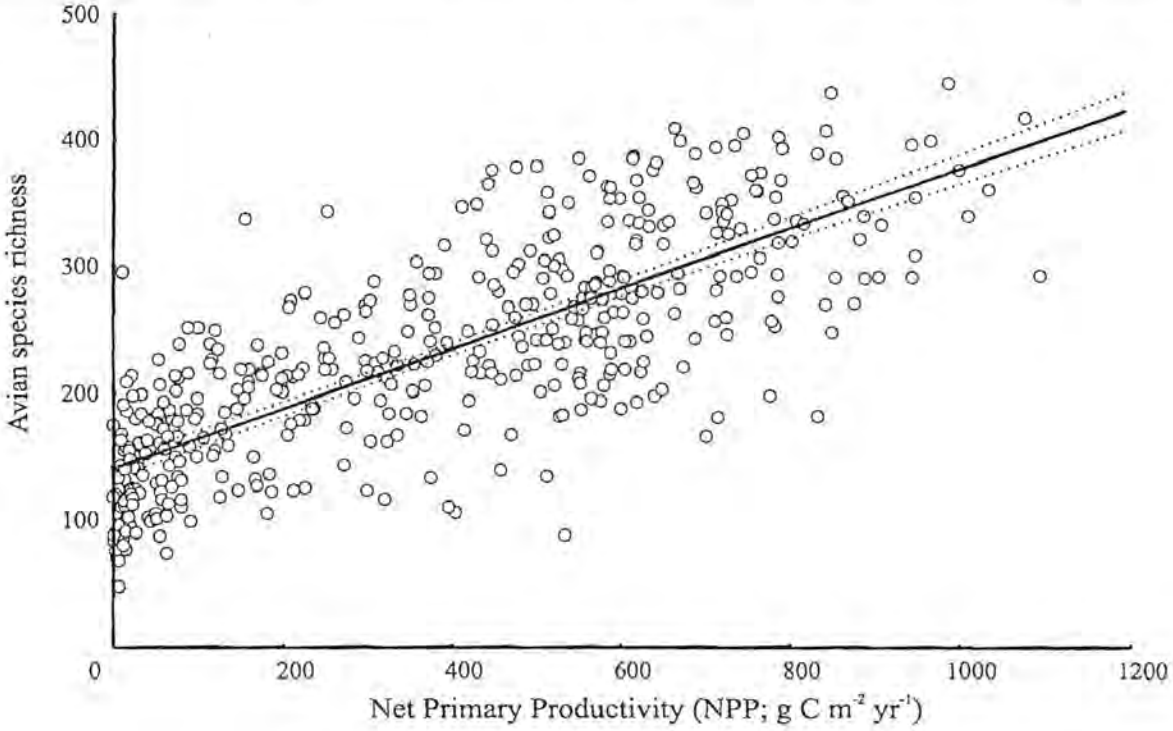
	Avian species richness		
Environmental variables	Quarter degree	Half degree	One degree
	r	r	r
PET	-.52***	-.64***	-.71***
MAX	.02 NS	.02 NS	-.25*
MIN	.39***	.42***	.27**
PPT	.65***	.77***	.82***
MAXMO	-.12***	-.13**	-.28**
MINMO	.42***	.45***	.29**
SRAD	-.47***	-.49***	-.60***
VEG	.32***	.43***	.70***
EVVEG	.04 NS	.10 NS	.22*
NPP		.79***	.71***
LAI		.80***	.71***

Note: Significance was calculated after a sequential Bonferroni correction was applied; df = 1, 1,856 at quarter degree; df = 1, 456 at half degree; df = 1, 100 at one degree. PET = mean annual potential evapotranspiration (mm yr^{-1}); MAX and MIN = mean absolute monthly maximum and minimum temperatures (^{0}C) averaged over the year; PPT = mean annual precipitation (mm yr^{-1}); MAXMO and MINMO = mean monthly maximum and minimum temperatures (^{0}C) of the hottest and coldest months; SRAD = mean annual solar radiation (MJ m^{-2} yr^{-1}); VEG = number of vegetation types; EVVEG = evenness of vegetation type cover; NPP = mean annual net primary productivity (g C m^{-2} yr^{-1}); LAI = leaf area index.

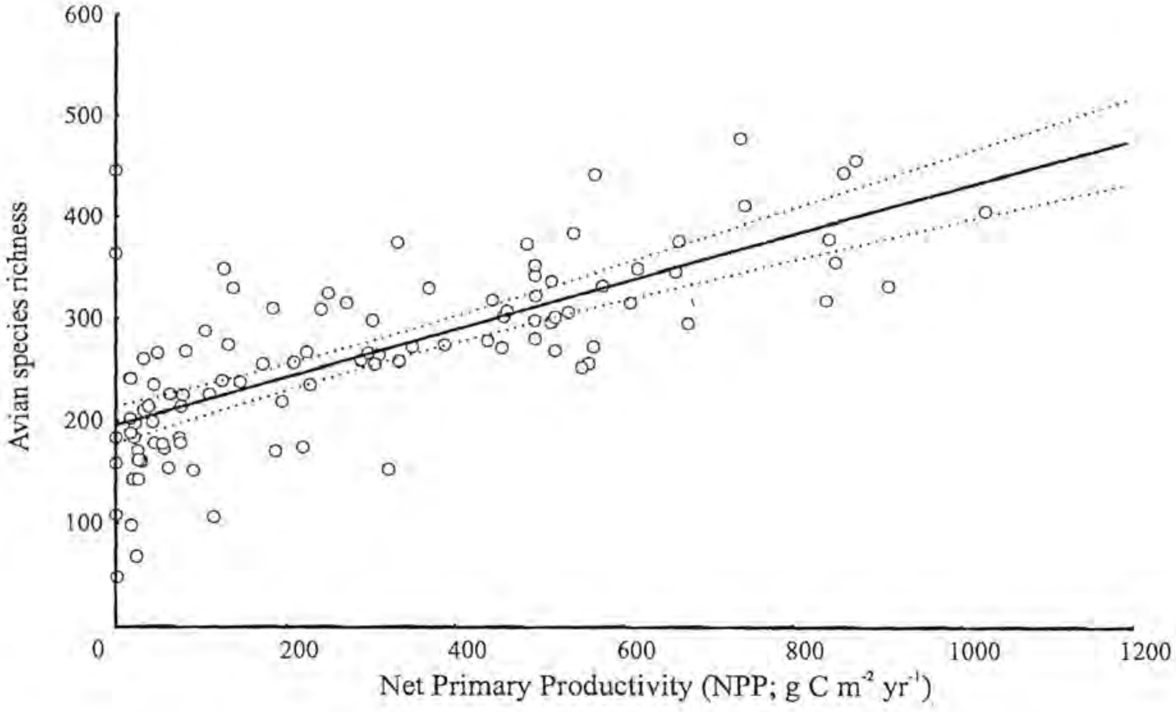
* $P < .05$.

** $P < .01$.

*** $P < .001$.



(*A*)



(*B*)

Figure 1: Relationships between avian species richness and NPP (mean annual net primary productivity). *A*, Half-degree resolution (avian species richness = 140.66 + 23.588 x NPP; $r = 0.79$). *B*, One-degree resolution (avian species richness = 195.61 + 23.100 x NPP; $r = 0.71$).

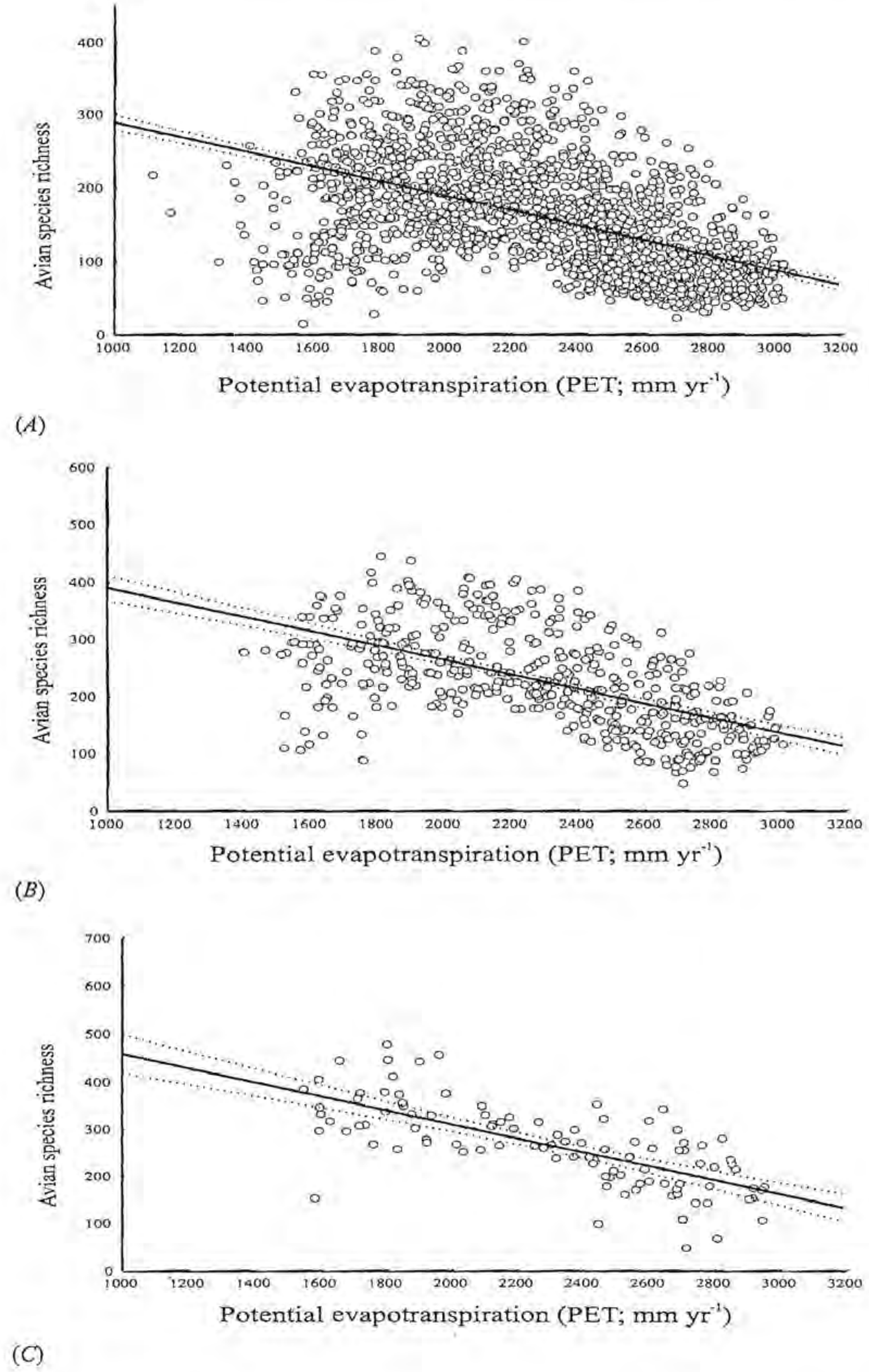


Figure 2: Relationships between avian species richness and PET (potential evapotranspiration). *A*, Quarter-degree resolution (avian species richness = 389.97 - 0.1009 x PET; $r = -0.52$). *B*, Half-degree resolution (avian species richness = 516.10 - 0.1261 x PET; $r = -0.64$). *C*, One-degree resolution (avian species richness = 606.79 - 0.1485 x PET; $r = -0.71$).

Table 2: Correlation coefficients for the best fit explanatory models of bird species richness incorporating two variables, in order of their fit, without taking spatial autocorrelation into account

Spatial resolution with significant two-environmental variable models	r
Quarter degree:	
PPT and MIN	.728***
PPT and MINMO	.722***
PPT + (PEMIN - PEMIN^2)	.670***
Half degree:	
PPT and MIN	.830***
NPP and MIN	.815***
NPP and MINMO	.815***
PPT + (PEMIN - PEMIN^2)	.766***
One degree:	
PPT and VEG	.867***
LAI and VEG	.839***
NPP and VEG	.839***
PPT + (PEMIN - PEMIN^2)	.821***

Note: Significance was calculated after a sequential Bonferroni correction was applied; df = 2, 1,856 at quarter degree; df = 2, 456 at half degree, df = 2, 100 at one degree. PPT = mean annual precipitation (mm yr^{-1}); MIN = mean absolute monthly minimum temperatures (^0C) averaged over the year; MINMO = mean monthly minimum temperatures (^0C) of the coldest months; NPP = mean annual net primary productivity (g C m^{-2} yr^{-1}); VEG = number of vegetation types; LAI = leaf area index. PPT + (PEMIN - PEMIN^2) is the model proposed by O'Brien et al (1998).
*** $P < .001$.

Despite pronounced collinearity among many of the independent variables, the relationships between these particular variables were generally not strong ($0.08 < r < 0.58$). The O'Brien et al. (1998) model, that is, species richness = PPT + (PEMIN – PEMIN^2), provided a poorer fit than did the other variable combinations at all resolutions (table 2).

In most cases, spatially structured environmental variation accounted for most of the variation in bird species richness (tables 3, 4), as might be expected given strong and similar spatial autocorrelation patterns in both the dependent and independent variables (fig. 3). Nonetheless, a reasonable proportion of the variation in bird species richness was accounted for by space only, while the environment only accounted for a small proportion of variation in avian richness.

The use of approximately equal area grid cells limited the likelihood of a direct effect of variation in local area on the relationships between species richness and the environmental variables. However, area might have had a role at the regional level. For example, if in a positive relationship between species richness and some environmental variable the highest values of the environmental variable cover the largest area (Chown and Gaston 1999), then the relationships between species richness and the environmental variable in question might be the consequence of an underlying species-area relationship. To test for this effect, we assigned grid cells to equal-sized classes for each of the abiotic environmental variables contributing most to variation in species richness (PPT, MIN, LAI). The precise number of classes used for each variable depended on the range of values in each case.

For each of the classes, and for each variable, we determined mean species richness and total area (number of grid cells) covered by each variable within each class. We examined the relationships between these variables using Pearson product-moment correlation coefficients, and then repeated this procedure for all resolutions. As we expected, species richness and the mean class value were positively correlated at all resolutions ($r > 0.748$). These relationships were all monotonic except for PPT, which exhibited a unimodal relationship at the quarter-degree resolution. The mean class value for PET also exhibited a unimodal relationship with species richness. Because the area covered by each class either tended to decrease (PPT and LAI, $r < -0.29$) or showed no change (PPT) with an increase in the mean value for that class, there were either no significant relationships, or a negative (PPT at quarter-degree resolution, $r = -0.779$) or weak positive (MIN at quarter-degree resolution, $r = 0.325$) relationship between area covered by the variable and species richness. Thus, underlying species-area effects do not appear to have significantly affected the relationships between species richness and the environmental variables.

Table 3: Coefficients of determination for the relationships between avian species richness and the environmental variables with the best fit at each resolution

	The proportions of variation in avian species richness (r^2)				
Spatial resolution with strongest single significant explanatory variables	Total ($a + b + c$)	Environment only (c)	Spatial structured environmental variation (b)	Space only (a)	Spatial structured environmental variation and space only ($a + b$)
Quarter degree:					
Potential evapotranspiration	.622***	.007	.267	.346	.614***
Precipitation	.618***	.003	.415	.199	.614***
Half degree:					
Net primary productivity	.779***	.018	.603	.158	.761***
Leaf area index	.771***	.009	.631	.129	.761***
Potential evapotranspiration	.776***	.015	.409	.351	.761***
One degree:					
Precipitation	.805***	.002	.672	.131	.803***
Net primary productivity	.806***	.003	.512	.291	.803***
Leaf area index	.812***	.008	.493	.310	.803***
Potential evapotranspiration	.830***	.026	.474	.329	.803***

Note: Variables partitioned into (*a*) nonenvironmental spatial component, (*b*) spatially structured environmental variation component, (*c*) nonspatial environmental component, and (*d*) unexplained component. All partial regression values reached significance after a sequential Bonferroni correction was applied.

*** $P < .05$.

Table 4: Coefficients of determination for the relationships between avian species richness and the two environmental variable models with the best fit at each resolution

	The proportions of variation in avian species richness (r^2)				
Spatial resolution with most significant explanatory two-environmental variable models	Total ($a+b+c$)	Environment only (c)	Spatial structured environmental variation (b)	Space only (a)	Spatial structured environmental variation and space only ($a+b$)
Quarter degree:					
PPT and MIN	.656***	.041	.489	.125	.614***
PPT and MINMO	.655***	.040	.481	.133	.614***
Half degree:					
PPT and MIN	.797***	.036	.653	.107	.761***
NPP and MIN	.794***	.032	.631	.129	.761***
NPP and MINMO	.797***	.035	.628	.133	.761***
One degree:					
PPT and VEG	.842***	.038	.666	.090	.757***
LAI and VEG	.847***	.043	.660	.143	.757***
NPP and VEG	.844***	.040	.663	.140	.757***

Note: Variables partitioned into (*a*) nonenvironmental spatial component, (*b*) spatially structured environmental variation component, (*c*) nonspatial environmental component, and (*d*) unexplained component. All partial regression values reached significance after a sequential Bonferroni correction was applied. PPT = mean annual precipitation (mm yr^{-1}); MIN = mean absolute monthly minimum temperatures (^0C) averaged over the year; MINMO = mean monthly minimum temperatures (^0C) of the coldest months; NPP = mean annual net primary productivity ($g\ C\ m^{-2}\ yr^{-1}$); VEG = number of vegetation types; LAI = leaf area index.

*** $P < .05$.

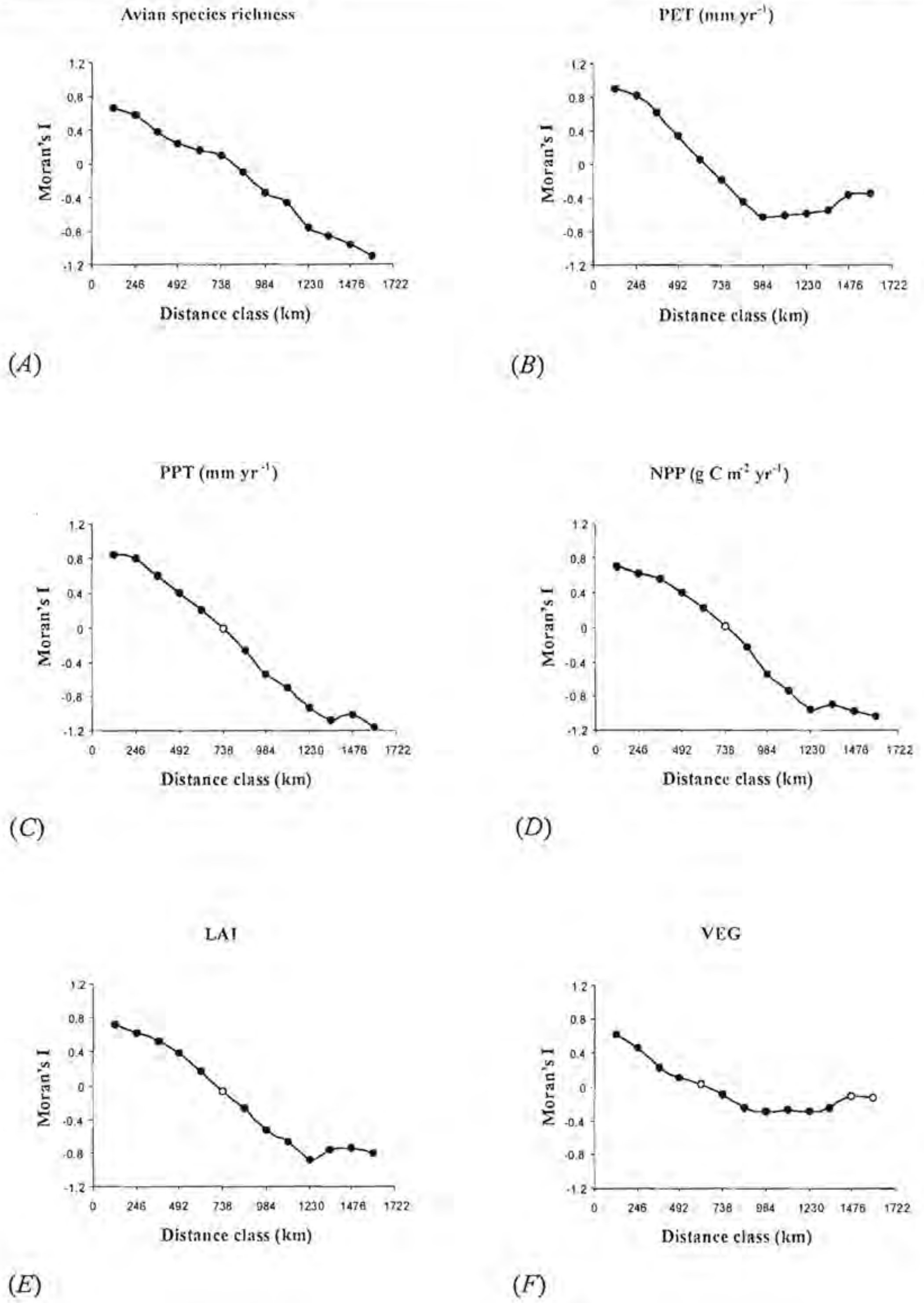


Figure 3: Spatial patterns in avian species richness and the most significant environmental correlates of this variation at the one-degree grid square resolution across South Africa based on equal distance classes (123 km). *Moran's I* = the coefficient of autocorrelation. Sequential Bonferroni correction was applied at $\alpha = 0.001$ to evaluate each *I* value and the overall significance of each correlogram. All correlograms proved significant, and the closed circles represent significant *I* values. *PPT* = mean annual precipitation; *PET* = mean annual potential evapotranspiration; *NPP* = mean annual net primary productivity; *LAI* = leaf area index; *VEG* = number of vegetation types.

Discussion

Mean annual precipitation (PPT), mean annual productivity (LAI or NPP), mean absolute monthly minimum temperature averaged over the year (MIN), and, at the coarser resolutions, the number of vegetation types (VEG), either singly or in combination, accounted for most of the variation in avian species richness across South Africa. Perhaps more significantly, it is clear that the spatially structured component of the variation in the environmental variables accounted for most of the variation in species richness. Few other studies explicitly account for the pronounced spatial autocorrelation that is characteristic of species richness (see, e.g., Currie 1991; O'Brien 1993; Kerr and Packer 1997; Jetz and Rahbek 2001), and investigations into the reasons for this spatial structure have generally been limited. In this case, it is clear that spatial structure of the environmental variables, which is plainly a reflection of the strong east-west gradients in precipitation, and associated gradients in both productivity and vegetation heterogeneity in South Africa (see fig. 3; Schulze 1997*a*, 1997*b*) are responsible for much of the variation in species richness. This undoubtedly also explains the small proportion of richness accounted for solely by the environment (a common feature of regional scale studies, Borcard et al. 1992; Smith 1994; Boone and Krohn 2000*a*). Furthermore, the variation accounted for solely by space indicates that species richness shows spatial autocorrelation independent of the spatial structure of the explanatory variable in question, although this was generally small compared to the spatially structured environmental variation. Thus, much of the variation in avian species richness across southern Africa is strongly related to and likely a consequence of the east-west spatial gradient in the environmental variables, particularly primary productivity and rainfall.

That primary productivity is strongly correlated with species richness is not surprising. This is considered the least contentious aspect of species-energy theory and there are sound mechanisms accounting for these relationships (Rosenzweig and Abramsky 1993; Wright et al. 1993; but see also Srivastava and Lawton 1998; Waide et al. 1999). The strong association between species richness and precipitation is also readily explained. Precipitation and primary productivity (measured as either NPP or LAI) are highly correlated and there is a clear, underlying causal relationship between these two variables. In semiarid areas, such as South Africa, precipitation sets limits to primary productivity, giving rise to the strong association between the two variables (see O'Brien 1993; Schulze 1997*a*; O'Brien et al. 1998, 2000; Andrews and O'Brien 2000). Thus, the correlations found in this study between species richness and both productivity and precipitation likely reflect underlying causation, though it remains unclear exactly what the mechanisms are through which energy and water availability might have such a pronounced causal effect on avian species richness (see also Gaston 2000).

