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).

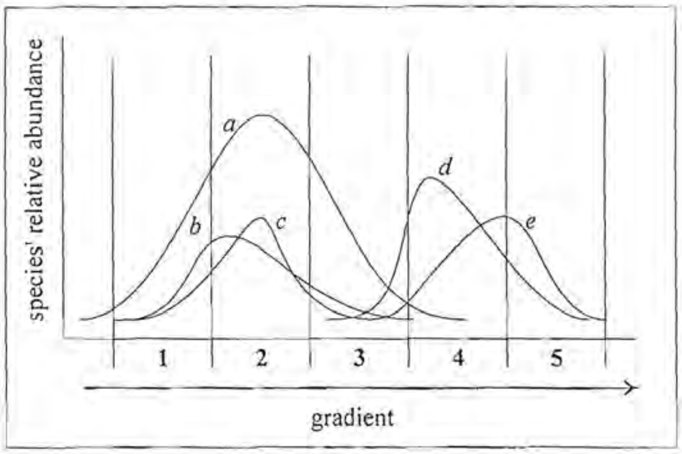

Figure 1. Hypothetical distribution of five species (*a* - *e*) across an environmental gradient. All species might be represented at the core of their ranges by two sites (2 and 4) or by a minimum set of just one site (3) in the transition between different species assemblages.

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):

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

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

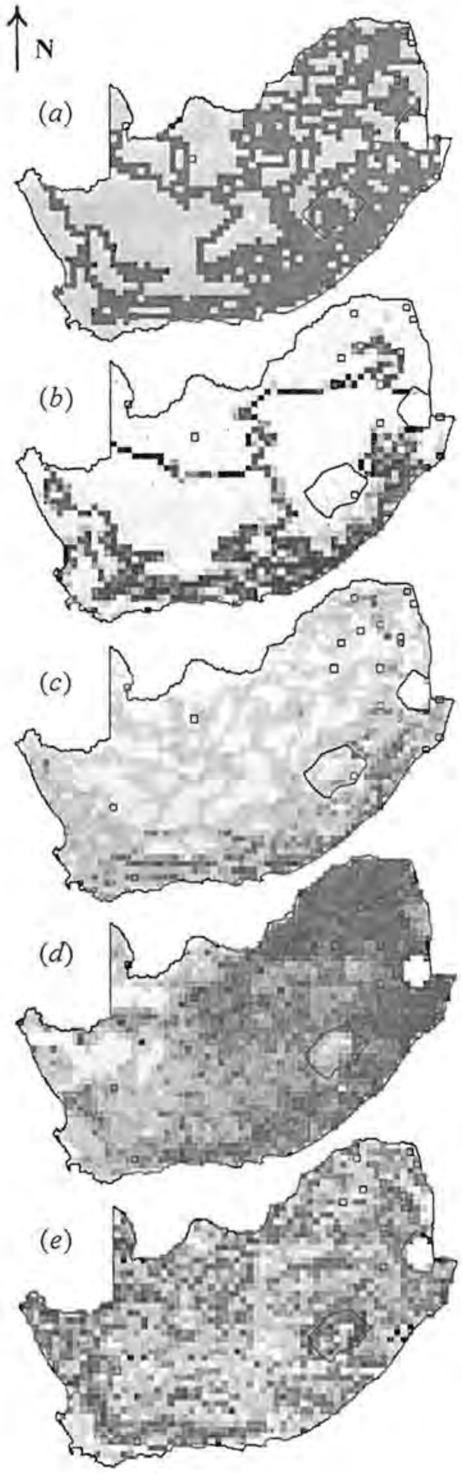

Figure 2. Measures of ecological transition: (*a*) presence of vegetation edges (darker cells correspond to edges); (*b*) biome heterogeneity; (*c*) number of vegetation types; (*d*) bird composition heterogeneity; and (*e*) β_g across South Africa and Lesotho. In (*b*), (*c*), (*d*) and (*e*), darker 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).