Unlike the other direct (NPP and LAI) and indirect (PPT) measures of primary productivity, annual potential evapotranspiration (PET) was negatively related to species richness, with the latter showing a strong decline above ~2,200 mm yr^{-1} (fig. 2). The lack of available precipitation is clearly responsible for this relationship too. Although potential evapotranspiration is high in the western arid regions of southern Africa, the rainfall here is low (hence the negative relationship between PPT and PET; table 1). In other words, even though there is potentially a considerable amount of energy available to be utilized for primary productivity in the western arid regions of the country, there is insufficient moisture to support utilization of the energy by plants. In a series of papers, O' Brien and her coworkers (O'Brien 1993, 1998; O'Brien et al. 1998, 2000; Andrews and O'Brien 2000), have suggested that a capacity rule based on geographic variation in and interactions between energy and water availability can explain variation in woody plant species richness in most geographic regions. Our findings show that this may be true of birds too, although the precise nature of the relationship between avian species richness and available energy and water differs from the model proposed for woody plants.

The relationship between PET and species richness found here shows a number of similarities and differences to that found by Currie (1991) for North American birds. Undoubtedly some of these differences are a consequence of the fact that the A-Pan measure of PET used here differs from the one used by Currie (1991). In particular, the absolute values of PET are likely to vary between methods, and the values we used are generally higher than those estimated using other models (see Rosenberg et al. 1979; Hulme et al. 1996). Nonetheless, these are unlikely to affect the comparison, because the most significant issue at hand is the trend in species richness relative to PET, rather than the absolute values of PET. In North America, the strong increase in PET is associated with a rapid rise in bird species richness from the Arctic to more temperate areas. In North America, there is likely to be little in the way of water limitation, and productivity rises rapidly in this region (or at least AET does, and this variable was used to estimate productivity in Currie's (1991) study). Indeed, it is clear from Currie's (1991) figure 5 that the relationship between avian species richness and productivity is positive in this region too. Thereafter, the relationship between PET and species richness is virtually asymptotic, with the variance increasing as PET increases. In southern Africa, there is also an initial rise in species richness in regions with low PET, but thereafter species richness declines dramatically, and it seems likely that this is caused by a water constraint that prevents PET from being translated into energy availability (see discussion above).

In contrast, species richness in both regions increases monotonically with primary productivity over a similar range of productivity values. Thus, the important distinction between southern Africa and North America appears to be that of water limitation. In southern Africa, high productivity areas are associated with areas of lower PET (i.e., a negative relationship between NPP and PET: r = -0.71 and –0.67 at the half- and one-degree resolution levels, respectively), whereas PET and productivity are more likely to be positively related in North America (see fig. 8 in Currie 1991), where water limitation is not as severe, at least over much of the range of PET. This influence of water availability on the translation of available energy into primary productivity (see also O'Brien et al. 1998, 2000), means that when surrogates of primary productivity are being used during investigations of species-energy relationships, care must be taken in interpreting the outcomes of the analyses.

In the multivariate analyses undertaken here, minimum temperature (both MIN, mean absolute monthly minimum temperatures averaged over the year, and MINMO, mean monthly minimum temperatures of the coldest months), which was not strongly correlated with NPP or PPT, entered most of the models as the most important explanatory variable together with either primary productivity or precipitation. Following the logic of Root (1988) and Blackburn et al. (1996), we propose that the importance of minimum temperature as a correlate of species richness is likely a consequence of interactions between resource abundance and the physiological capabilities (especially alterations of metabolic rate) of the species involved. Nonetheless, this effect of minimum temperature is relatively weak, probably because most of the region in question has a subtropical to warm temperate climate (see also O'Brien 1993; Andrews and O'Brien 2000).

At the largest scales, minimum temperature was replaced by vegetation heterogeneity as the independent variable, second to primary productivity or precipitation, contributing most to variation in species richness. The increase in the explanatory importance of habitat heterogeneity with a decline in spatial resolution can be attributed largely to an increase in the range of habitat heterogeneity included in the analysis with an increase in grid cell size (from 1-8 (quarter degree), to 1-12 (one degree) vegetation types). For statistical reasons, this increase in the range of vegetation types is likely to mean an increase in the importance of VEG as an explanatory variable (see the introduction to this article). Nonetheless, the increase in the importance of vegetation heterogeneity might also be caused by the strong positive effects that environmental and habitat heterogeneity have on species richness (see Rosenzweig 1995; Ricklefs and Lovette 1999; Waide et al. 1999 for discussion). These findings suggest that studies investigating the relationship between species richness and habitat heterogeneity, which are undertaken at large spatial scales using coarse resolutions (the two parameters are usually varied simultaneously), are almost certain to conclude that habitat heterogeneity is an important explanatory variable for species richness (see, e.g., Kerr and Packer 1997; Fraser 1998; Andrews and O' Brien 2000), even when this might not be the case. Thus, conclusions regarding the importance of vegetation heterogeneity in explaining species richness must be cautiously interpreted in the context of both the spatial extent and resolution of the study being undertaken.

In conclusion, we have shown that spatial variation in avian species richness in southern Africa is correlated with and likely is the consequence of considerable spatial variation in precipitation and energy availability, which affects primary productivity. In addition, we have demonstrated that these results are consistent across several spatial resolutions, but that vegetation heterogeneity is likely to increase in importance as an explanatory variable with declining spatial resolution, probably for statistical reasons. This provides at least a partial explanation for the conclusions of some studies (see, e.g., Kerr and Packer 1997; Fraser 1998) that, second to energy availability, vegetation heterogeneity forms a significant correlate of species richness. Finally, we have shown that surrogate measures of primary productivity must be interpreted cautiously when investigating species energy theory.

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CHAPTER 3

Spatial congruence of ecological transition at the regional scale in South Africa

Running title: Spatial congruence of ecological transition

In review: *Journal of Biogeography*

Abstract

Aim To determine whether patterns of avian species turnover reflect either biome or climate transitions at a regional scale, and whether anthropogenic landscape transformation affects those patterns.

Location South Africa and Lesotho.

Methods Biome and land transformation data were used to identify sets of transition areas, and avian species occurrence data were used to measure species turnover rates (β-diversity). Spatial congruence between areas of biome transition, areas of high vegetation heterogeneity, high climatic heterogeneity, and high β-diversity was assessed using random draw techniques. Spatial overlap in anthropogenically transformed areas, areas of high climatic heterogeneity and high β-diversity areas was also assessed.

Results Biome transition areas had greater vegetation heterogeneity, climatic heterogeneity, and β-diversity than expected by chance. For the land transformation transition areas, this was only true for land transformation heterogeneity values and for one of the β-diversity measures. Avian presence/absence data clearly separated the biome types but not the land transformation types.

Main conclusions Biome edges have elevated climatic and vegetation heterogeneity suggesting that the transition zones between biomes are more heterogeneous than other areas. Elevated β-diversity in the avifauna is clearly reflected in the heterogeneous biome transition areas but not in the land transformation transition areas. This suggests that anthropogenic landscape transformation has no substantive influence on the avifauna. However, it is likely that the quarter degree resolution of our study is too coarse to reveal finer-scale effects. Thus, future data should be collected at a finer scale to improve landscape planning.

Key words avian species turnover, β-diversity, heterogeneity, spatial congruence

INTRODUCTION

The composition of species assemblages changes in complex ways across space. Among some areas the numbers of species gained might be equalled by the number of those lost, whilst elsewhere there may be strong asymmetries in such gains and losses (Gaston, 2000; Bell, 2001). The result is a landscape comprising a spectrum of patterns of transition in species assemblages, from smooth gradients to sharp discontinuities (Cody, 1975; Wilson & Shmida, 1984; Ryti & Gilpin, 1987; Brown, 1995; Hanski & Gyllenberg, 1997; Desrochers & Fortin, 2000; Rahbek & Graves, 2001; Lennon *et al*., 2001).

Sharp discontinuities, or regions of considerable species turnover, have long fascinated biologists. At large scales, they have been used to define the spatial boundaries of biogeographical regions, which in turn have formed and continue to form a significant, though often contentious, basis for understanding the evolutionary history of life on earth (see e.g. Cox, 2001; Morrone, 2002). For example, the relationship of the biotas and areas surrounding the Wallace line has been one of considerable importance, though surrounded by controversy (Darlington, 1957; Cox, 2001). Likewise, elucidating the cryptic history of biotas of the Southern ocean islands remains critically dependent on whether the islands are considered part of a broader Insulantarctic region (Jeannel, 1964; Udvardy, 1987) with its own history, or whether the biotas of the islands should simply be thought of as a subset of those on the continents closest to them (Morrone, 1998; Cox, 2001). Moreover, it is only because biotas of different biogeographic regions are thought to have very different histories that community similarity and convergence can be assessed relatively free of the problems of phylogenetic or historical constraint that might confound similar investigations within regions (see Cowling & Campbell, 1980; Wiens, 1991 for examples).

At smaller scales, sharp discontinuities are often used to demonstrate regional faunal complexity that may require either historical or ecological explanation. For example, on the basis of turnover and endemism in amphibians in southern Africa, Poynton (1961) and Poynton & Boycott (1996) emphasized the co-occurrence of Afromontane and lowland tropical amphibian faunas on the Mozambique/KwaZulu-Natal eastern border area, and concluded that vegetation type played little role in the distribution of frog species. At these scales, the spatial delineation of discontinuities and the relatively homogenous regions between them is also important for understanding finer scale assemblage or community membership and the properties of community members (Bestelmeyer & Wiens, 2001). Not only is the richness of local communities determined by the region within which they are found (Cornell & Lawton, 1992; Cornell & Karlson, 1996; Caley & Schluter, 1997), but the identity and properties of the species comprising these communities is also significantly influenced by the regional species pool (Ricklefs, 1987; Blackburn & Gaston, 2001). Understanding transition zones and the areas they surround, and identifying the regional biotas to which assemblages belong, is therefore an important part of elucidating the processes that are responsible for the distribution and abundance of organisms (Gosz, 1992; Risser, 1995; Williams, 1996; Srivastava, 1999; Williams *et al*., 1999).

From a more pragmatic perspective, delineation of biotas may also serve as a framework for conservation actions (for discussion see Williams *et al*., 1999). For example, biome identification forms a significant component of the identification of Important Bird Areas, which are considered an important part of the conservation panoply (e.g. Barnes, 1998). In southern Africa, delineation of the Cape Floristic Region as a highly significant biogeographic unit has been instrumental in drawing attention to conservation threats facing the biota in the region (e.g. Huntley, 1989; Cowling, 1992; Richardson *et al.*, 1996). Identification of transitional areas may also be crucial from an area selection perspective because the algorithms used to identify minimal area networks often select ecotonal or transitional areas, which might not always be ideal for long-term persistence of a given assemblage or biota (Chapter, 4).

Early delineations of biogeographic regions and the transitional areas between them were generally based on qualitative assessments (see Hengeveld, 1990 for review), and these continue to form an important component of biogeographic debate. However, a suite of numerical methods is now available for classifying geographic areas by biotic similarity and difference (Hengeveld, 1990; Williams, 1996; Lennon *et al.*, 2001). Although these methods have been widely applied to identify biogeographic regions and their relationships, or areas of similarity and transition at finer scales (e.g. Poynton & Boycott, 1996; McInnes & Pugh, 1998; Morrone, 1998; Davis *et al.*, 1999; van Rensburg *et al.*, 2000), few studies have utilized these methods to determine whether areas of transition are congruent among taxa. Indeed, the search for congruent area relationships using methods such as Brooks Parsimony Analysis (see Brooks *et al.*, 2001) is much more frequently undertaken than the identification of congruence in transition zones (for review, examples and discussion see e.g. Endler, 1982; Cracraft & Prum, 1988; Myers & Giller, 1988; Brooks & McLennan, 1991; Cox & Moore, 1993; Smith, 1994; Morrone, 1994; Morrone & Crisci, 1995). Although there may be historical reasons for this focus (see Wallace, 1876; Newbegin, 1936; Darlington, 1957), the paucity of investigations of congruence in transitional areas may also be a consequence of the early absence of appropriate analytical methods. Moreover, even with the availability of such numerical techniques, the extent to which turnover in one group might be reflected in another has not been widely investigated (see Gosz & Sharpe, 1989; Risser, 1995; Bestelmeyer & Wiens, 2001 for discussion), despite the fact that changes to biogeographic classifications have been suggested based on apparently different responses of plants and animals to the landscape (Cox, 2001).

Clearly, investigations of spatial congruence in ecological transition are important for determining which processes result in large-scale changes in species assemblages in different taxa (Gosz, 1993; Krasnov & Shenbrot, 1998; Bestelmeyer & Wiens, 2001). However, they are also useful for determining how much influence landscape transformation by humans has had on biogeographic patterns. Although it is clear that humans have had a profound effect on the distributional ranges of many species (McKinney & Drake, 1994; Williamson & Fitter, 1996; Williamson, 1996, 1999; Channel & Lomolino, 2000; Ceballos & Ehrlich, 2002), whether biogeographic patterns have been influenced to the extent that broader scale analyses are likely to exhibit patterns that are predominantly anthropogenic is not well known. If current patterns are influenced to a greater extent by anthropogenic landscape transformation than by other ecological and historical factors, then using present patterns to understand intrinsic biological processes may produce answers that are partial at best or spurious at worst (see Gaston & Blackburn, 2000 for discussion). Clearly, understanding the extent to which humans have modified underlying biogeographic and ecological patterns is important.

In this study, we therefore examine the extent to which transitions in avian assemblages match those in vegetation (biomes) or climate at a regional scale, and the extent to which discontinuities in avian assemblages might be driven by anthropogenic landscape transformation rather than by differences in climate or vegetation. We use data on the South African avifauna (Harrison *et al.*, 1997) for several reasons. First, birds have regularly been used for delineation of biogeographic regions and for transitions among them (see Williams *et al.*, 1999 for partial review), and in southern Africa they are the most well-known and accurately surveyed taxon (Harrison *et al.*, 1997; Chapter, 2). Second, South Africa is characterized by several major biomes with reasonably sharp transitions between them (Rutherford & Westfall, 1994; Low & Rebelo, 1996) (Fig. 1), thus ensuring that transitions in vegetation can be readily identified. Third, biomes in South Africa, and their constituent vegetation types, are regularly used as a framework for generalizations concerning the ecology and biogeography of the region's fauna, and as a foundation for conservation assessments and actions (Barnes, 1998; Low & Rebelo, 1996; Huntley, 1989; van Rensburg *et al.*, 2000). However, the extent to which the biomes, which have been defined largely on plant functional groups and endemism, and climatic factors (Cowling *et al.*, 1989; Rutherford & Westfall, 1994; Low & Rebelo, 1996), reflect patterns in faunal assemblages remains poorly known. Although there have been some quantitative assessments of relationships between faunal assemblages in Afrotropical and Afrotemperate forests (Poynton & Boycott, 1996; Lawes, 1990; van Rensburg *et al.*, 2000), investigations of relationships and turnover between the other biomes is scanty (see Holm & Scholtz, 1985; Davis, 1997, 2002 for exceptions). Indeed, in a major treatment of the biotic diversity of southern Africa there is virtually no assessment of faunal relationships, despite careful assessments of the flora (e.g. Cowling *et al.*, 1989). It is well known that the avifauna responds to local vegetation heterogeneity in southern Africa (Hockey *et al.*, 1988; Bruderer & Bruderer, 1993), and this is true also of the avifauna in other regions (Cody, 1985; Verner & Larson, 1989; Gentilli, 1992; Blondel & Vigne, 1993; Cody, 1993; Bellamy *et al.*, 1996; MacNally, 1997; Catterall *et al.*, 1998; Wiebe & Martin, 1998). However, Allan *et al.* (1997a) have argued that these responses do not match vegetation patterns at larger scales. Finally, much of South Africa has been transformed by extensive human land use over the past 100 years (Macdonald, 1989; Scholtz & Chown, 1993). Indeed, the south-western region of the country has been farmed for the past 350 years, leading to massive landscape transformation over much of the region (e.g. Richardson *et al.*, 1996). Thus, if anthropogenic landscape transformation has an influence on broader scale patterns it should be detectable, at least in the heavily transformed south-western parts of South Africa.

METHODS

Data

The Southern African Bird Atlas Project (SABAP; Harrison *et al.*, 1997) provides the most comprehensive information available on the distribution of birds in southern Africa.

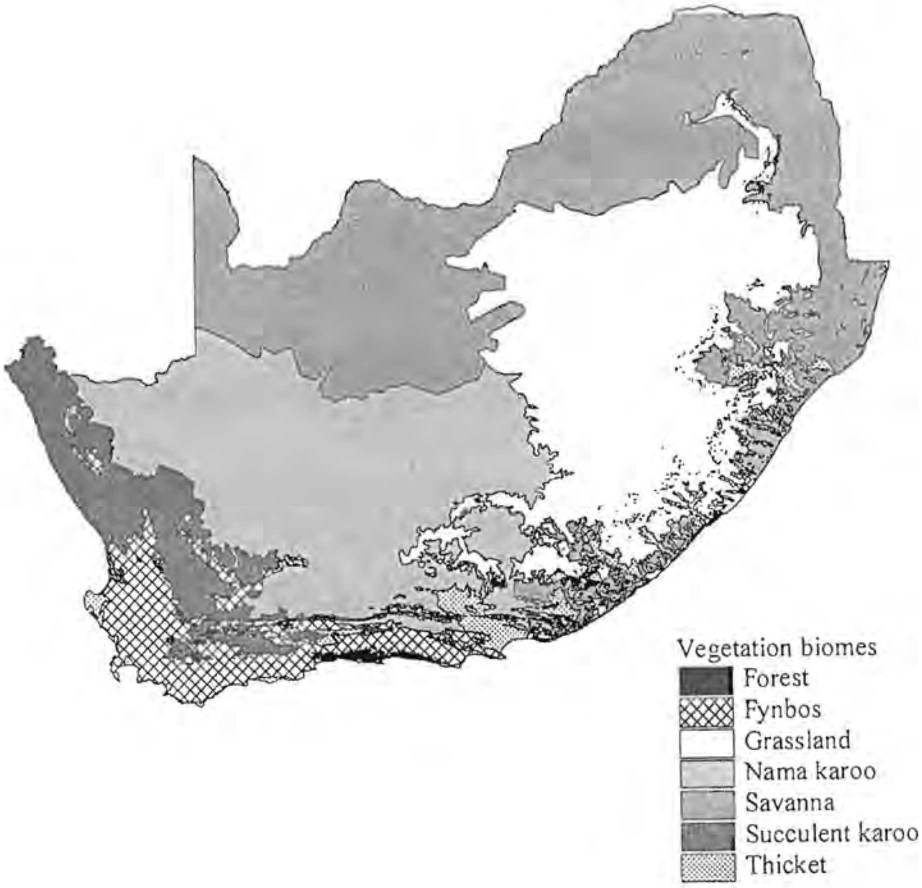

Figure 1 The vegetation biomes of South Africa and Lesotho based on Low & Rebelo (1996).

Data were collected mainly between 1987 and 1992, at a spatial resolution of a quarter-degree (15' x 15' ≈ 676 km^2) for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree (30' x 30' ≈ 2500 km^2) for Botswana (for a detailed description of methods see Harrison *et al.*, 1997). For the purpose of this study, the analyses were restricted to South Africa and Lesotho because of the availability of appropriate climatic and vegetation data. Those quarter-degree grid cells that included both land and ocean surfaces were excluded as well as those with low reporting rates, which might produce artificial species turnover patterns as a result of low sampling effort. Following Harrison *et al.* (1997), these latter, unreliable cells were identified as those cells with less than 10 checklists. For the remainder (1352 grid cells), the number and identity of bird species occurring in each grid cell was determined excluding marine, vagrant, marginal and escaped species (651 species were analysed). The species richness of those grid cells overlapping the national boundaries of South Africa may in some cases be somewhat underestimated, because part of their area lies outside the study region. However, such effects influence only a very small proportion (4%) of cells. These restrictions and the current data used make our results directly comparable to those of other investigations using the SABAP data (e.g. Rodrigues & Gaston, 2002; Gaston & Rodrigues, in press; Chapters, 2, 4).

Low & Rebelo's (1996) classification of the study area into seven biome types was used to calculate the percentage of each type in each quarter-degree cell. In southern Africa, biomes are defined based on five explicit criteria (i) they are the largest land community unit recognized at a continental or subcontinental level; (ii) they are units mappable at a scale of no larger than about 1:10 million; (iii) they are distinguished from other biomes primarily on the basis of dominant plant life form(s) in climax systems; (iv) they are from other biomes secondarily on the basis of those major climatic features that most affect the biota; and (v) they are not unnatural or major anthropogenic systems (see Rutherford & Westfall, 1994 for further discussion). This study included the forest, thicket, savanna, grassland, Nama karoo, succulent karoo, and fynbos biomes. Each of these is characterised by several vegetation types, giving a total of 68 different vegetation types for the study area (see Low & Rebelo, 1996 for further information).

Data on the extent and nature of anthropogenic activities for each quarter-degree cell were based on the ten land-cover types identified primarily during 1994-1995 by Thompson (1996) and Fairbanks *et al.* (2000). These land-cover types (and their proportional cover) are (i) cultivated lands (11.4%), (ii) forest plantations (1.3%), (iii) urban/built-up lands (0.9%), (iv) mines and quarries (0.1%), (v) degraded lands (5.2%), (vi) artificial water bodies (3.2%), (vii) forest and woodland (6.1%), (viii) thicket and bushland (49.7%), (ix) grassland (22.0%) and (x) wetlands (0.3%). After reclassifying these ten land-cover types into three land transformation categories, we calculated the percentage of (i) totally transformed (13.6%), (ii) partially transformed (8.4%), and (iii) untransformed (78%) values for each grid cell. Finally, we calculated the percentage values for two land transformation categories in each grid cell, namely (i) transformed (22%) and (ii) untransformed (78%).

Spatial turnover in avian assemblages

Beta diversity (hereafter referred to as β-diversity), a measure of species turnover in space, is commonly used to identify transition zones (see Williams, 1996; Williams *et al.*, 1999; Lennon *et al.*, 2001 for overviews), and was used here to identify areas of high turnover. Although there are a great variety of ways in which beta diversity can be calculated (see Magurran, 1988; Lande, 1996; Lennon *et al.*, 2001; Chapter, 4), we employed β_g and β_{sim} (Lennon *et al.*, 2001; Chapter, 4). We did so because the behaviour of these measures is well understood and because they have rather different properties, which we consider essential for investigating spatial congruence in turnover in this region, which is characterized by steep east-west gradients in species richness (O'Brien, 1993, 1998; O'Brien *et al.*, 1998; Andrews & O'Brien, 2000; Chapter, 2).

β_g is a measure of β-diversity based on the rate of species replacement across multidirectional gradients, and captures the directional gradients in composition (see Fig. 2 for an explanation) (Chapter, 4). In consequence, β_g can be used to detect sharp discontinuities that are primarily a result of differences in species richness. In contrast, β_{sim} highlights species compositional differences between focal and neighbouring cells. Calculations of β_{sim} are based on the matching components used in dissimilarity indices. Pairwise calculations of β_{sim} between a focal cell and each of its neighbours are made using the formula:

$$\beta_{sim} = \min(b,c) / [\min(b,c) + a] \qquad (1)$$

where a is the total number of species present in both quadrats, b is the number of species present in the neighbouring quadrat but not in the focal one, and c is the number present in the focal quadrat but not in the neighbouring one (Lennon *et al.*, 2001).

A β-diversity value was calculated for each grid cell based on the avian species occurrence data (Fig. 3). For each β-diversity measure, the top 10% of cells (135 cells) with the highest β-diversity values were arbitrarily defined as areas indicative of sharp transitions between avian species assemblages. Linear and curvilinear regressions were used to evaluate the degree of independence of these β-diversity measures. To minimize the problems for statistical inference caused by spatial autocorrelation, which tends to distort the significance levels of correlation coefficients and regression slopes (Clifford *et al.*, 1989; Lennon, 2000), we used the modified correlation test suggested by Clifford *et al.* (1989) (see also Lennon *et al.*, 2001). This corrects the significance of the standard product-moment correlation coefficient for the spatial dependency within and between two patterns, and uses the concept of 'effective sample size' (*ess*), the equivalent sample size for the two variables when the redundancy produced by spatial autocorrelation is removed and is a joint property of the two patterns. The *ess* depends on the product of their autocorrelation functions, and can be considerably smaller than the observed number of data points.

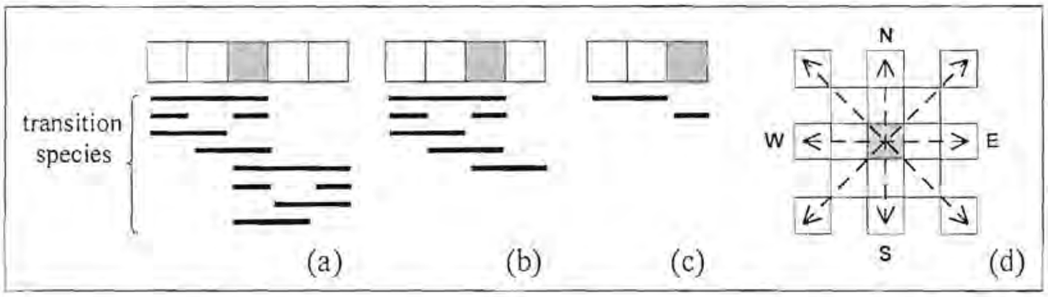

Figure 2 Illustration of the concept and measurement of β diversity based on multidirectional gradients (β_g). This measure highlights regions that have a high proportion of species that are on the edge of their ranges ('transition species'). (a) Considering a linear sequence of five adjacent cells centred on the focal cell (in grey) for which β_g is to be measured, species whose range within these five cells follows one of the patterns indicated by the thick horizontal lines were considered to be 'transition species'. The same applies when only four (b) or three (c) adjacent cells are possible (this happens for cells at the edge of the study area). The percentage of transition species in relation to the total number of species found in the sequence of adjacent cells measures the intensity of species replacement across that direction. (d) The intensity of species replacement is measured across four directions (dashed arrows): West-East (horizontal), North-South (vertical), NW-SE and NE-SW (two diagonals). The final β_g value is the maximum of these values.

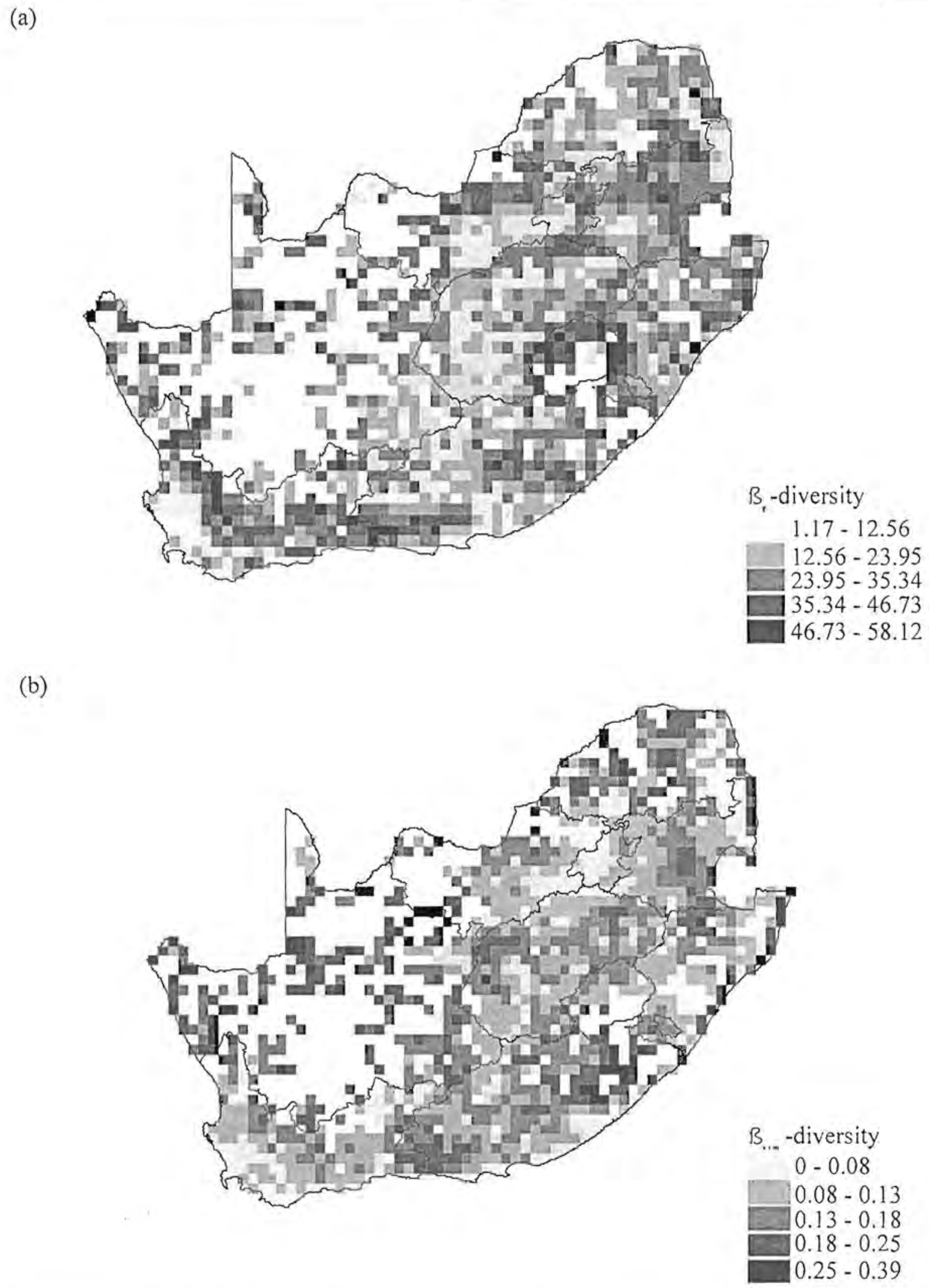

Figure 3 Patterns of: (a) β_g-diversity and (b) β_{sim}-diversity. The β-diversity values recorded ranged between 1.2% and 58.1%; 0% and 39.3% for the two β-measures respectively. Darker colours correspond to higher values of β-diversity and colour gradients represent 5 equal-interval classes. White is absence of data.

Biome and land transformation transitions

Biome edges were identified using two criteria. Using the 'overlapping edge criterion' (criterion I) a grid cell was considered to be at the edge of a biome if, whilst the focal biome covered > 5% of the focal cell, the focal biome covered $\leq$ 5% of at least one of its neighbouring cells. In the case of the 'dominant type criterion' (criterion II) each grid cell was first assigned to a single biome based on an assessment of which of the biomes present in the cell was most widespread. A cell was then considered to be at the edge of a biome if, whilst it belonged to that biome, at least one of its neighbouring cells did not. Jaccard's coefficient was used to determine the extent of the congruence (number of overlapping cells) between the two measures used to identify biome edges (Legendre & Legendre, 1998):

$$\text{Jaccard coefficient} = a / (a + b + c) \times 100 \qquad (2)$$

where a is the number of overlapping cells between the two measures used to identify biome edges, b is the number of additional grid cells identified from criterion I and c is the number of additional grid cells identified from criterion II.

Land transformation edges and their spatial congruence, for both the three-way and two-way land transformation classifications were identified in the same manner.

Environmental heterogeneity

In a previous study, relationships between avian species richness and several environmental variables at three spatial resolutions across South Africa were investigated (Chapter, 2). It was found that for the quarter-degree resolution, mean annual precipitation (PPT; mm yr^{-1}) and PPT in combination with mean absolute monthly minimum temperature (MIN; ^{0}C) averaged over the year (calculated using monthly data for the last 30 – 50 years supplied by the South African Computing Center for Water Research (see Schulze, 1998)) were the most significant, positive linear correlates of avian species richness. In this study, we used the same climatic variables to calculate the degree of climatic heterogeneity for each grid cell compared to its first order neighbouring cells (i.e. bordering cells). To do so, the S-PLUS 2000 for ArcView extension (ESRI Inc., 1998) was used to calculate a Moran's I value for each climatic variable in each grid cell based on the mean Moran's I value of each cell's first order neighbouring cells (i.e. point pairs were used to calculate the mean Moran's I value of each cell and the number of point pairs used for a cell was equal to the number of bordering cells). Following Reyers *et al.* (in press), the Moran's I values were used as the coefficient of autocorrelation to determine gradients in climatic values and therefore areas of transition between climatic values for each variable. A grid cell with a positive Moran's I value for a given climatic variable represents positive spatial autocorrelation, i.e. this focal cell is similar to its neighbouring grid cells leading to spatial clustering of similar values of the specific variable. Areas with high positive values of spatial autocorrelation for a specific climatic variable can therefore be interpreted as areas with similar climatic conditions along a gradient, i.e. no major climatic changes. Negative Moran's *I* values represent a clustering of dissimilar variable values and should therefore indicate areas with high levels of climatic transition or climatic heterogeneity. A Bonferroni corrected level at $\alpha = 0.001$ was used to evaluate the significance of each Moran's *I* value (Rice, 1989).

To further investigate environmental heterogeneity we calculated the number of vegetation types (i.e. vegetation heterogeneity) in each cell, from a total of 68 types defined by Low & Rebelo (1996). This is expected to be higher in areas of transition between different biome types, and in areas with high levels of climatic transition or climatic heterogeneity. The number of vegetation types recorded for each grid cell ranged from 1 to 8.

Identifying spatial congruence in turnover

For each of the overlapping edge (criterion I) and the dominant type (criterion II) biome edge cells we determined whether these cells had greater values of vegetation heterogeneity, climatic heterogeneity, and β-diversity than expected by chance. To do this the mean values for vegetation heterogeneity, climatic heterogeneity and β-diversity of the overlapping biome edge cells and the dominance type biome edge cells, respectively, were calculated. These mean values were then compared to the mean vegetation heterogeneity, mean climatic heterogeneity and mean β-diversity values, respectively, found for 10 000 sets of randomly selected grid cells. The number of randomly selected grid cells within each set was equivalent to the number of biome edge cells based on each of the biome edge cell criteria in question.

In a similar fashion, we determined whether each of the overlapping edge (criterion I), and the dominance type (criterion II) type land transformation edge cells had greater values of land transformation heterogeneity, climatic heterogeneity, and β-diversity than expected by chance. These relationships were examined for both the three-way and the two-way land transformation classifications. Following Chapter 4, land transformation heterogeneity in grid cells was determined using Simpson's index of diversity (Krebs, 1999):

$$H = 1 - \text{Sum}\,(p_i)^2 \qquad (3)$$

where p_i is the fraction of the grid cell's area occupied by land transformation type *i*. This was calculated for each of the three and the two land transformation categories used.

Finally, we determine whether cells with the highest 10% of β_g values and β_{sim} values (135 cells each) had greater values of vegetation heterogeneity, climatic heterogeneity, and land transformation heterogeneity than expected by chance. To do so, the mean values for vegetation heterogeneity, climatic heterogeneity and land transformation heterogeneity for the cells with the 10% highest β_g values, and the highest β_{sim} values, respectively, were calculated. These mean values were then compared to the mean vegetation heterogeneity, mean climatic heterogeneity and mean land transformation values, respectively, found for 10 000 sets of 135 randomly selected grid cells.

Highly transformed area

To further investigate interactions between avian spatial turnover, landscape heterogeneity and anthropogenic land transformation we repeated the above analyses for a subset of the region that has been highly transformed (the Western Cape Province comprising 153 of 1352 quarter-degree grid cells). This area includes 54% transformed (cultivated lands, urban/build-up lands and artificial water bodies) and 46% untransformed land-cover areas with three different biome types, i.e. succulent karoo, thicket and fynbos. The Western Cape region was the first region in southern Africa to be exploited by Europeans after the discovery of a sea route to India via the Cape of Good Hope by Portuguese sailors in the late 15th century (Theal, 1964; Hattersley, 1969). Land transformation was rapid over the next 500 years (Muller, 1969), especially after the Dutch set up permanent settlement in Cape Town in 1652 and began extensive crop farming.

We expected that within a highly transformed area such as the Western Cape, avian species assemblage patterns might be transformed to such an extent that the relationship between biome edge cells and high β-diversity values would be substantially weakened, and that the relationship between land transformation edge cells and high β-diversity values would predominate.

RESULTS

The correlation between β_g and β_{sim} was weak ($r = 0.12$, $n = 1352$, $ess = 600$, $p < 0.0022$), although significant. This weak relationship indicates that the two β measures are relatively independent of each other, as might be expected given that β_g primarily measures the rate of species turnover based on changes in species richness and β_{sim} measures the rate of species turnover based on changes in species composition.

The biome edge cells identified from the overlapping edge criterion and the dominant type criterion had significantly higher numbers of overlapping cells than expected by chance (Jaccard coefficient = 45%, $p <$ 0.05, 10 000 permutations). However, there was some, though generally limited, spatial displacement owing to the difference in the methods used to identify edges in each case. Both criteria were nonetheless successful in highlighting biome edges (Fig. 4). Much the same result was found for the land transformation edge cells (Three-way classification - Jaccard coefficient = 39%, $p < 0.05$, 10 000 permutations; Two-way classification - Jaccard coefficient = 34%, $p < 0.05$, 10 000 permutations), although the spatial congruence was often not as high as for the biome edge cells (Fig. 5). We consider these displacements in edge cells based on the two criteria helpful because they enhance the identification of transition areas between biome types and between land transformation types. Such transition areas are often not characterised by sharp boundaries but rather by boundaries where ecological change may be distributed over several kilometres especially in the case of biome transitions (Gosz & Sharpe, 1989). Thus, displacements of the kind identified here are useful in showing up

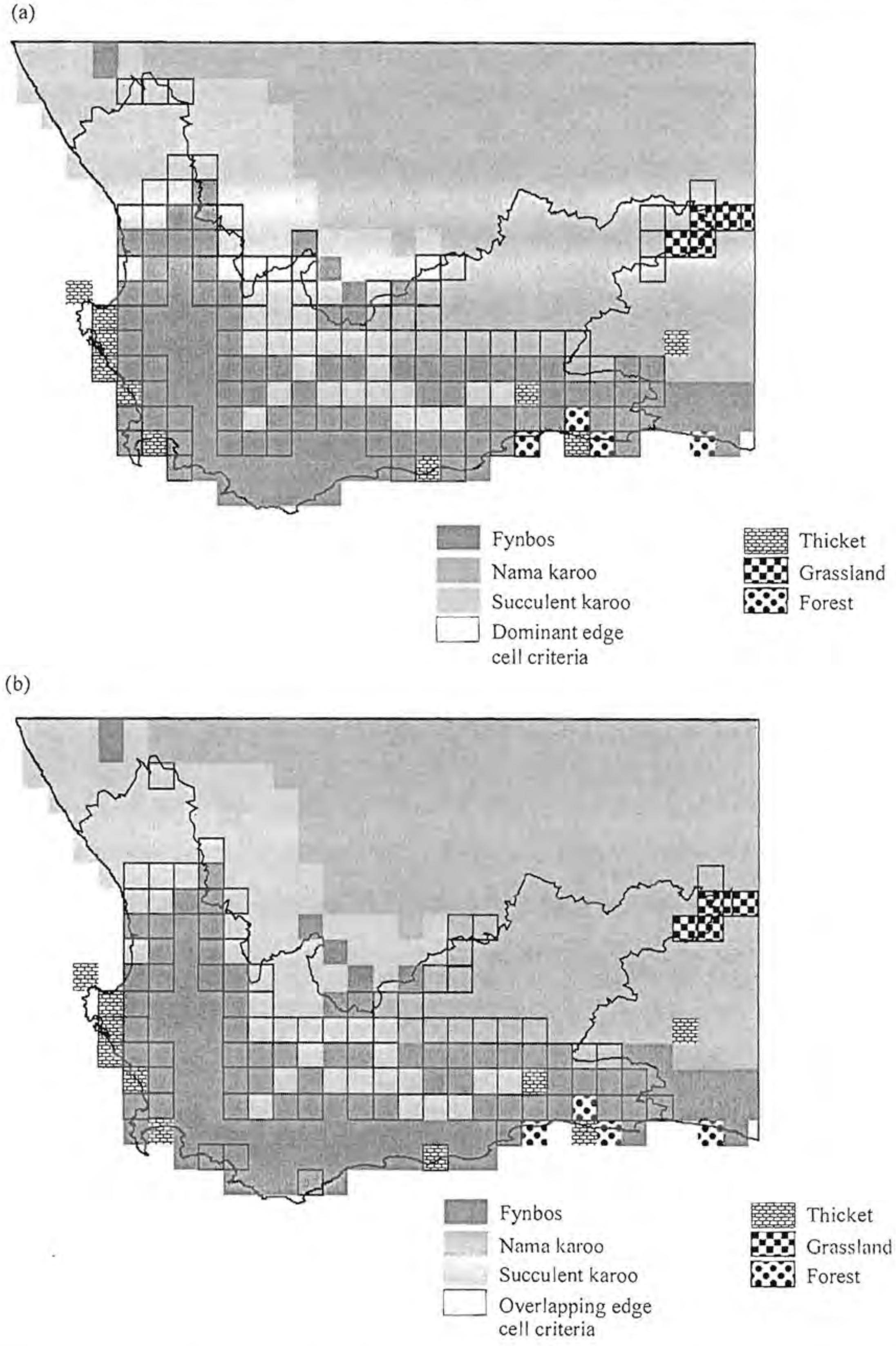

Figure 4 Biome edge cells for the Western Cape region based on the two different criteria used to detect edge cells namely, (a) the dominant edge criteria, and (b) the overlapping edge criteria.

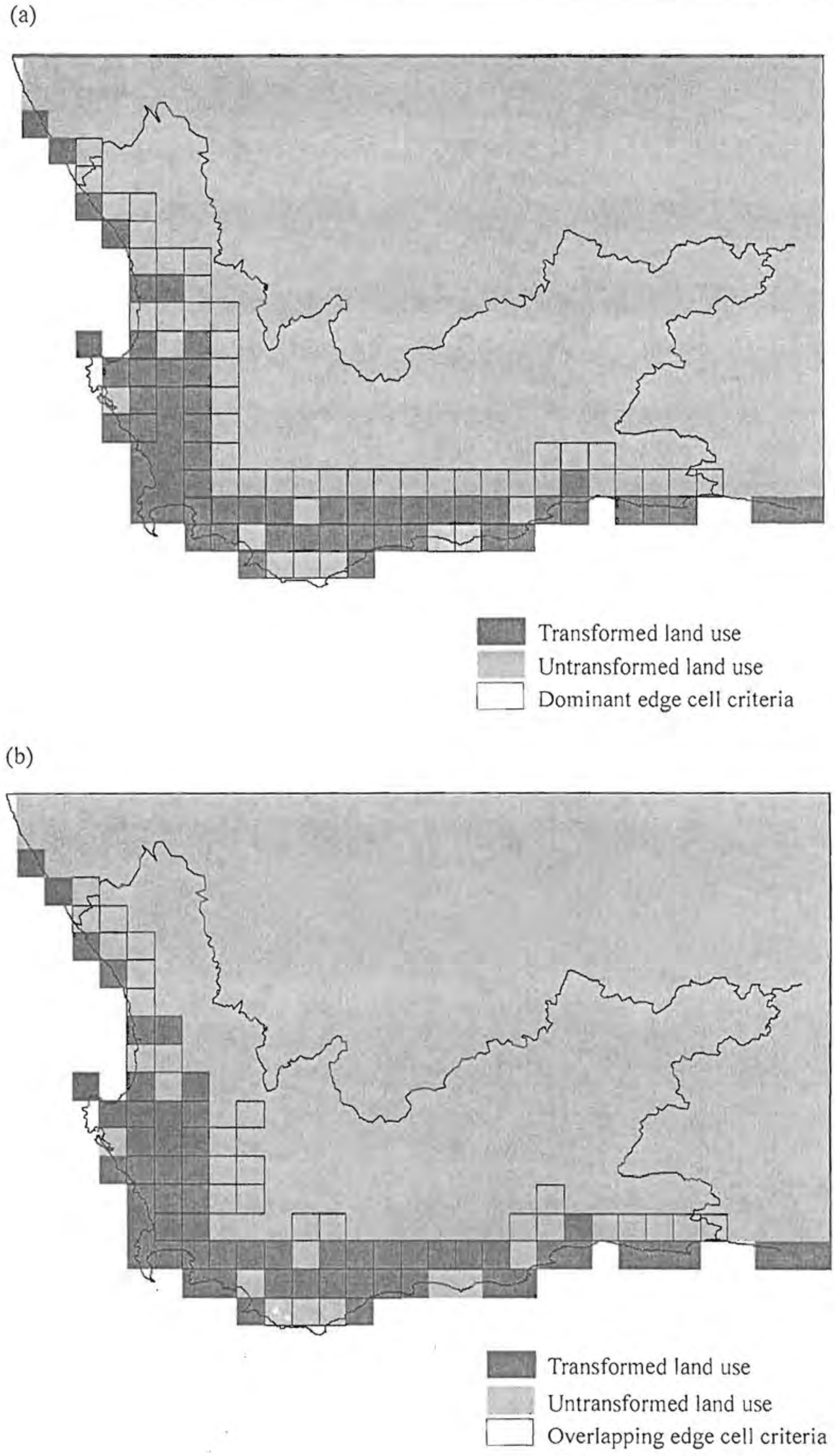

Figure 5 Land transformation edge cells for the Western Cape region based on the two different criteria used to detect edge cells namely, (a) the dominant edge criteria, and (b) the overlapping edge criteria.

areas of transition.

The biome and land transformation edge cells had significantly larger vegetation and land transformation heterogeneity values, respectively, than expected by chance ($p < 0.05$, 10 000 permutations – Tables 1 & 2). This result provides support for the idea that the biome edge cells and land transformation edge cells reflect biome and land transformation edges, respectively. Higher vegetation heterogeneity values in the biome edge cells are indicative of lack of homogeneity and therefore turnover between biomes. The increase in land transformation heterogeneity in the land transformation edge cells similarly supports the idea that the edge cells successfully identified transitional areas.

The biome edge cells had significantly larger climatic heterogeneity values (i.e. larger negative Moran's *I* values for both PPT and MIN) and β-diversity values (both β_g and β_{sim}) than expected by chance ($p < 0.05$, 10 000 permutations – Table 1). However, in the land transformation edge cells only β_g values were significantly larger than expected by chance (Table 2). Quarter-degree grid cells with the highest 10% of β_g values had significantly larger vegetation heterogeneity and climatic heterogeneity values (i.e. larger negative Moran's *I* values for both PPT and MIN) than expected by chance ($p < 0.05$, 10 000 permutations – Table 3). The land transformation heterogeneity values in these cells with high β_g values were significantly lower ($p < 0.05$, 10 000 permutations) than expected by chance. Similar relationships were found for the quarter-degree grid cells with the highest 10% of β_{sim} values (Table 3). However, it is evident from the significance values that the β_g values are more responsive to changes in climate heterogeneity than β_{sim} values, and that the latter are more responsive to changes in vegetation heterogeneity than the former (Table 3). Therefore, it appears that biome transitions are areas characterized by high levels of climatic and vegetation heterogeneity, and by high avian species turnover. Such spatial congruence was not found for areas transitional between land transformation types.

In the highly transformed Western Cape Province remarkably similar results were found. Within this subregion, the biome edge cells also had significantly larger climatic heterogeneity values and β-diversity values than expected by chance (Table 1). Likewise, the land transformation edge cells only had significantly larger β_g values than expected by chance (Table 2). The quarter-degree grid cells within the subregion with the highest 10% of β_g values had significantly larger vegetation heterogeneity and minimum temperature heterogeneity values than expected by chance (Table 3), and grid cells with the highest 10% of β_{sim} values had significantly larger vegetation heterogeneity values than expected by chance (Table 3). Land transformation heterogeneity values in the cells with high β_g values and high β_{sim} values were significantly lower than expected by chance (Table 3).

These results suggest that the avifauna is responding more strongly to biomes and transitions between them than to anthropogenic habitat transformation, at least at this resolution. To further demonstrate that, at the quarter degree resolution, biome identity has a larger influence on the avifauna than does land transformation we determined whether biomes and land transformation categories, respectively, remain significantly differentiated from each other based on avian species presence/absence data.

TABLE 1 Results indicating whether biome edge cells, identified based on both edge cell criteria used (criteria I and II), have significantly greater values of vegetation heterogeneity, climatic heterogeneity (PPT & MIN), and β-diversity than expected by chance based on 10 000 permutations. Results are given for both the regional scale and the smaller, highly transformed study area.

Study area and variables	Biome edge cells	
	Criterion I	Criterion II
Regional scale		
Vegetation heterogeneity	greater	greater
PPT heterogeneity	greater	greater
MIN heterogeneity	greater	greater
β_g-diversity	greater	greater
β_{sim}-diversity	greater	greater
Highly transformed region		
Vegetation heterogeneity	greater	greater
PPT heterogeneity	greater	greater
MIN heterogeneity	greater	greater
β_g-diversity	greater	greater
β_{sim}-diversity	greater	greater

Note: Significance ($p < 0.05$) was reached for all analyses showing a result = greater. MIN = mean absolute monthly minimum temperatures (^{0}C) averaged over the year; PPT = mean annual precipitation (mm yr $^{-1}$).

TABLE 2 Results indicating whether land transformation edge cells, identified based on both edge cell criteria used (criteria I and II), have significantly greater values of land transformation heterogeneity, climatic heterogeneity (PPT & MIN), and β-diversity than expected by chance based on 10 000 permutations. Results are given for both the three and the two land transformation categories used at the regional scale and at the smaller, highly transformed study area.

Study area and variables	Edge cells for three land transformation categories		Edge cells for two land transformation categories	
	Criterion I	Criterion II	Criterion I	Criterion II
Regional scale				
Land transformation heterogeneity	greater	greater	greater	greater
PPT heterogeneity	ns	ns	ns	ns
MIN heterogeneity	ns	ns	ns	ns
β_g-diversity	greater	greater	greater	greater
β_{sim}-diversity	lower	lower	lower	lower
Highly transformed region				
Land transformation heterogeneity	greater	greater	greater	greater
PPT heterogeneity	ns	ns	ns	ns
MIN heterogeneity	ns	ns	ns	ns
β_g-diversity	greater	greater	greater	greater
β_{sim}-diversity	lower	lower	lower	lower

Note: Significance ($p < 0.05$) was reached for all analyses showing a result = greater or lower. MIN = mean absolute monthly minimum temperatures (^{0}C) averaged over the year; PPT = mean annual precipitation (mm yr $^{-1}$). ns = value is not significantly greater or lower than the mean value.

TABLE 3 Results indicating whether cells with the highest 10% of β_g-diversity values and β_{sim}-diversity values have significantly greater values of vegetation heterogeneity, land transformation heterogeneity, and climatic heterogeneity (PPT & MIN) than expected by chance based on 10 000 permutations. The significance value (*p*) is given in parentheses. Results are given for both the regional scale and the smaller, highly transformed study area.

Study area and variables	10% Highest β-diversity values	
	β_g	β_{sim}
Regional scale		
Vegetation heterogeneity	greater (0.01)	greater (0.0007)
Land transformation heterogeneity	lower (0.0002)	lower (0.0001)
PPT heterogeneity	greater (0.002)	greater (0.02)
MIN heterogeneity	greater (0.0001)	greater (0.02)
Highly transformed region		
Vegetation heterogeneity	greater (0.03)	greater (0.01)
Land transformation heterogeneity	lower (0.03)	lower (0.002)
PPT heterogeneity	ns	ns
MIN heterogeneity	greater (0.0002)	ns

Note: Significance was calculated at $p < 0.05$. MIN = mean absolute monthly minimum temperatures (^{0}C) averaged over the year; PPT = mean annual precipitation (mm yr^{-1}). ns = value is not significantly greater or lower than the mean value.

If biomes have a large influence on the avifauna, then avifaunal presence/absence data should continue to distinguish these biomes. By similar reasoning, land transformation categories should remain distinguishable using the avian data if birds are responding strongly to transformation.

For this analysis, each grid cell was first assigned to a single biome and land transformation type, respectively, based on the most widespread biome and land transformation type in each cell. Analyses of similarity (ANOSIM – Clarke, 1993) using PRIMER v5.2 2001 (Clarke & Warwick, 1994) were used to establish the significance of differences between each of the seven biome types and between each of the three land transformation types based on avian species presence/absence data for each grid cell. ANOSIM is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke, 1993). A significant global R-statistic of close to zero indicates no clear differences between the biome types/land transformation types compared, and a significant global R-statistic of close to one indicates distinct differences between the biome types/land transformation types compared (Clarke & Gorley, 2001). We predicted that if biomes have a larger influence on the avifauna than land transformation, the biome analysis would be characterized by a larger global R-statistic value than the land transformation analysis.

From a total of 21 biome combination pairs (see Appendix 1), and following Clarke & Gorley's (2001) R-statistic classification, eleven (52%) biome pairs were either significantly well separated ($R \geq 0.75$, $p < 0.05$) or significantly clearly different ($R \geq 0.5$, $p < 0.05$), nine (43%) biome pairs were not clearly different ($0.5 > R > 0.25$), although significant, and only one (5%) biome pair was barely separable at all ($R \leq 0.25$), although significant. A significant overall global $R = 0.500$ ($p < 0.05$) was found for the biome comparison, indicating that, in the main, the avian presence/absence data were able clearly to distinguish the biomes.

From a total of three land transformation combination pairs, one (33%) land transformation pair was not clearly different ($0.5 > R > 0.25$) though significant, one land transformation pair was barely separable at all ($R \leq 0.25$) though significant, and finally, one land transformation pair was not significantly different (see Appendix 2). A non significant overall global $R = 0.004$ ($p > 0.05$) was found for the land transformation comparison, indicating that land transformation types could not be separated using avian presence/absence data.

DISCUSSION

Our results clearly show that biome edges have elevated climatic and vegetation heterogeneity. This is perhaps not surprising given that the biome classification we used for this study is based on differences in plant functional type and climate (Rutherford & Westfall, 1994; Low & Rebelo, 1996). Nonetheless, these findings do support the idea that the transition zones between biomes, like ecotones at finer scales, are more heterogeneous than other areas (Risser, 1995; Nekola & White, 1999; Bestelmeyer & Wiens, 2001).

The elevated heterogeneity at biome edges is clearly reflected in the avifauna. Both β_g and β_{sim} had larger values than expected by chance in the biome edge cells, which indicates that the biome edges are characterized not only by greater vegetation heterogeneity than cells elsewhere, but also by greater turnover in the avifauna than expected by chance. This demonstration of spatial congruence between biome transitions and avifaunal turnover is, to our knowledge, the first of its kind for the southern African avifauna (see Poynton, 1961; Poynton & Boycott, 1996 for amphibian analyses), and one of the few of its kind overall (see Risser, 1995; Krasnov & Shenbrot, 1998; Bestelmeyer & Wiens, 2001 for discussion, and Boone & Krohn, 2000 for examples). It also supports a widely held idea that bird assemblages respond strongly to changes in vegetation structure (Pitelka, 1941; Recher, 1969, Rotenberry & Wiens, 1980; Polo & Carrascal, 1999; Williams *et al.*, 1999; Boone & Krohn, 2000; Bestelmeyer & Wiens, 2001) even at large spatial scales. The idea that vegetation structure and its heterogeneity contribute substantially to changes in avian assemblages has long been appreciated for the southern African region (Winterbottom, 1978; Osborne & Tigar, 1992; Allan *et al.*, 1997b; van Rensburg *et al.*, 2000), and is supported by the outcome of the analyses of similarity undertaken here. Indeed, in a similar approach, van Rensburg *et al.* (2000) demonstrated that the relationships between the biomes based on avian species presence/absence data are similar to those found using analyses of the flora (see e.g. Cowling *et al.*, 1989), and our results using finer scale analyses support this outcome. Our results and those of van Rensburg *et al.* (2000) contrast strongly with the statements made by Allan *et al.* (1997a) that the botanically defined biomes are not entirely relevant to the avifauna.

The relationships between avian assemblages and vegetation structure and heterogeneity might appear contrary to the results of Chapter 2. There it was found that net primary productivity and precipitation are major correlates of avian diversity at the quarter degree grid cell resolution, whereas vegetation heterogeneity is only important as a correlate of diversity at a coarser resolution (one degree grid cell). However, Chapter 2 was concerned only with the relationships between species richness, productivity, climate and vegetation heterogeneity, whereas the analyses presented here concern changes both in species richness and in species identity. These differences between analyses based solely on richness and those including identity are mirrored, to some extent, in the outcomes of our analyses. β_g is a measure of turnover that is primarily a result of differences in species richness, whereas β_{sim} is far more responsive to species compositional differences between neighbouring cells (Lennon *et al.*, 2001). Here, there was a larger difference in climate heterogeneity between the 10% cells with the largest β_g values and a random sample of cells, than in the 10% cells with the largest β_{sim} and a random sample of cells. In addition, the opposite was found for vegetation heterogeneity. These results clearly support those that have shown a pronounced influence of climate on species richness in the region (O'Brien, 1993, 1998; O'Brien *et al.*, 1998, 2000; Andrews & O'Brien, 2000; Chapter, 2). Moreover, they indicate that whilst climate is likely to contribute most to changes in richness in the region, vegetation heterogeneity is likely to have a pronounced second-order effect on changes in species identity, a major component of turnover. These results are also consistent with Williams *et al.*'s (1999) conclusions that Afrotropical birds show broad latitudinal trends in β-diversity patterns. Their results suggested that transition zones based on differences in species richness are dominant further away from the equator (where variation in climatic conditions increases), and that transition zones based on species compositional differences are important in equatorial areas (where variation in climatic conditions is low).

In contrast, human land transformation patterns were not associated with particularly climatically variable areas and seem to have had no substantive influence on the avifauna, at least at the spatial scale of our analyses. Land transformation categories could not be recovered in the analyses of similarity, and the cells that constituted those with the 10% highest β_g and β_{sim} values had lower land transformation heterogeneity values than expected by chance. Furthermore, land transformation edge cells tended to have β_{sim} values that were no different to cells selected at random. In other words, species compositional differences, that are generally indicative of human land transformation (see Rosenzweig, 1995; Stotz 1998), were not discernible. However, β_g, which is associated with changes in species richness, was significantly higher in land transformation edge cells than expected by chance. This might reflect changes in either species gains or losses because, in southern Africa, several indigenous species are known to be associated with both agricultural (e.g. several dove species) and urban (e.g. hadeda ibis, *Bostrychia hagedash*, olive thrush, *Turdus olivaceus*) land transformation (Harrison *et al.*, 1997). That land transformation heterogeneity was lower than expected by chance in the 10% highest β-diversity cells, but that β_g was higher than expected by chance in the land transformation edge cells is not surprising. The spatial congruence of the top 135 β_g cells and the land transformation edge cells is low (Three-way classification for criteria I and II - Jaccard coefficient = 5% and 5%, respectively; Two-way classification for criteria I and II - Jaccard coefficient = 7% and 8%, respectively), and certainly lower than expected from a random draw ($p < 0.05$, 10 000 permutations). Thus, cells with high β_g values are mostly from areas where land transformation is intermediate when compared to random ($p = 0.14$, 10 000 permutations). The same significantly low ($p < 0.05$, 10 000 permutations) spatial congruence is also true of the top 135 β_{sim} cells (Three-way classification for criteria I and II - Jaccard coefficient = 4% and 5%, respectively; Two-way classification for criteria I and II - Jaccard coefficient = 6% and 7%, respectively). These cells with high β_{sim} values are mostly from areas where land transformation is minimal ($p = 0.04$, 10 000 permutations).

The virtual absence of an effect of land transformation on avian diversity patterns persisted when the analyses were confined to the highly transformed Western Cape Province. Why this should be the case is not entirely clear. It might be expected that 350 years of commercial farming and other forms of anthropogenic landscape transformation (see review in Cowling *et al.*, 1996; Dean, 2000; Fairbanks *et al.*, 2002) would have obscured natural patterns shown by the avifauna. However, there are several reasons why this might not be the case. First, the quarter degree resolution of our study might be too coarse to reveal finer-scale effects. For example, within the larger fynbos biome region, quarter-degree cells representing the edges of the dominant land-cover types (i.e. cultivated lands, urbanized areas and artificial water body areas), contained 85% of the total fynbos avian species richness. In other words, highly transformed cells still contain sufficient natural vegetation to allow species, which would otherwise be compromised by landscape transformation, to persist at abundances high enough to be detected during atlassing surveys (see also Redford & Dinerstein, 1994). Second, much of the landscape transformation might be too recent for there to have been any affect on avian transition patterns (Brooks *et al.*, 1999; Chapter, 5). Third, African birds might be capable of withstanding considerable habitat modification and disturbance (the resilience of the African fauna to human activities has repeatedly been discussed in the context of the low levels of recorded Quaternary extinctions; see MacPhee (1999) and references therein). Finally, it may well be that the influence of biome transitions, which are large and stable (i.e. historically old) areas across space (Gosz & Sharpe, 1989; Risser, 1995), are capable of overwhelming even substantial human land transformation patterns (Thompson, 1996; Brooks *et al.*, 1999). For example, Gaston & Blackburn (2000) have argued that even in the highly modified landscapes of the United Kingdom (see Collar *et al.*, 1994; Bellamy *et al.*, 1996), at large spatial scales, natural processes continue to exercise a large enough influence on avian diversity for these natural processes to remain discernible.

Currently, there are insufficient data, collected at a wide enough variety of scales, to further resolve these questions, at least for southern Africa. Given the rate at which landscapes are being modified in the subregion (Richardson *et al.*, 1996; Thompson, 1996; Fairbanks *et al.*, 2000), and projections for even greater modification in the future (Richardson *et al.*, 1996; Erasmus & van Jaarsveld, 2002) such studies will be critical for ensuring that landscape planning can be done in such a way that it will both ensure species survival and meet human aspirations. This is, after all, the *raison d'etre* of sustainable development. It is ironic, in this context, that South Africa should simultaneously host the World Summit on Sustainable Development and continue downsizing its biological research and conservation capabilities.

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APPENDIX 1 Analyses of similarity between each biome combination pair based on avian distribution data to establish the significance of differences between each of these pairs. The *R*-statistic is a measure of similarity between each biome pair. If *R* is significantly different from zero, then there are significant differences between biome pairs. All pairwise *R*-statistic values reached significance after a sequential Bonferroni correction was applied. An overall significant *R*-value of 0.5 ($p < 0.05$) was found for all biome combination pairs in total.

Biome pairs	*R*-statistic	Significance level
Savanna vs. grassland	0.396	0.001
Savanna vs. succelent karoo	0.607	0.001
Savanna vs. Nama karoo	0.504	0.001
Savanna vs. fynbos	0.371	0.001
Savanna vs. thicket	0.194	0.010
Savanna vs. forest	0.411	0.004
Grassland vs. succelent karoo	0.795	0.001
Grassland vs. Nama karoo	0.609	0.001
Grassland vs. fynbos	0.336	0.001
Grassland vs. thicket	0.311	0.003
Grassland vs. forest	0.396	0.002
Succelent karoo vs. Nama karoo	0.26	0.001
Succelent karoo vs. fynbos	0.666	0.001
Succelent karoo vs. thicket	0.751	0.001
Succelent karoo vs. forest	0.891	0.001
Nama karoo vs. fynbos	0.510	0.001
Nama karoo vs. thicket	0.487	0.001
Nama karoo vs. forest	0.806	0.001
Fynbos vs. thicket	0.723	0.001
Fynbos vs. forest	0.510	0.024
Thicket vs. forest	0.377	0.043

APPENDIX 2 Analyses of similarity between each land transformation combination pair based on avian distribution data to establish the significance of differences between each of these pairs. The *R*-statistic is a measure of similarity between each land transformation pair. If *R* is significantly different from zero, then there are significant differences between land transformation pairs. Sequential Bonferroni correction was applied to all pairwise significance values. An overall non significant *R*-value of 0.004 ($p > 0.05$) was found for all land-cover combination pairs in total.

Land transformation pairs	*R*-statistic	Significance level
Untransformed vs. totally transformed	0.063	0.285
Untransformed vs. partially transformed	0.24	0.001
Totally transformed vs. partially transformed	0.413	0.001

CHAPTER 4

Complementary representation and zones of ecological transition

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Abstract

Minimum complementary sets of sites that represent each species at least once have been argued to provide a nominal core reserve network and the starting point for regional conservation programs. However, this approach may be inadequate if there is a tendency to represent several species at marginal areas within their ranges, which may occur if high efficiency results from preferential selection of sites in areas of ecological transition. Here we use data on the distributions of birds in South Africa and Lesotho to explore this idea. We found that for five measures that are expected to reflect the location of areas of ecological transition, complementary sets tend to select higher values of these measures than expected by chance. We recommend that methods for the identification of priority areas for conservation that incorporate viability concerns be preferred to minimum representation sets, even if this results in more costly reserve networks.

Key words: beta diversity, complementarity, efficiency, reserve selection.

INTRODUCTION

Approaches to the selection of priority areas for conservation based on the complementarity principle are becoming increasingly popular in the conservation literature (e.g. Pressey *et al.* 1993; Howard *et al.* 1998; Margules & Pressey 2000). Most commonly, these methods look for a set of sites such that all species of concern are represented in the minimum possible total area.

One potential drawback of such minimum sets is that some species may be represented at sites that are inadequate for their long-term persistence in the final conservation network (Harrison & Martinez 1995; Turpie 1995). For example, Branch *et al.* (1995) found that seven of the eight sites selected to represent all species of land tortoises and terrapins in southern Africa were inadequate for the protection of the species that justified their selection. Likewise, Nicholls (1998) found that in a near-minimum set selected to represent species of snakes in South Africa, most species were mainly represented in grid cells covering the periphery of their spatial distributions. Such outcomes might explain the finding by other studies that minimum sets are ineffective in maintaining species over time (Margules *et al.* 1994; Virolainen *et al.* 1999; Rodrigues *et al.* 2000*a*, 2000*b*).

To date, there has been no investigation of whether there is reason to suspect an inherent tendency in minimum complementary sets to select sites that are of marginal value for the conservation of species. The high efficiency of minimum sets (i.e. the ability to represent a maximum of diversity in the minimum number of sites; Pressey & Nicholls 1989) is their most acclaimed trait, and derives from the selection of sites that are highly complementary in terms of species composition. It is implicitly assumed that this complementarity is obtained by selecting sites representative of different ecological regions, which therefore have species assemblages that complement each other. However, it can be envisaged that an even more efficient way of representing all species would be to select areas in the transition between ecological regions, with species assemblages resultant from a mixture of floras or faunas, which would allow the simultaneous representation of species belonging to different ecological regions (Fig. 1). If so, then the high efficiency of minimum sets may be attained at the cost of a preferential selection of sites which are not truly representative of any ecological region and where several species are represented at marginal sites within their ranges.

In this paper, we use data on the distribution of birds in South Africa and Lesotho to test this idea, by investigating whether minimum complementary sets tend to select sites in areas of ecological transition.

DATA

The Southern African Bird Atlas Project (SABAP; Harrison *et al.* 1997) has provided the most comprehensive information currently available on the distribution of birds in southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid for Botswana (for a detailed description of the methods used in the SABAP, see Harrison *et al.* 1997).

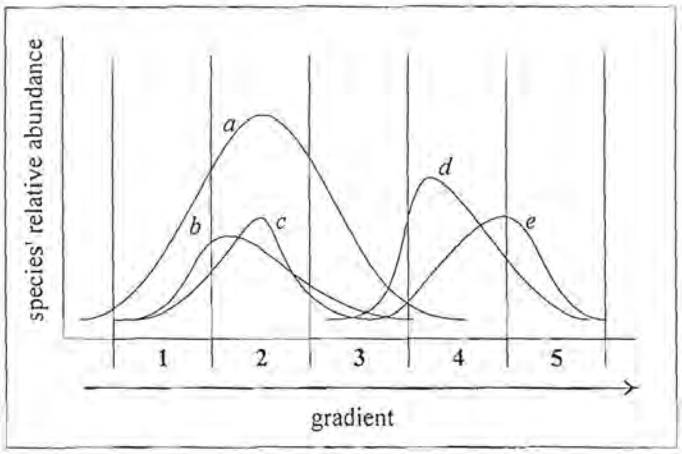

Figure 1. Hypothetical distribution of five species (*a* - *e*) across an environmental gradient. All species might be represented at the core of their ranges by two sites (2 and 4) or by a minimum set of just one site (3) in the transition between different species assemblages.

In this study, we used the presence/absence data for South Africa and Lesotho (1858 grid cells), excluding marine, vagrant, marginal (species with only one occurrence in the study area and substantial populations outside of it) and escaped species from the analysis (651 species were analysed).

We used Low & Rebelo's (1996) classification of the study area in seven biomes, obtaining the percentage of each cell occupied by each biome by digitising the corresponding maps. We also used two classification systems of vegetation types: that into 16 types by Harrison *et al.* (1997), who provided corresponding distribution maps; and a finer classification into 68 types by Low & Rebelo (1996) for which we knew only the number of types present in each cell.

ANALYSES

Thirty complementary sets were obtained that represent all 651 bird species in South Africa and Lesotho by solving the integer linear problem of minimising the number of grid cells such that each species is represented at least once (Underhill 1994). This was solved using the CPLEX optimisation software (ILOG 1999), and the minimum number of cells needed to represent all species was 19. Numerous equally optimal solutions exist for this problem, and the specific solution found depends on the order in which variables (sites) are introduced. To obtain 30 representatives of the entire set of optimal solutions, the problem was solved 30 times after re-ordering the data set randomly. To avoid repeated selection of solutions, each time one was sought an additional restriction was added to the problem that excluded the solution previously found (Rodrigues *et al.* 2000*c*). This procedure obtains a random set of optimal solutions without replacement.

Five measures that are expected to reflect the location of areas of ecological transition were calculated for each grid cell:

(i) **Presence of vegetation edges.** A cell was considered to be at the edge of one of the 16 vegetation types considered if it belongs to that type but at least one of its neighbours (one of the eight surrounding cells) does not (Fig. 2*a*).

(ii) **Biome heterogeneity**, obtained using Simpson's index of diversity (Krebs 1999):

$1 - \text{Sum}\ (p_i)^2$

where p_i is the fraction of the grid cell's area occupied by biome i. This index ranges from zero (only one biome present in a cell) to 0.86 (all seven biomes present in the same proportions) and is expected to reach high values in areas of transition between biomes. The values recorded ranged between 0-0.76 (Fig. 2*b*).

(iii) **Number of vegetation types** in each cell, out of the 68 types defined by Low & Rebelo (1996) (Fig. 2*c*). This is expected to be higher in areas of transition between different vegetation compositions. The values recorded ranged between 1-8.

(iv) **Bird composition heterogeneity.** A dissimilarity measure was obtained for each pair of neighbouring cells using the complement of the simple matching coefficient (Krebs 1999):

$1 - (a + d)/(a + b + c + d)$

where a is the number of species occurring in both cells (A and B) of a pair, b is the number of species occurring in A but not in B, c is the number of species occurring in B but not in A, and d is the number of

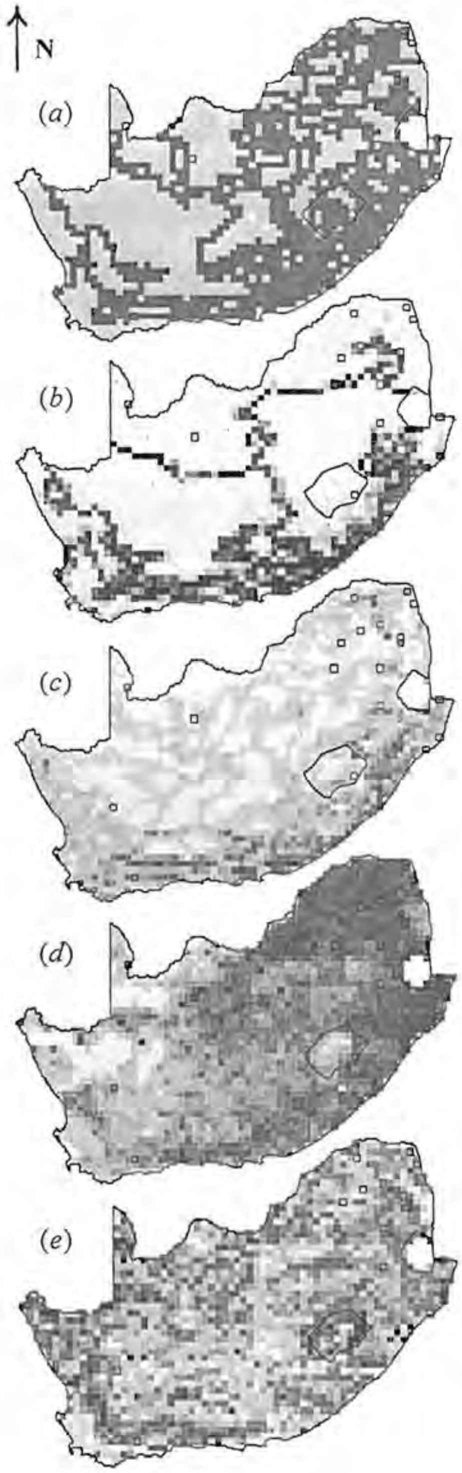

Figure 2. Measures of ecological transition: (*a*) presence of vegetation edges (darker cells correspond to edges); (*b*) biome heterogeneity; (*c*) number of vegetation types; (*d*) bird composition heterogeneity; and (*e*) β_g across South Africa and Lesotho. In (*b*), (*c*), (*d*) and (*e*), darker colours correspond to higher values of ecological transition and colour gradients represent 10 equal-interval classes. White is absence of data. The cells outlined in black correspond to one of the complementary solutions found.

species absent from both cells. For each cell, the value of bird composition heterogeneity was obtained by calculating the average dissimilarity between the cell and each of its neighbours. This index ranges between zero (the cell has the same species composition as all of its neighbours) and one (it does not share any species with its neighbours). This measure is expected to capture the transition between areas of different species composition. The values recorded ranged from 0.03-0.26 (Fig. 2*d*).

(v) β_g, is a measure of β-diversity based on the rate of species replacement across multidirectional gradients (see Fig. 3 for an explanation). As with the previous measure, this is expected to highlight transition areas between different species assemblages, but it is more effective in capturing directional gradients in composition. It is also less sensitive to fragmentation, whether real or artificially imposed on the data set by uneven sampling effort, and to local species richness. The values recorded ranged between 1.2-58.1% (Fig. 2*e*).

For each measure, it was determined whether complementary sets tend to select higher values of transition than expected by chance. For measures (i), (iii), (iv) and (v), the mean value across the cells in each of the 30 complementary sets was found always to fall within the 5% upper tail (i.e. a one-tailed test) of a random distribution of means obtained by selecting 10,000 random sets of 19 cells each. For the biome heterogeneity (ii), which has a markedly skewed frequency distribution (Fig. 4*b*), the median value of complementary sets was found always to be above the median for all cells.

For each of the measures, we also compared the frequency distribution of values in the cells selected by complementarity to the frequency distribution for all the 1858 cells in the study area (see legend to Fig. 3 for an explanation). In all cases, the mean frequency distribution for the 30 complementary sets showed a displacement to the right (Fig. 4), which was very marked for all measures except perhaps biome heterogeneity (Fig. 4*b*).

Overall, these results suggest a clear tendency for minimum sets for birds in South Africa and Lesotho to coincide with areas of ecological transition, an outcome that was consistent for all the five measures of transition considered.

DISCUSSION

The simplicity of minimum sets as a way of representing a maximum of biodiversity features at minimum cost makes them extremely appealing for conservation planning. In practice, of course, few proponents of complementarity-based methods would argue that representing each species only once in a conservation network is a sensible planning strategy (although several published studies have actually used this simple representation target in analysing methods for the definition of priority areas for conservation; e.g. Sætersdal *et al.* 1993; Castro Parga *et al.* 1996; Howard *et al.* 1998; Nantel *et al.* 1998). Nevertheless, it has been advocated that these minimum sets can constitute a nominal core reserve network and the starting point for the development of regional conservation programs (Nicholls and Margules 1993; Margules *et al.* 1994).

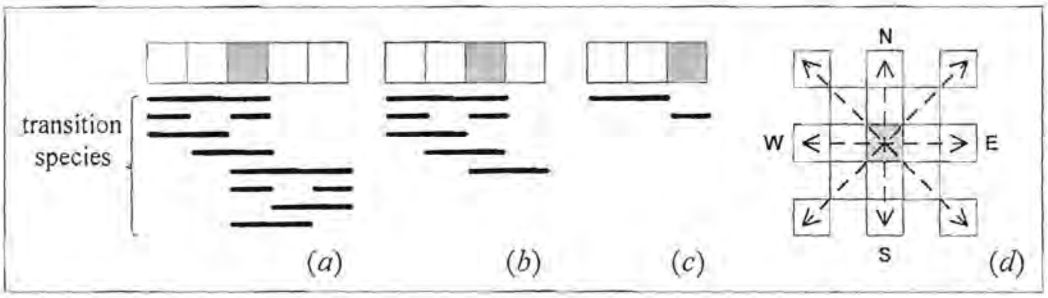

Figure 3. Illustration of the concept and measurement of diversity based on multidirectional gradients (β_g). This measure highlights regions that have a high proportion of species that are on the edge of their ranges ('transition species'). (*a*) Considering a linear sequence of five adjacent cells centred on the focal cell (in grey) for which β_g is to be measured, species whose range within these five cells follows one of the patterns indicated by the thick horizontal lines were considered to be 'transition species'. The same applies when only four (*b*) or three (*c*) adjacent cells are possible (this happens for cells at the edge of the study area). The percentage of transition species in relation to the total number of species found in the sequence of adjacent cells measures the intensity of species replacement across that direction. (*d*) The intensity of species replacement is measured across four directions (dashed arrows): West-East (horizontal), North-South (vertical), NW-SE and NE-SW (two diagonals). The final β_g value is the maximum of these values.

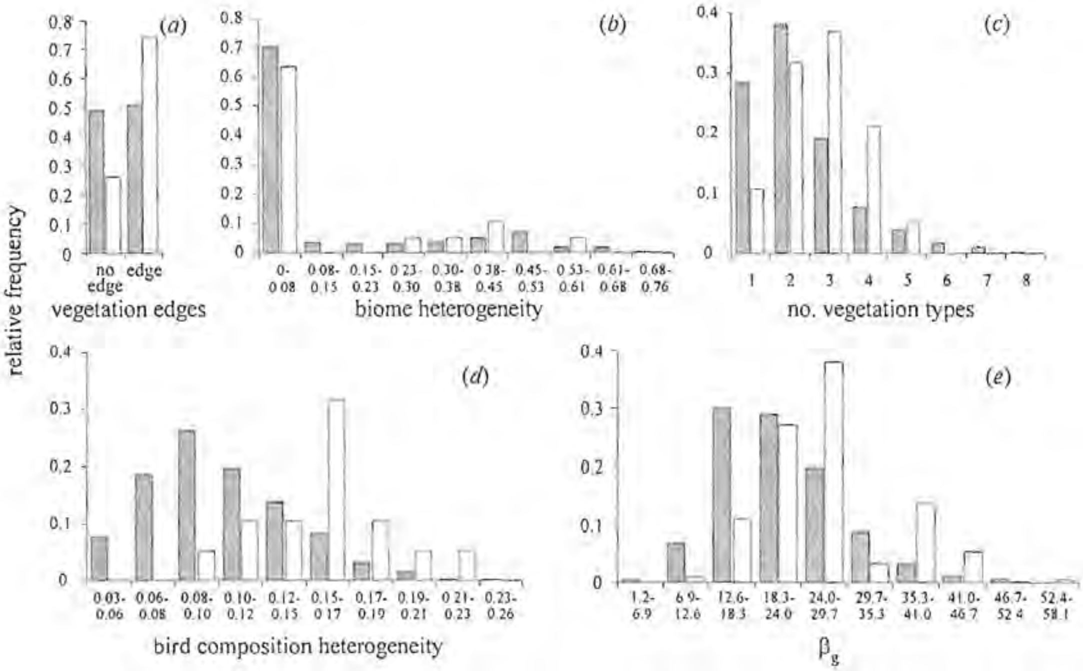

Figure 4. Comparison between the frequency distributions obtained for all grid cells in the study area (grey bars) and the mean frequency distributions of the 30 complementary sets (white bars), for each of the measures of ecological transition: (*a*) presence of vegetation edges, (*b*) biome heterogeneity, (*c*) number of vegetation types, (*d*) bird composition heterogeneity, and (*e*) β_g. In (*a*) only two classes were considered (cells which are edges and cells which are not); in the other histograms, ten (eight in *b*) equal width classes were considered between the minimum and the maximum values recorded in all cells. The frequency distribution for all cells was obtained by computing the fraction of all cells in the study area whose values fall within each class (relative frequency). The mean frequency distribution for the complementarity sets was obtained by calculating the mean relative frequency in each of those classes for the 30 complementary sets.

However, even this approach may be inadequate if these minimum set nodes form a poor or unsuitable basis for reserves aimed at the conservation of the species that they are supposed to represent (Branch *et al.* 1995; van Jaarsveld 1995).

Our results for birds in South Africa and Lesotho confirm that there is a tendency for minimum sets representing each species once to coincide with areas of ecological transition. If, as seems likely commonly to be the case, the high efficiency of minimum complementary sets is obtained by a preferential selection of transition areas, then these results may not be exclusive to this particular data set, and may translate into a more general tendency for representing at least some species at peripheral areas within their ranges (indeed, we found that in our data set an average of 21% of all species were represented in the complementary sets by edge cells of their ranges only). Without denying the potential importance of peripheral populations for the conservation of species (Lesica & Allendorf 1995; Channell & Lomolino 2000), it may be a questionable strategy preferentially to select these areas, where species are expected to exhibit lower abundance (Maurer & Brown 1989; Lawton 1993; Brown 1995; Brown *et al.* 1995) and therefore be more vulnerable to local extinction. A reserve network built on these sites is likely to be very ineffective in ensuring the maintenance of species over time if the surrounding habitats are degraded (Brown *et al.* 1995), especially in a scenario of future climate change, which would probably have stronger effects in areas of transition between different ecological regions.

These results do not refute the value of applying complementarity-based methods to the selection of networks of nature reserves. They are a powerful and flexible tool that allows the integration of a wide range of concerns in the simultaneous evaluation of many sites for the conservation of many species, and that can be used in much more sophisticated ways than simply looking for minimum representation sets (Rodrigues *et al.* 2000*c*). Although reserve networks obtained taking viability concerns into account are expected to be significantly more costly than those obtained by minimum representation sets (e.g. Nicholls 1998; Rodrigues *et al.* 2000*a*, 2000*b*), they should be preferred, as they are likely to perform considerably better in achieving long-term conservation, the reason for the designation of reserves in the first place.

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CHAPTER 5

SPECIES RICHNESS, HUMAN POPULATION SIZE AND ENERGY: CONSERVATION IMPLICATIONS AT A NATIONAL SCALE

Running title: Conservation conflicts

In review: *Ecological Applications*

Abstract. The maintenance of biodiversity rests on understanding and resolving conflict between patterns of species occurrence and human activity. Recent debate has centred on the relationship between species richness and human population density. However, conclusions have been limited by the lack of investigations of these relationships for individual countries, at which level most practical conservation actions are determined, and for a spatial resolution at which practical conservation planning takes place. Here, we report the results of the first such analysis, for birds in South Africa. Species richness and human density are positively correlated, apparently because both respond positively to increasing levels of primary productivity. High species richness is maintained by currently designated reserves, but the areas surrounding these have higher human population densities than expected by chance, placing the reserves under increasing external pressure. Not all species lie within protected areas, but the options are limited for building on the present network to generate a more comprehensive one, which protects all species and significantly reduces the conflict with human activities by designating new reserves in areas with lower human populations. Ultimately, the only solution to the conflict between biodiversity and people is likely to be individual-based regulation of human population size.

Key words: species richness; human population size; primary productivity; scale; reserves.

Introduction

It is widely accepted that habitat destruction is a key component of species extinction (Bibby 1995, Brooks et al. 1997, Brooks et al. 1999*a*), that human activities are responsible for the vast majority of current habitat loss (Soulé 1991, Ehrlich 1995, Bawa and Dayanandan 1997), and that human population density is correlated with habitat modification (Harcourt et al. 2001). What is much less clear is whether areas of high human activity and high species richness are spatially congruent. If, on the one hand, the two are inversely related, areas rich in species might not be severely compromised by the ongoing development required to sustain growth in human numbers and expectations. On the other hand, if the relationship between species richness and human impact is positive, conservation conflicts can be expected to increase, because increasing human resource demands will pose ever greater threats to biodiversity. Under the latter scenario, considerably larger efforts will have to be made to set aside and protect conservation areas in species rich regions (Soulé and Sanjayan 1998), and to integrate more carefully conservation requirements into land use planning, than is currently the case.

Despite the existence of several studies that have examined these issues (e.g., Kerr and Currie 1995, Thompson and Jones 1999, Cincotta et al. 2000), debate (Margules and Gaston 1994, Redford and Dinerstein 1994, Faith 2001, Huston 2001, Balmford et al. 2001*a*) has been polarized around two recent studies. In the first, Huston (1993) concluded that because agricultural productivity is low and plant species richness generally high in low productivity areas (and *vice versa*), conflicts between conservation and other human land uses (especially agriculture) can be avoided. In contrast, Balmford et al. (2001*b*) showed that at the one-degree resolution across Africa, the relationship between primary productivity and species richness of vertebrates, and primary productivity and human population density, were both unimodal, resulting in a positive relationship between species richness and human population density. They concluded that future conflicts between conservation and development cannot readily be avoided, and that maintaining reserves in high human population density areas would become increasingly difficult.

Given that increasing human demand for resources, and especially for agricultural resources, is likely to mean significant future environmental change (Tilman et al. 2001), understanding the relationship between human activity and biodiversity is critical for reducing the rate at which species continue to be lost. This is particularly true for the scale at which conservation is likely to be implemented. That is, within countries, and using data that are at the finest resolution available for the region (e.g., Lombard 1995*a*, *b*, van Jaarsveld et al. 1998). The form of the relationship between productivity and species richness might change significantly at smaller spatial extents, thus providing different outcomes to those of studies undertaken over larger areas (Margules and Gaston 1994, Redford and Dinerstein 1994). If, at a finer spatial scale (both extent and resolution), the relationships between productivity, human activity and biodiversity are positive, then efforts to integrate land use planning at the national level clearly need to be stepped up in synchrony with broader scale, often global, initiatives (Mace et al. 2000, Myers et al. 2000). Likewise, if finer resolution information is available, local heterogeneity might mean that in at least some areas conservation and human development needs can be integrated with less compromise (Balmford et al. 2001*b*).

Investigations of the relationships between human activity, species richness and conservation requirements have, to date, not been undertaken at the within-country scale, and using the data resolution employed for local conservation. Thus, it is not clear what the sign or form of the relationships are, a significant gap in the knowledge required to undertake rational conservation planning within a framework of ongoing human need (see Faith 2001). Here, we address this lacuna by examining relationships between bird species richness, human population density, landscape transformation, and conservation areas in South Africa at three spatial resolutions (quarter-, half- and one-degree). Following Harcourt et al. (2001) we also determine whether existing conservation areas are located in areas of unusually high population density, whether small reserves are particularly prone to this effect, and whether conservation agencies are proclaiming increasingly smaller protected areas in regions of high population density. If fine scale heterogeneity in species distributions and human land use can potentially be used to minimize conflict between conservation and development, but conservation agencies are not making use of this opportunity, then longer-term maintenance of biodiversity could be under greater risk than is presently thought to be the case (see e.g., Woodroffe and Ginsburg 1998, Inamdar et al. 1999, Liu et al. 2001).

We chose South Africa and data on birds for several reasons. First, although South Africa is considered a developing country (O'Riordan 1998), it has a well-developed, mechanized agricultural infrastructure, which means both local food security and substantial export-based agricultural contributions to its GDP (World Development Report 2000/2001). Huston (2001) argued that such an infrastructure is likely to reduce the correlation between human population density and net primary productivity that is apparently a characteristic of developing nations. That is, people can occupy areas for reasons other than those associated with the exploitation of local resources for subsistence agriculture.

Second, species richness data (here considered a reasonable surrogate for biodiversity – see Gaston 2000) at a quarter-degree resolution are generally used for conservation planning in South Africa (Lombard 1995*b*, Anonymous 1997, SA-ISIS 2001). Although reserves are often smaller in area than an entire quarter-degree grid cell, this resolution is regularly used to identify areas in need of conservation attention (e.g., Lombard et al. 1995). Third, the most comprehensively surveyed taxon at the quarter degree resolution is the birds (Harrison et al. 1997). Fourth, there are modern data available on human population density (Statistics South Africa 1996) and landscape transformation (Fairbanks et al. 2000), as well as for the relationships between net primary productivity (NPP), rainfall (a major correlate of NPP) and species richness (Chapter 2), thus making it possible to explore explicitly the interrelationships between these variables.

Methods

Avian species richness data for South Africa (including Lesotho) were obtained from the Southern African Bird Atlas Project (SABAP, Harrison et al. 1997), which compiled data on species occurrences at a quarter-degree grid (15' x 15' ≈ 676-km^2) (Fig. 1). In a previous study (Chapter 2) the relationships between avian species richness and several environmental variables were investigated at three spatial resolutions, viz. quarter-degree (1 858 grid cells of approximately equal area, but varying from 635-km^2 in the north to 712-km^2

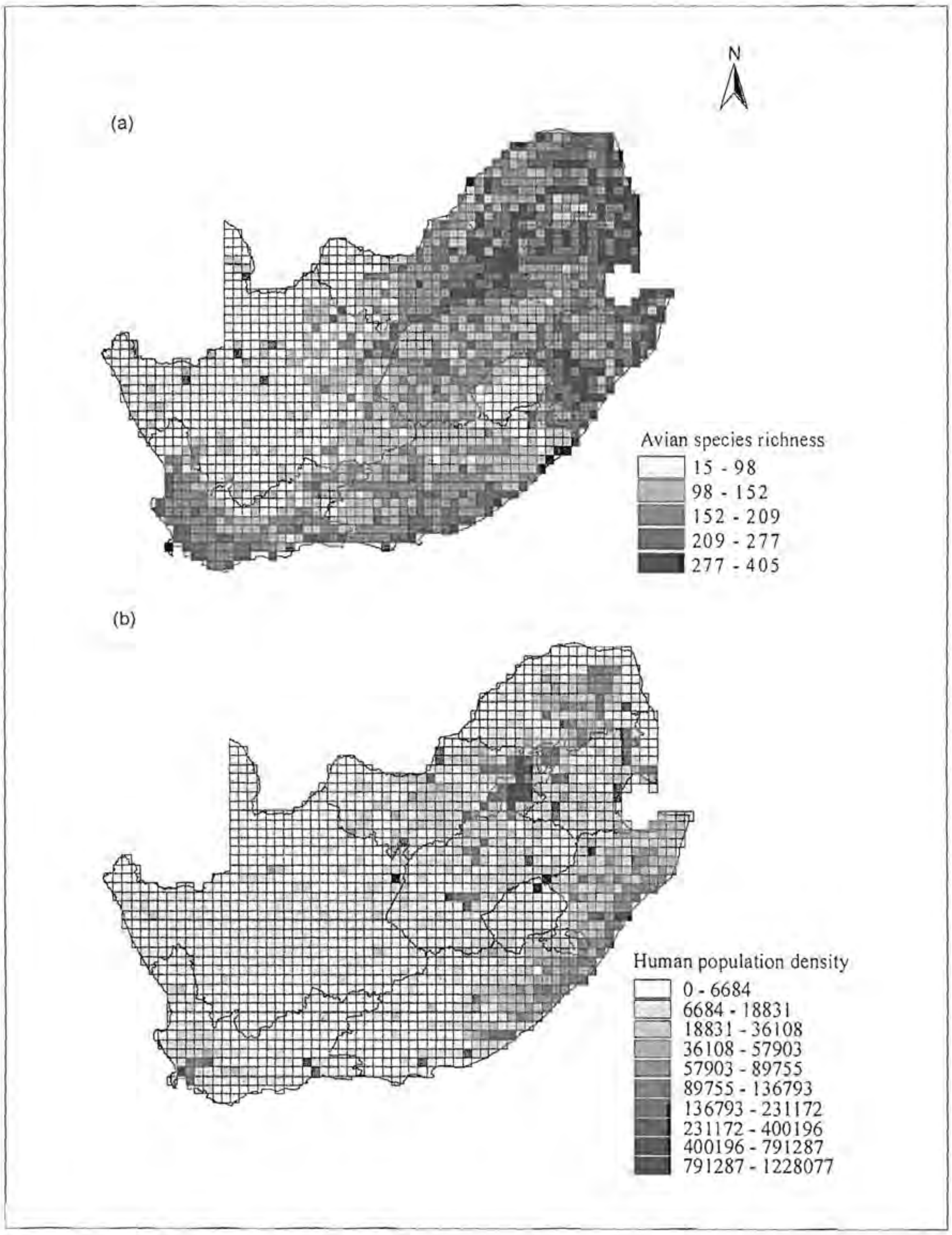

Fig. 1. Avian species richness (a) and human population size (b) variation across South Africa.

in the south), half-degree (458 cells), and one-degree (102 cells of *ca.* 100-km x 100-km). It has been shown that net primary productivity (NPP) (at the half-degree and one-degree resolutions) and precipitation (PPT) were strongly correlated, and were significant, strong positive, linear correlates of avian species richness at all spatial scales (Table 1). For this analysis, we use the same species richness data, precipitation and NPP data, but now include additional data on human population density, land transformation, and the position, extent and date of declaration of conservation areas. We also examine four species richness categories, based on Balmford et al.'s (2001*b*) finding that the relationships between human population density and species richness differ between groups with different range sizes. The four avian species richness categories calculated for each quarter-degree cell were (i) all 651 species, (ii) the 25% most widespread species (163 of 651 species), (iii) the 25% most range restricted species (163 species), and (iv) only those 152 species classified as red data species based on Baillie and Groombridge (1996) and Barnes (2000) red list categories.

Data on land transformation in the study area were obtained by calculating the percentage of each land-cover class in each quarter-degree cell, based on six transformed land-cover classes provided by Thompson (1996) and Fairbanks et al. (2000). These percentage land-cover values were then summed in each grid cell. These classes were based on seasonally standardized Landsat TM satellite imagery captured primarily during 1994-1995 and included cultivated lands, forest plantations, urban/built-up lands, mines and quarries, degraded lands and water bodies. As was the case with the avian richness data, percentage land-cover was rescaled for grid cell sizes of half-degree and one-degree. The most recent South African population census data (1996) were supplied as numbers of humans per quarter degree grid cell by Statistics South Africa (1996) (Fig. 1), and were appropriately rescaled for the half-degree and one-degree analyses. Finally, based on the 1997 United Nations list of protected areas for South Africa (WCMC 1997, see http://www.wcmc.org.ukindexshock.html/), information on the size and year of proclamation for 264 protected areas were obtained, and these areas were mapped using ArcView GIS (ESRI Inc. 1998). While acknowledging that there are other areas utilized for conservation on a less formal basis, and a small turnover of formal reserve designations, this list covers the large majority of the established conservation network in South Africa.

For each resolution, Pearson product-moment correlation coefficients were used to investigate relationships between human population density and NPP/PPT, human population density and each of the avian species richness categories, and human population density and percentage land transformation. Tabulated results were subject to sequential Bonferroni corrections. Spatial structure in the data (see Legendre and Legendre 1998) was examined using partial regression analyses to partition variation in the dependent variable of interest into its non-environmental spatial, spatially structured environmental, non-spatial environmental and residual variation (see Legendre and Legendre 1998).

In Chapter 4, 30 optimal solutions were identified, each one requiring 19 quarter degree cells, to represent each avian species in at least one grid cell across South Africa and Lesotho (overlapped, these 30 solutions occupy 53 cells). To determine whether these minimum complementary cells represent areas with larger human population densities than expected by chance, the total human population size for each of the 30 optimal solutions (consisting of 19 cells each) was calculated.

Table 1. Pearson correlation coefficients between mean annual net primary productivity (NPP, g C m^{-2} yr^{-1}), and mean annual precipitation (PPT, mm yr^{-1}) and avian species richness and human population density at the quarter-, half- and one-degree resolutions before taking spatial autocorrelation into account. Significance was calculated after a sequential Bonferroni correction was applied. (*df* at quarter-degree = 1, 1856, half-degree = 1, 456, one-degree = 1, 100).

Variables	Quarter degree	Half degree	One degree
NPP vs. PPT	-	0.90***	0.80***
Avian richness vs. PPT	0.65***	0.77***	0.82***
Avian richness vs. NPP	-	0.79***	0.71***
Human population density vs. PPT	0.71***	0.76**	0.80***
Human population density vs. NPP	-	0.78**	0.73***

** $P < 0.01$.
*** $P < 0.001$.

This value was then compared with the mean total human population found for 10 000 sets of 19 randomly selected grid cells. To determine whether human population density in the cells bordering protected areas tends to be higher than expected by chance, the total population of the 588 cells which are neighbors (i.e. one of the eight bordering cells) of a cell containing a protected area (but excluding those that include a protected area themselves), was calculated. This value was then compared to the mean population size found in 10 000 random draws of 588 cells.

Results and Discussion

Avian species richness, primary productivity and mean annual precipitation showed strong, significant positive correlations at all spatial scales (Table 1), with no strong non-linear or asymptotic effects (checked using a quadratic term, see also Chapter 2). Much of this covariation between richness and the environmental variables was a consequence of spatially structured environmental variation (Table 2), largely the result of a strong east-west moisture gradient in southern Africa (O'Brien 1993, Chapter 2). Human population density was likewise significantly correlated with both precipitation and primary productivity at all of the scales examined, and here too the covariation was largely a consequence of spatially structured environmental variation (Tables 1 and 2). Thus, at all three spatial resolutions, human population density and bird species richness respond positively to increases in net primary productivity and rainfall (a strong surrogate for NPP). Consequently, it is not surprising that at all spatial scales strong correlations between human population density and avian species richness were found (for all species as well as common and range-restricted species) (Table 3). The large contribution of the spatially structured environmental variation component in the partial regression analyses of avian richness and human population density (Table 2) indicates that the covariation is probably a result of similar responses by both humans and birds to the aridity gradient in southern Africa.

Irrespective of the underlying cause, it is clear that at the extent and resolution at which conservation is usually undertaken there are strong relationships between NPP, human population density and avian species richness. These results provide considerable support for Balmford et al.'s (2001*a*, *b*) conclusions, and cast some doubt on Huston's (2001) suggestion that a well-developed agricultural infrastructure, such as that characteristic of South Africa, is likely to obscure these relationships. Furthermore, the magnitude of the relationships found at the one-degree resolution were quite similar to those of Balmford et al. (2001*b*), suggesting that in other regions, investigations at finer resolutions are likely to reveal qualitatively similar results. This means that both species rich areas, and areas containing range-restricted taxa are likely to contain high numbers of humans.

These high population densities clearly translate into considerable landscape transformation (Table 3), as has previously been suggested for Africa and other regions (Ehrlich 1995, Bawa and Dayanandan 1997). In consequence, it is not clear why the relationship between avian species richness and human population density has persisted. If landscapes were massively transformed it might be expected that the relationship between human population density and avian species richness would be considerably weakened. There are several reasons why this might not be the case: (i) African birds might be capable of withstanding considerable habitat modification and disturbance (the resilience of the African fauna to human activities has repeatedly been

Table 2. Results from partial regression analyses indicating the extent to which, at each spatial resolution, variation in the relationships between the two variables of interest is partitioned into: (a) non-environmental spatial component; (b) spatially structured environmental variation component; (c) non-spatial environmental component. The unexplained component (d) is not provided here. The total variation, excluding the residual component, is given by a + b + c, while the variation accounted for by the spatially structured components in combination is given by a + b (see Legendre and Legendre 1998)[1]. All partial regression values remained significant after a sequential Bonferroni correction was applied.

Variables/resolution	Coefficients of determination				
Species richness and PPT	a + b + c	a	b	c	a + b
Quarter-degree	0.618***	0.199	0.415	0.003	0.614***
Half-degree	0.822***	0.229	0.532	0.061	0.761***
One-degree	0.805***	0.131	0.672	0.002	0.803***
Population density and PPT					
Quarter-degree	0.568***	0.051	0.503	0.014	0.554***
Half-degree	0.628***	0.051	0.403	0.174	0.454***
One-degree	0.721***	0.051	0.652	0.018	0.703***
Spp. richness and Population density					
Quarter-degree	0.659***	0.167	0.447	0.045	0.614***
Half-degree	0.855***	0.168	0.593	0.094	0.761***
One-degree	0.906***	0.024	0.779	0.103	0.803***

*** $P < 0.001$.

[1] The spatial component of the dependent variable was modeled using a third-order polynomial of the form:

$$f(x,y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \quad (1)$$

where x and y represent longitude and latitude respectively. The coefficient of determination (r^2) for this relationship was used as a measure of that component of the variation in the dependent variable that is explained by a combination of components a + b. The variation in the dependent variable explained by components b + c was determined from a model only incorporating the independent variable. The variation in the dependent variable explained by components a + b + c was determined from a model incorporating both the independent and spatial variables.

Table 3. Pearson correlation coefficients between human population density and four avian species richness categories, and percentage land transformation at each resolution before taking spatial autocorrelation into account. Significance was calculated after a sequential Bonferroni correction was applied. (*df* at quarter-degree = 1, 1856, half-degree = 1, 456, one-degree = 1, 100).

	Quarter-degree	Half-degree	One-degree
All species	0.67***	0.79***	0.90***
Widely distributed species	0.56***	0.60***	0.69***
Narrowly distributed species	0.35**	0.45***	0.59***
Red data species	0.52**	0.69**	0.88**
% Land transformation	0.58**	0.63**	0.57***

** $P < 0.01$.
*** $P < 0.001$.

discussed in the context of the low levels of recorded Quaternary extinctions; see MacPhee 1999 and references therein); (ii) there is sufficient habitat heterogeneity at the quarter degree level to allow persistence of birds despite apparently high human population densities (Redford and Dinerstein 1994); (iii) landscape transformation is too recent for there to have been any effect (Brooks et al. 1999*b*), and therefore there is a pending extinction crisis as the debt run up by habitat transformation is collected (Brooks et al. 1999*b*, Baillie et al. 2001); (iv) some combination of these factors. Whatever the reason, it seems likely that over time the relationships between species richness, NPP and human population density should change substantially as populations in the region continue to increase (estimated population growth rate in South Africa between 1996 and 2001 is 2.2% per annum; Statistics South Africa 1996). Conservation agencies will increasingly have to consider these changes when assessing both future policies and the likely success of their current actions.

The relationships between avian species richness and human population size raise the question of whether cells containing currently designated reserves are likely to be characterized by higher numbers of humans, and whether such a problem might be avoided during designation of new potential conservation areas. Quarter degree grid cells bordering on currently designated conservation areas have significantly greater human population densities than expected by chance ($P < 0.025$, 10 000 permutations). In addition, this effect is stronger for smaller conservation areas because there is a significant negative relationship between human population density and protected area size ($r = -0.3$, $P < 0.0001$, $df = 1, 263$). These relationships, and the significant decline in size of newly proclaimed conservation areas ($r = -0.2$, $P < 0.05$, $df = 1, 263$), suggest that, in future, currently designated conservation areas are going to face increasing human pressure. This situation is not unique to South Africa (Harcourt et al. 2001). It also suggests that unless conservation authorities resist external demands on the resources they are protecting, or seek alternative and additional means to protect both plants and animals (McNeely 1994), species face an increasingly uncertain future (Thompson and Jones 1999, Terborgh 1999, Liu et al. 2001).

One form that such action could take is the selection of additional areas for species conservation. Balmford et al. (2001*b*) suggested that at fine scales this option does appear to be promising, though actual designation of such sites will still depend on integration of competing land uses (Vane-Wright 1996). Here, total human population size in the 30 minimum representation complementary sets of 19 quarter degree cells (Chapter 4) was either slightly higher than or not different from that of randomly drawn cells (in 18 out of 30 cases, the mean human population size of the minimum complementary sets was significantly higher than expected for a random selection of sites). However, there is a diversity of equally optimal complementary networks (representing all species in 19 cells), which are distinct in terms of the spatial location of particular sites (Rodrigues and Gaston in press *a*). This may provide some flexibility for minimizing the human population in reserve networks while still representing all species efficiently. To explore this flexibility (see Rodrigues et al. 2000*a*), we determined the maximum and minimum human population size contained within optimal reserve networks representing all species. This was done by solving the integer linear problems that maximize or minimize (respectively) the total human population in the cells selected, subject to all species being represented in 19 cells. We found that for optimal complementary sets representing all species, the total human population can vary between 360 733 and 947 142. When compared with the limits of the 95%

confidence intervals for 10 000 random draws of 19 cells (390 183 – 401 630), these values indicate a wide variation in the total population of optimal complementary sets. Although the maximum possible total population in these sets is much larger (more than twice) that of randomly selected cells, the minimum possible population is only slightly smaller. This indicates that there is some, but not much, flexibility in optimal complementary sets for the selection of reserve networks that minimize conservation conflict by minimizing the total human population contained in them.

Further flexibility may be achieved by relaxing the restriction that 19 cells are selected, that is, by searching for the set of cells with minimum human population that represents all species at least once without restricting the number of cells selected. This results in a set of 23 cells with a total population of 287 271, indicating that it is possible to obtain a reserve network representing all species while having a smaller total human population (79.6% of the best possible option for sets of 19 cells), at the expense of selecting additional sites. Unfortunately, this flexibility does not include much of the currently designated reserve network, because only six of these 23 cells have a considerable fraction of their area (>25%) currently reserved. Forcing the inclusion of other reserved cells raises substantially the human population included in the network: a set of 22 cells also representing all species but now maximizing the overlap with cells having more than 25% of their area reserved (without any restriction on the total human population) includes 13 of these cells but has a total population of 441 929. Thus, not only is the current reserve network subject to the threat of land use conflict because of pressure from high population density areas surrounding reserves, but there may also be little room left for minimizing potential land use conflicts by selecting new reserve areas in the context of the current reserve network (Lombard 1995*b*, Freitag et al. 1998). Given the considerable significance of undisturbed areas for the conservation of intact ecosystems (Redford 1992), other ways must be sought to minimize conflicts while retaining the currently designated network of reserves.

One way in which the potential for such conflicts could be minimized, and the problem of high human population densities surrounding reserve areas could be addressed, might be to relax the requirement that all species are represented. While such a compromise might be unappealing from a conservation perspective, and philosophically problematic (see Morowitz 1991), it is a question that should be addressed given that land use (and consequently species survival) trade-offs are likely to be made because of competing demands for the same areas. This procedure can be implemented by solving two coupled optimization problems. The first obtains a set of cells that minimizes the total human population subject to representing a given number of species. If more than one solution exists, a second problem is solved which finds the smallest number of cells while keeping the total human population equal to the minimum value found in the first problem (see Rodrigues et al. 2000*a*, Chown et al. 2001). When this is done, it becomes clear that as the requirement for species inclusiveness is relaxed, so the total population included in the minimum representation complementary set declines (Fig. 2). Because total human population decreases very rapidly as fewer species are selected, 96% of the bird species can be represented in cells with a total human population of 9.1% of that where all species are required. This result is not simply a consequence of a reduction in the total number of sites selected (Fig. 2). In other words, most avian species can be represented in cells with low human population density.

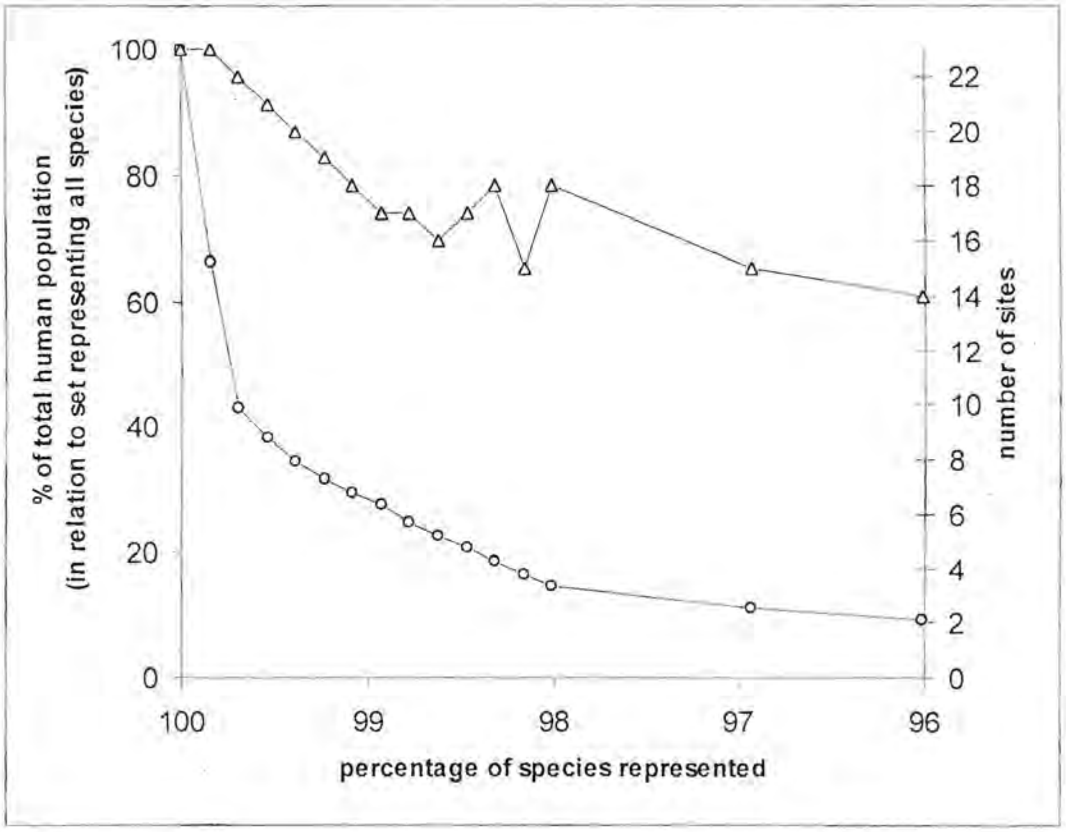

Fig. 2. Trade-off between species represented and total human population included in complementary reserve networks. Circles represent the minimum total population (as a percentage of the population in the set of 23 cells representing all 651 species) that is represented in selected sites (cells) while representing at least a given percentage of species (see text for details). Triangles represent the variation in the number of sites selected in each case.

It is just a few, often rare species (such as Green Barbet *Stactolaema olivacea*) that can only be represented in a single or just a few cells (see Rodrigues and Gaston in press *b*) characterized by high human population density. This result echoes Balmford et al.'s (2001*b*) statement that conservation conflicts cannot be totally avoided because some species are found in densely populated areas and nowhere else. Nonetheless, if these species are disregarded then it is possible to select sites that can represent the majority of species in areas where human population density and thus the likelihood of land transformation is low.

Unfortunately, these sites include only a small proportion (*c.* 10) of the 264 currently protected areas in South Africa. It is therefore clear that areas immediately adjacent to currently protected areas have much higher human population densities, and consequently a higher risk of habitat modification (see Terborgh 1999, Liu et al. 2001), than areas selected to reduce these risks. Although we are not suggesting that the currently protected areas be relinquished, we are of the opinion that programmes of new protected area acquisitions should be done in a way to minimize conflict. Furthermore, if areas with low human population density are selected, then the opportunity cost (see Vane-Wright 1996, Faith 2001) of establishing the protected area might also be lower. In short, it appears that there may be ways of addressing conservation conflicts at fine spatial scales (Balmford et al. 2001*b*).

However, such optimism (if acceptance of species losses could be called optimism) is based on the assumption that the physical and biotic landscape is static, and that a single representation is sufficient to conserve a species. It is widely appreciated that using single representations represents only a starting point for conservation planning (Cabeza and Moilanen 2001). Here, a requirement for several representations is likely to mean even fewer opportunities to minimize land use conflicts. Moreover, several studies have shown that for the long-term survival of species, reserve networks must be selected in ways that not only ensure species representation, but also their long-term persistence (Rodrigues et al. 2000*b*, *c*), and this is likely to be particularly true under scenarios of climate change (see Erasmus et al. 2002). Likewise, protected areas might act as attractors for humans, so changing the population density in the surrounding area and thus compromising conservation (Oates 1999, Terborgh 1999).

Conservation solutions could explicitly incorporate changing landscapes and the need for multiple representation in one, or a combination, of three ways. First, larger areas could be set aside for conservation (see Soulé and Sanjayan 1998). Despite arguments to the effect that the economic difficulties of doing so are insurmountable (Musters et al. 2000), in relative terms the cost of conservation is low (Balmford and Gaston 1999, James et al. 2001, Pimm et al. 2001). Second, conservation (biodiversity remediation) in as much of the landscape outside conservation areas as is possible could be undertaken (McNeely 1994, James et al. 2001). Unfortunately, even in countries where this requirement has long been recognized, once common species are now in decline (Baillie et al. 2001). Finally, the conservation conflicts associated with human expectations and the changing landscapes they bring could be ameliorated by altering the variable that is rarely considered: human population size. Individual-based regulation of human population size to a point that ensures both species survival and the satisfaction of human expectations appears to us to be one of the most effective means of ensuring a reduction in the rates of species loss over the longer term. Such regulation amounts to prevention of a problem that is unlikely to be solved by tinkering with alternative cures.

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CHAPTER 6

Thoughts for the World Summit on Sustainable Development - Priority bird areas and human development needs in South Africa

Running title: Priority bird areas and human development needs

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Abstract

Land acquisition for conservation purposes remains a main priority for conservation agencies. However, when site selection is used in an attempt to maximize species protection and simultaneously avoid areas of high human density it is immediately apparent that options for land acquisition are severely constrained. To assist conservation agencies in arriving at a "real world" solution for systematic land acquisition, we report the feasibility of adding previously identified priority bird conservation areas to an existing reserve network, after taking the constraints of human activities and climate change into account. Our evaluation of the potential of these areas is based on either increasing the size of existing protected areas or establishing linkages between core reserves as a form of matrix conservation management. We show that although the current human demand on natural resources is high in most of these priority areas (and is likely to escalate given current population trends and limited water resources), there are some areas outside of the current protected area network with lower human population densities than expected by chance both prior to and after taking climate change into account. These areas would be ideal candidates for reserve expansion, not only because they can contribute to the existing reserve network as important bird areas, but, most importantly, they contribute by minimizing potential future conflict between human resource needs and conservation as a legitimate land use form.

Introduction

A recurrent theme in landscape ecology is the need to integrate regional conservation needs with human demography, behaviour and socio-economics using appropriate policy interventions.[1-14] Given the rate at which landscapes are being modified,[15-18] and projections for even greater modification rates in future,[19-22] it is essential to ensure that landscape planning is done in a way that will provide for species survival and meet human needs.

Recent studies have shown that areas of high human activity and high species richness are spatially congruent,[23,24] apparently because both variables respond positively to increasing levels of primary productivity,[11,Chapter 5] but see also.[25] This overlap has several profound conservation implications. First, it has been shown that in areas subjected to significant human land transformation, which correlates strongly with high human densities,[12,26,27] both population viability[14] and species richness are negatively affected.[28-32,Chapter 5] Second, there is a tendency for human population densities to be higher than expected by chance in areas surrounding currently designated reserves which, in turn, have high species richness values.[12,33-37,Chapter 5] In consequence, reserves, and the species they are designed to protect are under considerable, and often increasing, external pressure.[12,34] Third, a positive correlation between species richness and human density leads to escalating conflict between human development and conservation needs.[11,38,39,Chapter 5]

These conservation conflicts are likely to increase as human populations increase.[7] This is especially true of countries such as South Africa where the estimated population growth rate of 2.2% yr^{-1} (estimated between 1996 and 2001)[40] is substantially higher than the population growth rate of the rest of the world (1.3% yr^{-1}), and above that of most developing countries (1.6% yr^{-1}).[7] Indeed, high human densities generally correlate strongly with habitat modification,[12,27,Chapter 5] and therefore increase the risk of local species extinctions.[29,31,32] Changes in human population growth will therefore bring about a change in the form of the relationship between species richness and human densities. Consequently, it is inevitable that land-use decision makers will increasingly have to consider ways of incorporating these changes into their conservation strategies if they are to succeed in their long-term goals of sustainable development.[41-43]

An additional factor that is likely to bring about changes in the relationship between human density and species richness patterns, and therefore alter the degree of conflict between conservation and human development needs, is climate change.[44-49] Recent evidence suggests that, in response to current changes in climate, the northern distributional range limits of many species in both Europe and North America have extended northwards owing to anthropogenically induced climate change.[50-58] Such range shifts and other responses to climate change are affecting both species and communities in the northern and southern hemispheres,[54,59-62] and the frequency of these shifts is likely to increase as climate change becomes more obvious.[63-65] The dynamic nature of the environment within which conservation must take place means that simple representation of the more tangible elements of the landscape in static protected areas[41,42,66,67] is unlikely to be sufficient for long-term protection and hence sustainability.

In consequence, conservation authorities will increasingly have to take into account that changes in the underlying drivers of human population densities and species richness patterns will influence the future efficacy of conservation areas and, in turn, impact on future human development options.[3,41-43] Incorporating system dynamics into conservation policy will require considerable flexibility that will be difficult to achieve under current reserve allocation procedures that rely on *ad hoc*- space available, or political feasibility-based approaches.[68-71] Several recent studies have specifically addressed the issue of effective conservation responses to factors such as climate change, by advocating approaches such as regional reserve networks, landscape connectivity, and matrix management models.[72-74] In other words, conserving as much of the landscape outside the current conservation area network is one way to partially incorporate these changing patterns of human activity and species distributions.[75,76]

Approaches to identifying additional conservation areas vary widely. For example, for birds, the "Important Bird Areas" programme was established to create a global network of sites to protect the world's bird fauna over the long-term.[77,78] Such IBAs are selected using four criteria determined by BirdLife International: the presence of globally threatened, restricted-range, or biome-restricted species, or the presence of major congregations of individuals.[78] There are several other examples of programs concerned with the identification of geographic priorities for conservation (see e.g. Conservation International's "Hotspots";[79,80] and WWF-US's "Global 200 Ecoregions"[81,82]). Because many of these priority areas show little overlap with existing reserves, and therefore have no formal conservation status, the aim of these programmes is not only to set geographic priorities for conservation, but also to persuade governments to incorporate as many of these areas into their National Biodiversity strategies as possible.

Another very different approach for setting geographic conservation priorities is systematic conservation planning.[83,Chapter 4] This approach employs algorithms to identify seed areas for the development of regional conservation networks.[66,84-87] Balmford *et al.*[11] have emphasized that the actual designation of such sites will nonetheless depend on effective integration of these areas with competing land-uses.[66,88]

One major problem faced by all of these approaches is that the available options for expanding present conservation networks are limited in most regions, especially if among their aims the priority setting exercises seek to minimize conflict with other land use requirements and with humans.[12,34,38,39,88,89,Chapter 5] Moreover, the opportunity costs of conservation efforts (i.e. the compensation of local people living in the vicinity of proposed protected areas)[90] will also limit the expansion of conservation areas. This cost will increase as human density increases, but in many cases conservation efforts are needed where human density or activity is at its highest,[10,11,Chapter 5] but see also.[25] Therefore, as is the case in many countries (e.g. the United Kingdom),[89] conservation agencies are faced with limited adaptation options. This makes the requirement for sustainable development[9,22,91] seem all the more difficult to achieve, at least if it means the maintenance of current biodiversity.

In this study, we use the South African avifauna as a case study to examine current and future human resource demands on (i) existing conservation areas, and (ii), priority conservation areas identified both in- and outside existing conservation area networks. To date, studies on the relationship between human activity and areas important for bird conservation have received little attention at a national scale. Here, we address this lacuna by examining, at the quarter-degree resolution, whether areas important for bird conservation are located in areas of unusually high human density, prior to and after human density and avian richness patterns change in response to climate change. This approach provides an initial, broad indication of the extent to which previously identified priority bird areas are subjected to the threat of land-use conflict owing to high current or future human densities in their vicinity. If, for example, priority bird areas outside protected areas are not characterized by high numbers of humans, then these areas may be identified as potential new reserve areas following Huston's[3] argument that priority conservation areas should maximize species conservation and minimize the negative impacts of proposed conservation areas on human welfare and economics.[22,66]

Methods

Avian species richness data and human population data for South Africa and Lesotho were obtained from the Southern African Bird Atlas Project (SABAP),[5] and from the most recent published South African population census data,[40] respectively. Data were compiled on species occurrences and the numbers of humans per quarter-degree grid cell (1 858 grid cells of approximately equal area, but varying from 635 km^2 in the north to 712 km^2 in the south). Marine, vagrant, marginal (species with only one occurrence in the study area and substantial populations outside of it) and escaped species were excluded from the analysis (651 species were analysed).

To determine the extent of conflict between human development needs and areas important for bird conservation, we made use of seven categories of previously identified priority bird areas. First, based on Barnes's[78] list of 112 Important Bird Areas (IBAs) located within the 1 858 quarter-degree grid cells used, we made use of ArcView GIS[92] to map information on the size of each IBA from maps published by Barnes.[78] From this we obtained the number of quarter-degree grid cells occupied by each IBA (424 cells). Second, we used 30, previously identified optimal solutions which represent each bird species in at least one grid cell across South Africa and Lesotho, each one requiring 19 quarter-degree cells (overlapped, these 30 solutions occupy 53 quarter-degree cells).[Chapter 4] Third, based on the 1997 United Nations list of protected areas for South Africa,[93] we mapped information on the size of 423 protected areas using ArcView GIS[92] and obtained the percentage of protected area in each quarter degree cell (485 cells). IBAs and protected areas are, with a few exceptions, generally smaller in area than an entire quarter-degree grid cell. Fourth, the number of quarter-degree grid cells that contain IBAs but without any degree of formal protection was calculated (hereafter referred to as IBAs outside protected areas) (127 cells). Fifth, the number of minimum complementary grid cells identified previously[Chapter 4] without any formal protected areas in them was calculated (hereafter referred to as minimum complementary cells outside protected areas) (30 cells). Sixth, the number of quarter-degree grid cells with both IBAs and protected area in the grid cell was calculated (hereafter referred to as IBAs inside protected areas) (297 cells). Seventh, the number of minimum complementary grid cells identified previously[Chapter 4] with some protected areas in them was calculated (hereafter referred to as minimum complementary cells inside protected areas) (23 cells).

Quantifying human densities in priority bird areas

To address the question of whether cells representing priority bird areas are likely to be characterized by higher numbers of humans, we first calculated the total human population of the 424 cells representing all IBAs (i.e. cells representing the first priority bird area category mentioned above). This value was then compared to the mean population size found in 10 000 random draws of 424 cells. These grid cells were selected from a pool of all possible grid cells with human density values, i.e. 1 858 quarter degree grid cells covering South Africa. In a similar fashion, we then determined whether each of the remaining six categories of priority bird areas had higher values of human density than expected by chance. Finally, using the same priority bird areas identified for each category, we repeated these analyses after taking the effect of climate change on human distribution patterns into account.

Climate change

The effects of climate change on the form and the strength of the relationship between human density and avian species richness across South Africa was investigated based on mean annual precipitation (PPT; mm yr^{-1}) values predicted for each grid cell (1 858 cells) given a doubling in pre-industrial CO_2 levels using the HadCM2 (no sulphates) model.[48,61] Precipitation, which sets the upper limit to net primary productivity, and therefore the amount of available environmental energy for a given area,[94-98] has been identified as an important correlate of spatial variation for both human density patterns[Chapter 5] and avian species richness patterns[Chapter 2] across South Africa.

Using the same species richness and human density data as for Chapter 5 at the quarter-degree resolution, the predicted PPT values were used to calculate new, climate-adjusted avian species richness and human density values for each grid cell by substituting the climate adjusted PPT values into the regression equations explaining avian species richness and human density values as a function of current PPT[Chapter 5] (Avian species richness = 68.055 + .1977 X PPT, r = .65 and Log_{10} human density = 2.7549 + .00208 X PPT, r = .71). The human density values in grid cells entirely protected by nature reserves and therefore with zero human density were not adjusted by the climate-adjusted PPT values.

Ordinary least squares regression was used to investigate the relationship between human density and avian species richness after both avian species richness patterns and human density patterns had been altered based on predicted climate change. Tabulated results were subject to sequential Bonferroni corrections.[99] The regression equation obtained from this relationship was then compared with the equation for the relationship between human density and avian species richness before taking climate change into account using analysis of covariance (ANCOVA).[100] We predicted that increasing conflict between human development needs and avian conservation requirements, as a consequence of climate change, would be indicated by an increase in the y-intercept value (i.e. for a given value of avian richness there are more humans per grid cell) and/ or the regression coefficient value (i.e. high species richness areas will have even higher human densities than before, although low richness areas might not be affected to the same degree).[61]

Results

Human densities in priority bird areas before climate change

The 424 quarter-degree grid cells representing IBAs had significantly greater human densities than expected by chance ($p < 0.05$, 10 000 permutations – Table 1). This was also true for the grid cells representing formal protected areas (485 cells), and for the grid cells representing IBAs inside protected areas

Table 1. Results indicating whether grid cells within each priority bird area category have significantly greater values of human densities than expected by chance based on 10 000 permutations. Analyses were conducted using both current human density values and climate adjusted human density values calculated from predicted precipitation values. The significance value (*p*) is given in parentheses. IBAs = Important Bird Areas.

Priority bird area categories	Mean human population densities	Climate adjusted mean human population densities
IBA cells	greater (0.0007)	greater (0.0013)
Minimum complementary cells	ns (0.0550)	greater (0.0002)
Protected area cells	greater (0.0006)	greater (0.0005)
IBA cells outside protected areas	ns (0.2235)	ns (0.1686)
Minimum complementary cells outside protected areas	ns (0.9201)	ns (0.1248)
IBA cells inside protected areas	greater (0.0145)	greater (0.0001)
Minimum complementary cells inside protected areas	ns (0.0889)	greater (0.0103)

Note: Significance was calculated at $p < 0.05$. ns = value is not significantly greater than the mean value.

(297 cells) (Table 1). There is considerable spatial overlap (70%) between the grid cells representing protected areas and the grid cells representing IBAs, therefore it is reasonable to suggest that most protected areas and IBAs are either located relatively close to one another (within a ~25 km radius from each other), show some degree of spatial overlap, or tend to represent the same areas within grid cells. Consequently, it appears that most IBAs are affected by factors similar to those that result in high human densities in protected area grid cells (see Discussion).

High human population densities generally lead to high levels of land transformation. This explains our finding that 413 (85%) of the 485 cells identified as protected areas are also transformed to some degree by anthropogenic activities, and 177 (43%) of these transformed cells are more than 25% transformed, based on Fairbanks and Thompson's[101] National Land-Cover database for South Africa. This was also true for the grid cells representing IBAs, where we found that 354 (83%) of the 424 cells are transformed to some degree, and 158 (37%) of these cells are more than 25% transformed. This is mostly because the protected areas and/ or IBAs are often smaller in area than an entire quarter-degree grid cell, which means that human land transformation, conservation activities, and areas important for conservation often occur within the same quarter-degree grid cell.

Moreover, as has been found for protected areas on the rest of the African continent,[12] and in the United States,[34] we found that small-protected areas are likely to be more prone to the effects of high human population densities than larger ones. This follows from a significant negative relationship between human density and the size of protected areas (r = -0.38, $p < 0.0001$, df = 1, 422),[Chapter 5] and IBAs (r = -0.13, $p <$ 0.0001, df = 1, 111). In addition, there is a significant positive relationship between the perimeter to area ratio values (smaller values being larger protected areas) and human density values for both protected areas and IBAs (r = 0.32, $p < 0.0001$, df = 1, 422 and r = 0.21, $p < 0.0001$, df = 1, 111, respectively). As a consequence of these relationships, and because areas important for bird conservation in South Africa are generally small (protected areas: 70% < 5 000 ha; IBAs: 36% < 5 000 ha) avian conservation would benefit considerably from an increase in the size and/ or number of priority bird areas under protection.

That quarter-degree grid cells representing IBAs outside protected areas did not show significantly greater human densities than expected by chance (Table 1), suggests that some of these IBAs may be favorable candidates for conservation. However, this approach would be further enhanced if it were possible to identify a subset of IBAs outside protected areas with significantly lower human densities than expected by chance. Based on a random draw technique (see Methods), we examined the IBA grid cells outside protected areas (127 cells) by comparing the mean human density value of these cells to the mean human density value found for 10 000 sets of (n) randomly selected grid cells after eliminating the IBA grid cell with the highest human density value. In other words, the number of randomly selected grid cells within each set (n) was equivalent to the number of IBA cells minus the cell with the highest human density value. After several eliminations, to identify the maximum number of IBA cells (found outside protected areas) with significantly lower human densities than expected by chance, a total of 111 grid cells was identified (see Fig. 1).

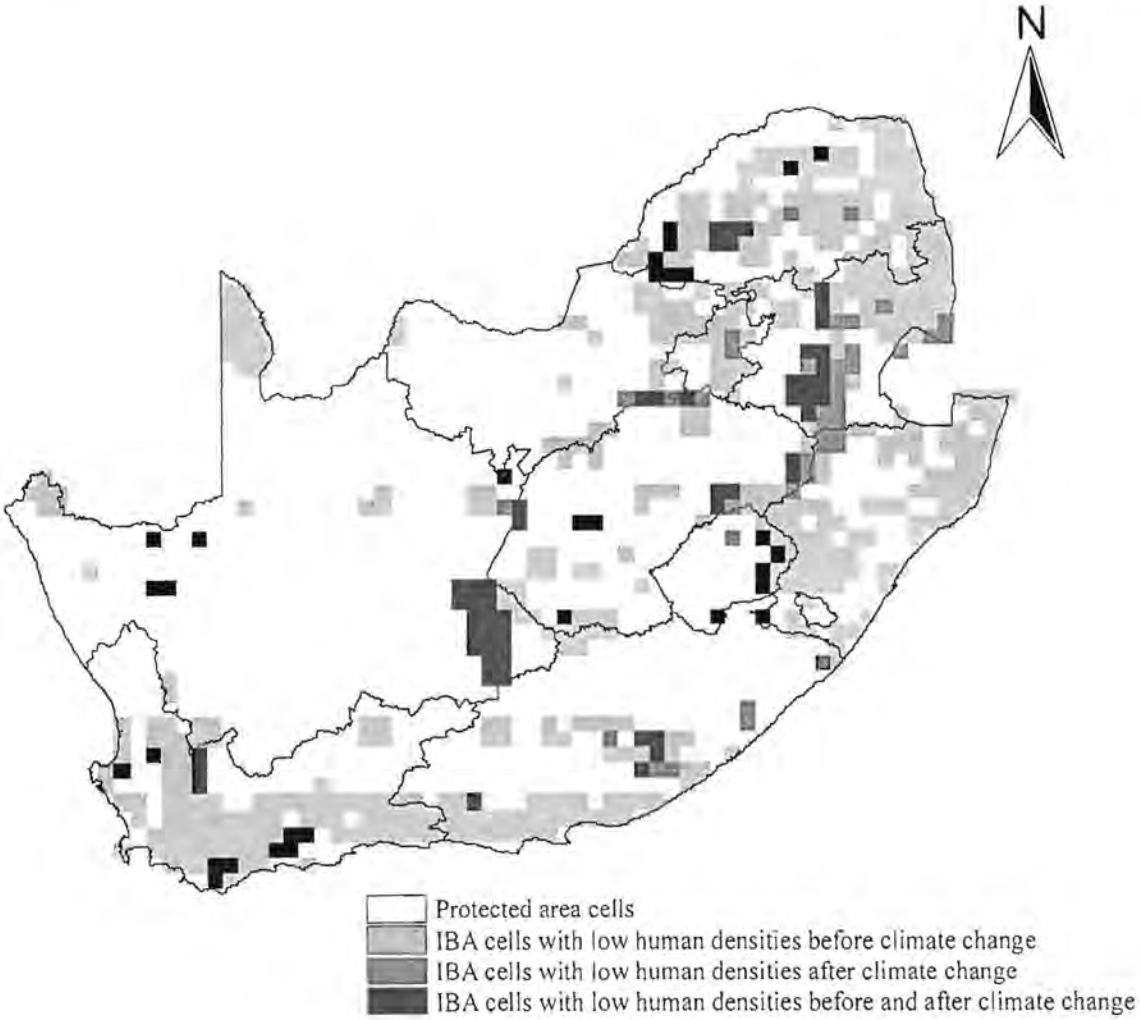

Fig. 1. The spatial distribution of protected area cells in relation to IBA (Important Bird Area) cells outside the current protected area network with lower than expected human density values prior to and after human population density responses to climate adjusted precipitation values across South Africa.

The total human population contained in the quarter-degree grid cells representing all 30 of the different minimum complementary set solutions (53 grid cells) was not different from that of the randomly drawn grid cells (Table 1). This was true also of those complementary cells found outside the current protected area network (30 cells) and for those complementary cells inside the current protected area network (23 cells - Table 1). However, the collection of 30 complementary solutions contain a sub-set of solutions that are equally efficient (representing all species in 19 cells), but which differ in terms of the specific sites they require.[102] This provides some flexibility for minimizing the human population in reserve networks while still representing all species. After taking this limited flexibility into account,[41] the total human population size in the 30 complementary solution sets was either slightly higher than (significantly so for 18 out of 30 cases) or not different from randomly drawn cells.[Chapter 5]

Avian richness and human density before and after climate change

Bird species richness showed a strong, significant positive correlation with human densities (Table 2), with no strong non-linear or asymptotic effects (checked using a quadratic term). Much of the correlation between richness and human density is a consequence of spatially structured environmental variation to which both birds and humans respond similarly.[Chapters 2,5] This strong spatially structured pattern of environmental variation is largely the result of a strong east-west moisture gradient in southern Africa.[94,Chapters 2,5] As can be expected, when using human density and species richness values calculated from the climate affected PPT values, the correlation between species richness and human density remained positive (Table 2). More interestingly, the linear regressions between human densities and avian species richness before and after climate change showed significant differences in both the *y*-intercept values ($p < 0.001$; $F = 206.72$; $df = 1, 3712$) and in the regression coefficient values ($p < 0.001$; $F = 235.15$; $df = 1, 3712$) (see Fig. 2). Based on these linear regressions, a decrease in conflict between human development and bird species richness can be expected in areas with avian species richness values presently lower than *c.* 180 species, and an increase in conflict between human development and bird species richness can be expected in areas with avian species richness values presently higher that *c.* 180 species (see Fig. 3 for these areas).

Human densities in priority bird areas after climate change

The likely increase in conflict between humans and birds in some areas of South Africa, following climate change, raises the question of whether the cells that currently represent priority bird areas are likely to be characterized by higher numbers of humans after human density patterns respond to climate change.

Quarter-degree grid cells representing IBAs had significantly greater human densities than expected by chance after taking climate change effects into account (Table 1). Although this was also the case before the potential effects of climate change were taken into account, the difference between the climate adjusted density values for the IBAs and those of the randomly drawn cells was less pronounced (i.e. not as large) in this case (Table 1). This suggests that elevated human population density is unlikely to have a pronounced effect on the IBAs following climate change.

Table 2. Pearson correlation coefficients between human population density and avian species richness prior to and after the values for both variables were calculated from predicted precipitation values. Significance was calculated after a sequential Bonferroni correction was applied. (*df* = 1, 1856).

Variables	Before climate change	After climate change
Spp. richness vs. Population density	0.659***	0.820***

*** $p < 0.001$.

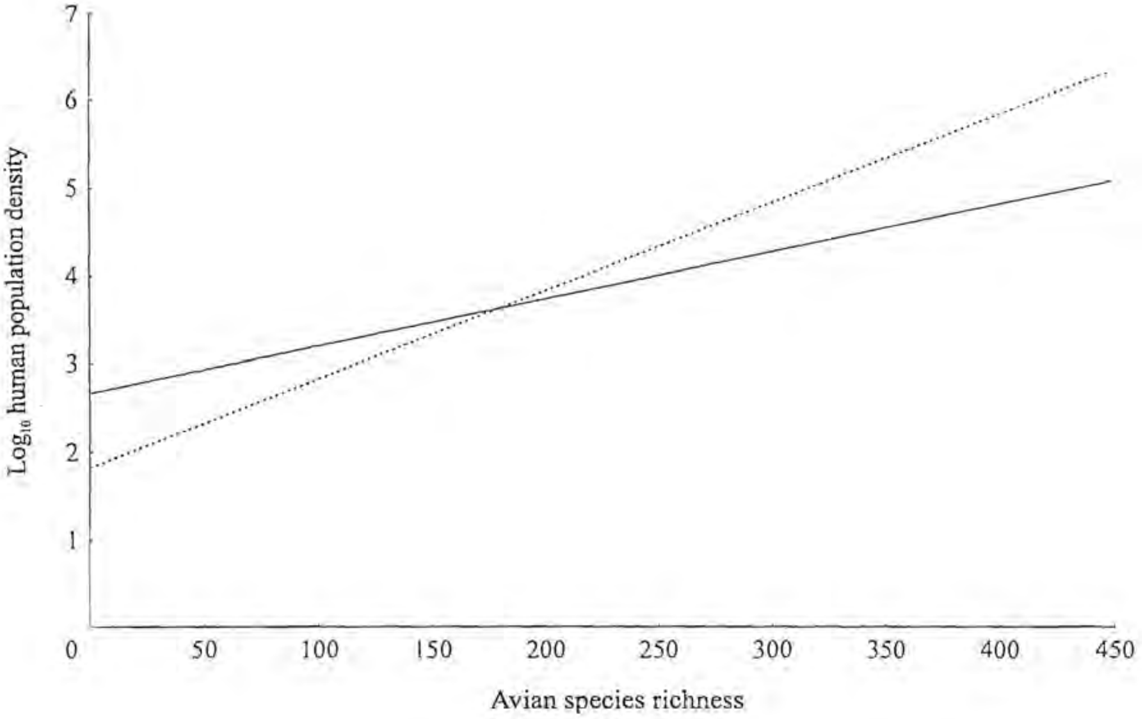

Fig. 2. The linear regressions between Log_{10} human population densities and avian species richness (——) before variable values were calculated based on climate adjusted PPT values (Log_{10} human density = 2.7235 + .006 X Avian species richness; r = .66), and (------) after variable values were calculated based on climate adjusted PPT values (Log_{10} human density = 1.8257 + .010 X Avian species richness; r = .82).

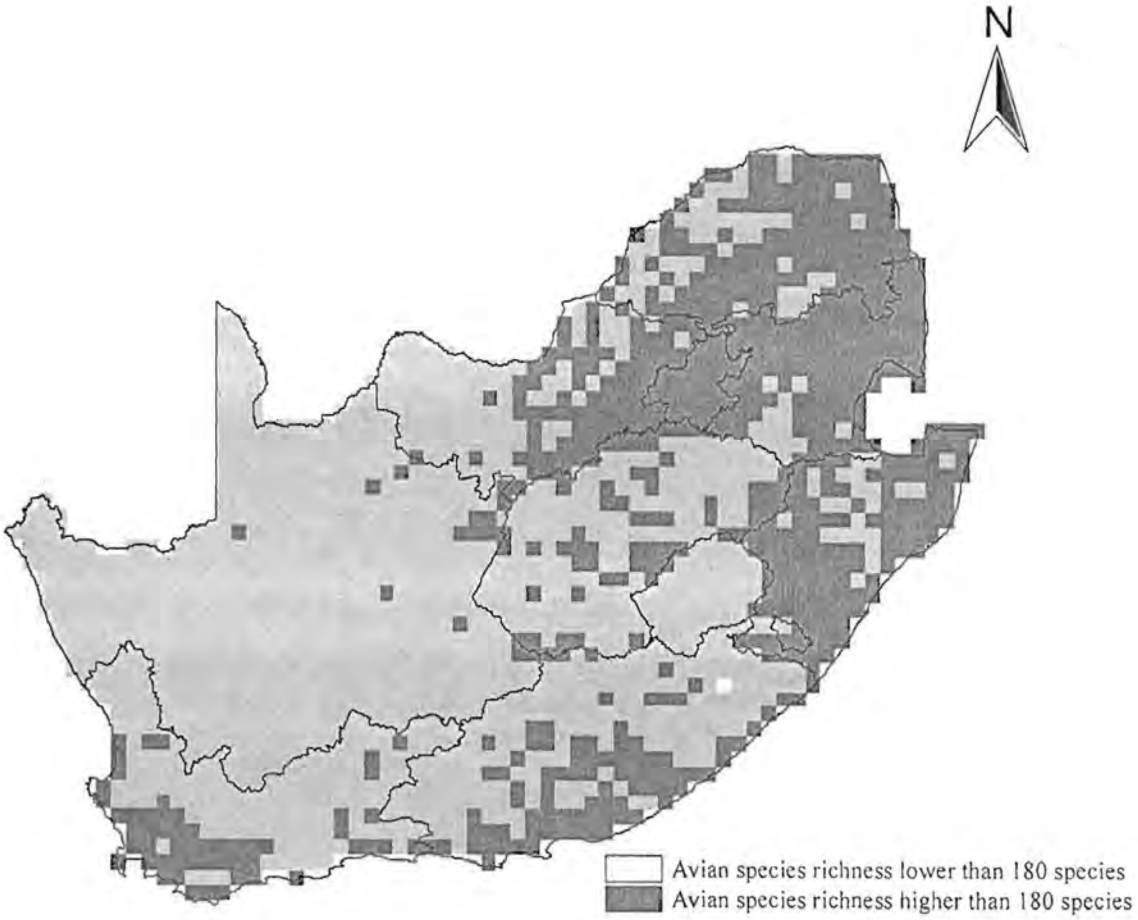

Fig. 3. The spatial distribution of quarter-degree grid cells with avian species richness values presently lower than 180 species per cell, and those grid cells with avian species richness values presently higher than 180 species per cell.

By contrast, quarter-degree grid cells representing all combinations of the 30 different minimum complementary site solutions (i.e. the 53 quarter-degree cells occupied by these 30 solutions) had significantly greater human densities than expected by chance after taking climate change into account (Table 1). Moreover, because the densities were higher than expected from a random draw, it is clear that these minimum complementary cells are likely to be characterized by higher numbers of humans following climate change. A similar result was also obtained for the grid cells representing minimum complementary cells inside protected areas (Table 1). Quarter-degree grid cells representing protected areas also had significantly greater human densities than expected by chance both before and after taking climate change into account (Table 1), and there was little difference between the two results. In the case of IBAs inside protected areas, it appears that following climate change, human population size would be considerably larger than expected from random (Table 1).

Finally, the total climate adjusted human population size in the IBA cells outside protected areas, and the total climate adjusted human population size in the minimum complementary cells outside protected areas, was not different from that of randomly drawn cells (Table 1). However, both here, and in the previous analyses, the overall number of humans in the cells generally increases. Thus, like the regression analyses, the random draw results also suggest that conflict between human requirements and avian conservation needs is likely to escalate considerably under a climate change scenario.

Discussion

Human population density and avian species richness show a strong positive relationship, indicating that areas with the highest richness are located in areas of greatest human population density. This means that there is substantial scope for conservation conflicts in the region, as has been demonstrated both elsewhere in Africa and in other regions.[10,11,24,103] This conflict is also likely to affect conservation areas for two main reasons. First, human population densities are higher immediately adjacent to all protected areas in the region than they are elsewhere.[Chapter 5] Protected areas generally provide access to improved resources such as bush meat and/ or fuel-wood, and employment opportunities associated with tourism.[12,33,35,37] Moreover, because formal conservation can often not take place without compensation (i.e. covering of opportunity costs),[90] protected areas in developing countries sometimes also attract people who have the expectation that should conservation agencies purchase land adjacent to existing reserves to expand the size of these areas (W. S. Matthews, personal communication), they will derive compensation associated with the purchase. In consequence, reserves in developing countries such as South Africa are frequently considered centers of economic opportunity within an otherwise impoverished economic landscape.[33,37] Second, small reserves, which represent the majority of formally protected areas in the region (70% < 5000 ha),[104] are more prone to intense edge effects caused by human land transformation than large reserves.[12,34] This is mostly a result of the fact that smaller reserves tend to have higher surrounding human population densities than larger ones. Thus, in Southern Africa conflicts between human requirements and conservation needs are a feature both of conservation areas and the matrix within which they are embedded.[70,104-107]

One way in which the conflict between human needs and conservation requirements might be alleviated is to expand the existing reserve network by formally protecting additional areas.[75,76,108] However, whether such reserve network expansion would actually alleviate human-conservation conflict depends on which of the areas (identified as important for conservation) are selected. Conservation is more feasible to achieve in areas with low human presence compared to areas already dominated by humans.[109,110]

In the case of the optimal complementary networks (30 sets of $n = 19$ cells, a total of 53 cells) we found that the human population ranged between 360 733 - 947 142. When compared with the 95% confidence limits for 10 000 random draws for similar sets of 19 cells (390 183 – 401 630), these values indicate considerable variation in the human population found in the complementary sets. Although the maximum achievable population in these sets is more than twice that of randomly selected cells, the minimum possible human population encountered is only slightly smaller. This suggests that there is some, but not much, flexibility for avoiding human conflict in the most efficient complementary sets.[Chapter 5] Moreover, the potential for these optimal complementary networks to be treated as acquisition areas is also limited. The primary reason underlying their limited utility is the fact that many of these cells reflect areas of ecological transition,[Chapter 4] and therefore represent species at the edge of their distribution ranges. Such representations are unlikely to provide long-term security for the species involved.[66,111]

By contrast, the options for increasing the conservation network by adding IBAs with low human population density seem more promising. Indeed, 111 IBA grid cells (found outside protected areas) with human densities that are lower than expected by chance were successfully identified in our analysis (see Fig. 1). Formal protection of these areas would certainly contribute to minimization of conflicts between human development and conservation needs, although in some cases only a few species might be involved owing to the ways in which IBAs are selected.[78]

Owing to the spatial location of these IBAs that have no formal protection but lower human densities than expected by chance, at least some, and perhaps the majority of these IBAs could contribute towards increasing the size of formally protected areas. The incorporation of grid cells containing IBAs adjacent to protected areas would be most advantageous. However, it is imperative that grid cells containing human attraction zones, situated directly adjacent to established conservation areas and that could undermine effective conservation management, be avoided whenever possible. The small sizes of the majority of South African protected areas (< 5000 ha ~ 13% of grid cells used in this study)[104] means that such human attraction zones are frequently contained within the analytical units used in the present study. This scale disparity explains why certain grid cells containing IBAs appear to have lower human densities than some grid cells containing protected areas with high human concentrations along their borders.

However, under a climate change scenario it seems likely that conservation conflicts will increase. This is due mostly to the fact that both human population and species richness change dramatically in the same grid cells, owing to similar responses to changes in water availability (Fig. 2). In Southern Africa, water availability is an important driving factor for biodiversity patterns,[94,96-98,112-114,Chapter 2] and human population density responds to water availability in a similar fashion (i.e. increasing with increasing water availability).[Chapter 5] Any change in water availability will therefore be translated into a corresponding change in both richness and population density.[55,61] Schultze *et al.*[115] point out that the climate model they used forecasts a general decline in rainfall across South Africa, and this was also borne out by the investigation undertaken by Erasmus *et al.*.[61] Thus, fewer areas across the country will harbour both high species richness and greater population density than is presently the case, and these are mostly areas that currently have a high rainfall (Fig. 4). Effectively these are the grid cells with species richness presently greater than about 180 species. If the estimated 2.2% per annum population growth continues, then the high species richness cells will have even higher population densities than estimated by the simple forecast adopted here. Thus, there is likely to be a large increase in conflict between conservation and other land use requirements. This conflict is also likely to be exacerbated by future human demands for agricultural resources, especially water,[116] as human populations continue to expand. Indeed, anthropogenic desertification and competition between human and animal needs for water utilization have been identified as important drivers leading to mammal population extinctions in Africa,[32] and there seems to be no reason why this should not also be the case for the avifauna, or at least several major avian groups.

Unfortunately, much of the flexibility required to expand the current conservation network, which might alleviate some of the conflict, also disappears under a climate-change scenario. Following predicted climate change, the quarter-degree grid cells representing all combinations of the 30 different minimum complementary site solutions (i.e. the 53 quarter-degree cells occupied by these 30 solutions) had significantly greater human densities than expected by chance. Therefore, these sites are unlikely to minimize conservation conflicts, and this is perhaps not surprising given their low initial utility for this purpose. However, the currently designated IBAs might continue to serve an important conservation role, even when climate change is taken into account. After taking projected climate changes into account (human responses), some 99 grid cells that fall outside protected areas continue to have lower human densities than expected by chance (Fig. 1). This is in contrast with the 111 grid cells identified before human related climate changes were considered. Of these 99 cells, 86 (87%) were common to the pre- and post climate change analyses and fell outside protected areas (Fig. 1). Therefore, currently designated IBAs, and especially those outside protected areas, form an extremely valuable component of the avian conservation network. Not only are they important for avian conservation now, but they are also less likely to be affected by conservation conflict in the future than many other areas. Of course, following climate change at least some of these areas might no longer be useful for the purpose they were originally identified because of changes to the population size of the focal species, or changes to the species composition of the original IBA. Nonetheless, low human population density in the grid cells within which they are found means that they are likely to form valuable conservation areas in an otherwise highly transformed landscape.[15,18,24,31]

Although conservation conflicts are likely to increase in many areas, in at least some regions, and especially the western parts of Southern Africa, conservation conflicts are likely to decline as both human population density and species richness decline with declining rainfall.[61,Chapter 5] Whether conservation areas and other priority bird areas (such as IBAs) would retain their utility is not clear, largely because the exact changes in species composition forecast for these areas are not particularly clear.[61]

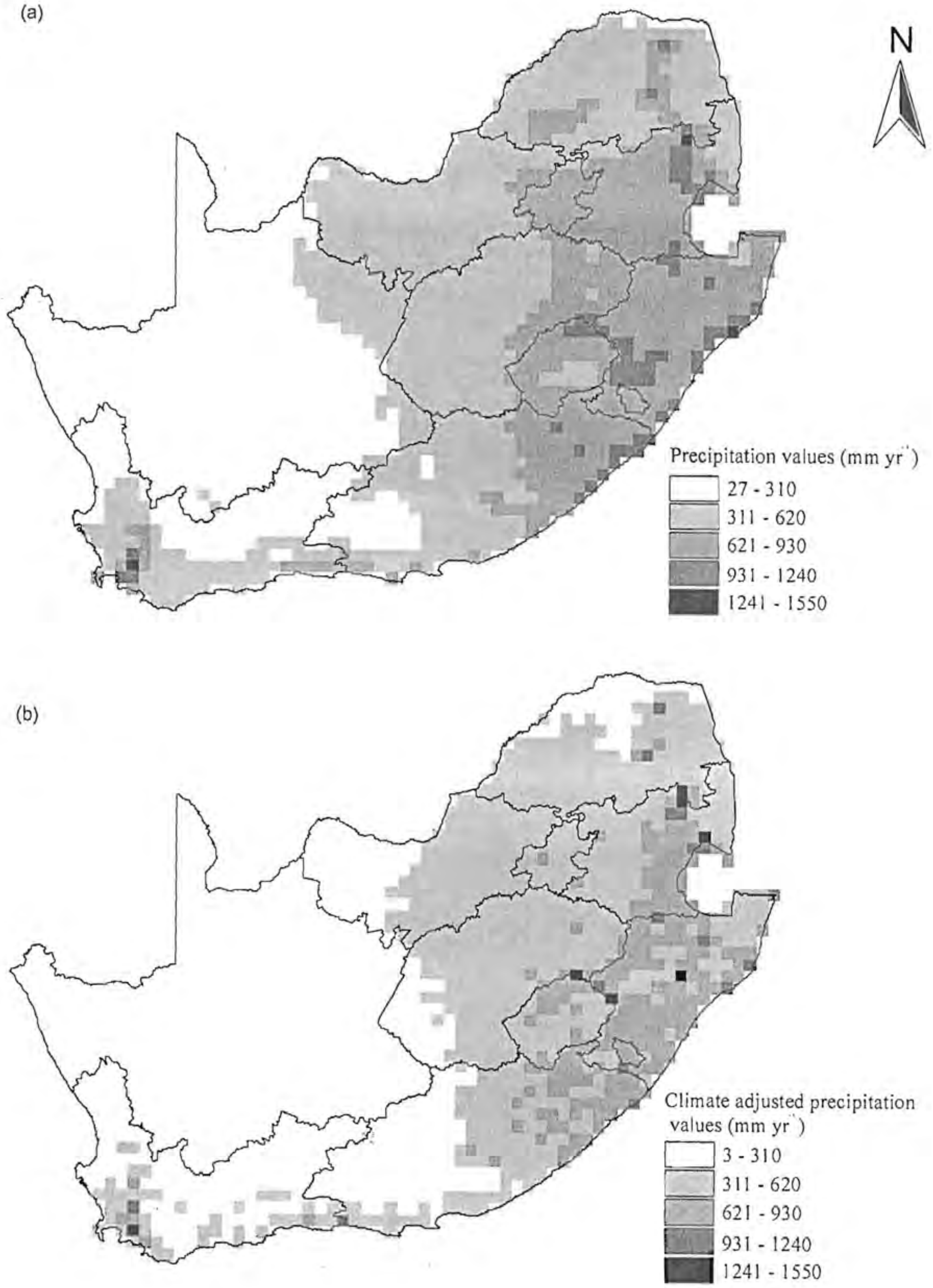

Fig. 4. Variation in precipitation (mm yr^{-1}) values across South Africa (a) before taking climate adjusted precipitation values into account and (b) after taking climate adjusted precipitation values into account as predicted by Shannon.[48]

Given this rather gloomy scenario it is important to point out that our approach is a something of a broad brush assessment of the extent to which conservation can be realized under current and future climate change scenarios. We have made very simple adjustments to human population density and avian richness, and we realize that more realistic adjustments, such as those undertaken by Erasmus and van Jaarsveld[22] might have been more insightful. Indeed, they might well have been able to include single species information, as well as information on migration, adaptation, and the likely impacts of HIV/ Aids.[117,118] However, at the moment, such a detailed approach is not yet possible, although we would certainly advocate its adoption. Thus, we regard our approach as sufficient to highlight the extent to which sustainable development might prove difficult both at present, and in the future.

Indeed, our investigations have raised two key points that are especially significant in the context of the World Summit on Sustainable Development.[91] First, current human resource demand is high on most of the previously identified priority bird conservation areas. This is especially true for those areas that contain some degree of existing formal protection. In other words, conservation areas in Southern Africa are either already under considerable threat or will be faced with such threat in the very near future. Second, mean human population size in several of the IBA grid cells outside the current protected area network is lower than expected by chance. Although the options are more limited under a climate change scenario, this result was also found following an initial assessment of the likely response of human population density to climate change. Therefore, IBAs show considerable potential for expanding conservation needs outside current protected areas while minimizing conflict with human development requirements.

These two points translate into a simple message. First, that sustainable development means an increasing focus on protection of protected areas to ensure that they do not suffer the same fate as many of those elsewhere.[33,37] High population densities surrounding protected areas mean that formal protection will be increasingly difficult, though necessary. The litany of examples of adverse effects of even low-level human utilization of resources on many species[14,119] is sufficient to show that formally protected areas should be just that. Second, that there are several options for ensuring that species continue to have some future under scenarios of both human population growth and climate change. These options should be carefully considered when planning future land use in Southern Africa. Failure to incorporate these options is likely to compromise substantially any sustainable development goal. Finally, that the most obvious way to ensure that sustainable development takes place to the benefit of both humans and the species on which they depend is to manipulate that part of the equation which is most within human grasp. Clearly, it is far easier to alter rates of human population growth and habitat modification, than it is to reverse the industrial revolution or to ensure that species can move through a maximally modified landscape.

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CHAPTER 7

General Discussion

Although macroecology (e.g. examining broad geographical patterns of spatial variation in biotic diversity) has its weaknesses and inadequacies, it is still an essential component of effective biodiversity conservation (Gaston & Blackburn 2000). Understanding patterns of species richness through space and time contributes substantially towards the increasing need to understand the mechanisms underlying biodiversity, and human impacts on species and populations. This thesis has addressed four major themes that have emerged from recent broad-scale studies namely: (i) the species-energy hypothesis which is thought to be a prime contender for explaining variation in richness across latitude; (ii) understanding broad-scale spatial turnover patterns in species richness and species identity; (iii) examining the effects of spatial autocorrelation on the outcomes of investigations of large scale patterns; and (iv) examining the influence of human activities on large scale patterns in biodiversity. Consequently, this thesis has not only contributed towards a better understanding of broad-scale patterns in species richness, but has also made a contribution to achieving sustainable development in South Africa. In the South African context, the shortage of conservation resources, land redistribution issues, as well as high annual human growth, mean that the information and insights provided by this thesis should prove most useful because conservation planning faces many current and future difficulties. Indeed, based on the findings from this thesis several recommendations can be made to further assist future conservation planning strategies in South Africa.

First, the importance of scale (resolution and extent) at which studies are undertaken to examine correlates of, or causal mechanisms underlying the variation in species richness patterns is critical, as this can affect the outcome of a study (Blackburn & Gaston 2002). Therefore, when examining the relationship between human activity and avian species diversity to reveal finer-scale effects, such as distinguishing species transition areas in response to subtle land transformation activities, fine resolution data are needed. The importance of these data is clearly evident in this thesis, given that no effects of land transformation on avian species turnover patterns were found even within the most highly transformed region in South Africa (see Chapter 3). Because of the unavailability of fine resolution information on animal diversity and distribution in South Africa, the question of assessing the degree of conflict between human and conservation needs at the national scale could not be adequately resolved. Substantial improvements in the quality of atlas data at a finer resolution than a quarter-degree are therefore needed for South Africa to further resolve fine-scale effects of habitat alterations and land-use patterns on biodiversity (see also Redford & Dinerstein 1994, Cowling et al. 1999).

Second, because the environment we live in is not static (Hannah et al. 2002, Reyers et al. 2002), South Africa needs more sophisticated studies to determine the likely effects of predicted climate change on human population patterns and biodiversity patterns. In a previous study examining south-eastern Africa's vulnerability to water shortages and surpluses, Schulze et al. (2001) identified South Africa as the country with the highest annual water demands and the largest respective area currently experiencing water shortages (>

50% of the region's area surface). In addition, South Africa showed the greatest increase in areas with severe water shortages based on projected water availability scenarios for 2050 (Schulze et al. 2001). As elsewhere, water availability is an important driving factor for observed biodiversity and human density patterns in South Africa (O'Brien 1993, 1998, O'Brien et al. 1998, 2000, Cueto & de Casenave 1999, Andrews & O'Brien 2000, Rahbek & Graves 2001, see also Chapters 2, 5, 6). Any change in water availability will therefore be translated into a corresponding change in these patterns (see e.g. Sillett et al. 2000, Erasmus et al. 2002), and therefore also a different conflict profile between humans and other species (see Chapter 6). Such changes in patterns of conflict are especially likely with increasing human demand for resources, especially agricultural resources (Tilman et al. 2001), where water often dominates production and therefore the economy (Schulze et al. 2001).

The availability of detailed information on the likely effects of predicted climate change is therefore essential to determine the extent of potential future conflict between human and conservation needs, and how best to incorporate these changes into the future conservation matrix. To date, only one attempt has been made to document the response of South African fauna to climate change events based on individual animal species responses (see Erasmus et al. 2002; and for a discussion of effects on the South African flora see McDonald & Midgley 1996, Rutherford et al. 1999). Erasmus et al. (2002) modelled and discussed the conservation consequences of distribution range shifts for several individual bird species after a doubling in pre-industrial CO_2 levels using the HadCM2 model (Shannon 2000). They showed that the majority of species analysed (78%) displayed some degree of range contraction and a large percentage of species loss (up to 66%) may occur in South Africa's flagship conservation area, the Kruger National Park. Future information, such as that provided by Erasmus et al. (2002), would be especially useful for land-use planners to identify the effectiveness of current and potential future conservation areas in protecting species after taking climate change into account. For example, there are areas specifically designed to conserve a single threatened species, like the Important Bird Area "Collywobbles Vulture Colony", which was designed to protect the globally threatened Cape Vulture (*Gyps coprotheres*) (see Barnes 1998). If the possible distribution range for the Cape Vulture can be predicted for certain climate change scenarios, then the effectiveness of the Collywobbles Vulture Colony area can be assessed. This type of information will be critical for future land-use planning in South Africa, especially after this thesis showed that when site selection is used in an attempt to maximize species protection and simultaneously avoid areas of high human density, options for such land acquisition are severely constrained (see Chapters 5, 6). Moreover, a further decrease in the flexibility to selecting such conservation areas becomes evident after taking climate change scenarios into account (Chapter 6).

Third, despite the fact that the South African Bird Atlas Project (SABAP – see Harrison et al. 1997) successfully provided the first up-to-date distribution maps for all of southern Africa's bird species, only limited programmes are currently in place for obtaining time-series data for taxa in South Africa. The Coordinated Waterbird Counts (CWAC – Taylor et al. 1999), which are the monitoring scheme for South Africa's waterbird populations and their associated habitats for the last ten years is most likely the best example of such a programme. The long-term aim of the CWAC programme is to create a data network which will provide time-series data on waterbird populations from all of South Africa's major wetlands. Data obtained from such programmes can enable scientists to calculate seasonal movements and therefore clarify the direction of trends and the rate at which population change is happening. In other words, annual population indices can be calculated from regular updates to trace the fluctuations, increases and declines of populations. From this, conservation solutions that explicitly incorporate changing landscapes and changing populations can be provided. The need for such conservation solutions was clearly evident in this study after it was found that under a climate change scenario, much of the flexibility to expand the current conservation network disappears (see Chapters 5, 6). However, to further test the increasing conservation conflict assumptions made from this thesis, not only will it be necessary to repeat the SABAP at regular intervals to monitor change, but because these assumptions were based solely on one taxon (birds), programmes providing time-series data are also desperately needed for other taxa. When selecting a taxon for long-term monitoring purposes, different taxa must be chosen carefully depending on practical considerations such as the taxonomic stability, degree of survey ease, their representativeness of regional ecosystems, and finally, their public conservation appeal. These considerations, although not always consistent with objective science practices, are real world issues that require attention if long-term monitoring programmes over large areas using professional and amateur volunteers are to be successfully undertaken.

Finally, at least for the foreseeable future, politicians ultimately have the final say when dealing with social and economic issues such as land-use and human population planning. These in turn affect the sustainability of the environment over time. Therefore, to try to bridge the communication gap between biologists and politicians (Chown & McGeoch 1995), and for politicians to make use of research findings that focus on conservation planning strategies, it is critical to incorporate research questions that relate to human expectations. Complex modelling approaches exploring different policy intervention strategies to provide sustainable development outcomes in South Africa are therefore necessary as they can be successfully used to narrow the gap between biological and political agendas (see e.g. Erasmus & van Jaarsveld 2002). Such sophisticated approaches will be critical for providing the necessary information needed to ensure that landscape planning can be done in such a way that it will ensure both species survival and human aspirations. For example, although the human population of South Africa displayed 2.2% per annum growth over the last six years (Statistics South Africa 1996), the HIV/Aids pandemic may precipitate a strong decline over the next 20 years (see Erasmus & van Jaarsveld 2002 for different human population growth rate scenarios in South Africa). Such a strong and rapid decline in South Africa's human population size will undoubtedly negatively affect social, economic and environmental issues in the region and, therefore, also negatively affect the outcome of sustainable development in the region. Ultimately, both human welfare and biodiversity protection will be negatively affected if sustainable development solutions cannot be achieved. The need to address these problems is clearly evident in this thesis after it was shown that most of the core sites for conservation are under immense pressure due to over-utilization by humans (Chapters 5, 6), which can most likely only be alleviated by addressing several issues related to human expectations (see Chapters 5, 6).

In conclusion, achieving sustainable development is no easy task. Significant changes will be needed in decision-making at the highest levels, and in day-to-day behaviour by producers and consumers, if we are to reach our goal of development that meets the needs of today without sacrificing the ability of future generations to meet their needs. Like other countries, to achieve sustainable development in one of the world's most species rich regions (see WCMC 1992), South Africa will ultimately need to produce more flexible conservation matrixes to allow for changing landscapes and areas with low human densities; stimulate economic growth to eradicate poverty especially among communities living on the periphery of reserves to reduce human use of core conservation areas; and reduce human population growth in the region. With these issues on the main agenda of the 2002 Johannesburg World Summit on Sustainable Development, we can only hope that practical solutions will be put in place to do away with the large number of unsustainable practices that have led to the current predicament not only in South Africa, but also across the globe.

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