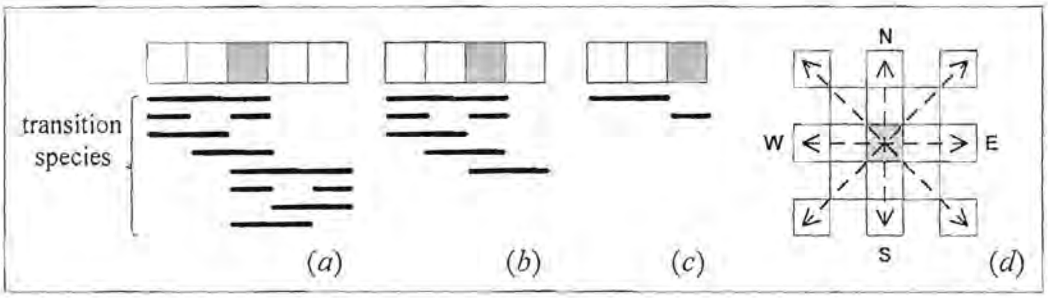

Figure 3. Illustration of the concept and measurement of diversity based on multidirectional gradients (β_g). This measure highlights regions that have a high proportion of species that are on the edge of their ranges ('transition species'). (*a*) Considering a linear sequence of five adjacent cells 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.

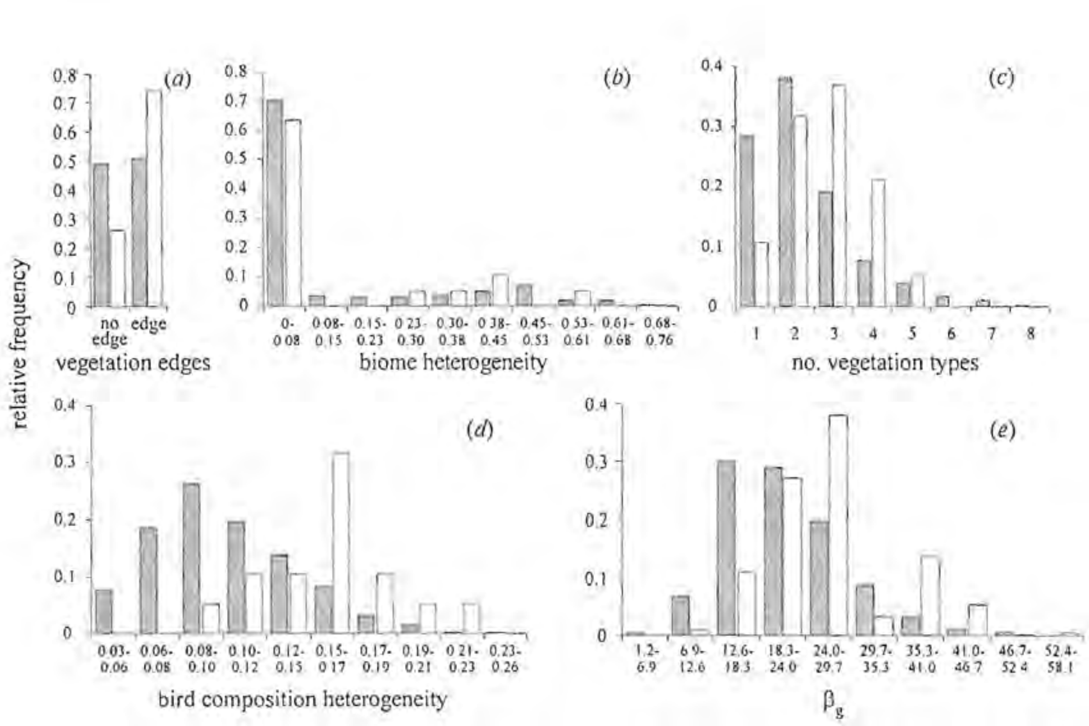

Figure 4. Comparison between the frequency distributions obtained for all grid cells in the study area (grey bars) and the mean frequency distributions of the 30 complementary sets (white bars), for each of the measures of ecological transition: (*a*) presence of vegetation edges, (*b*) biome heterogeneity, (*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

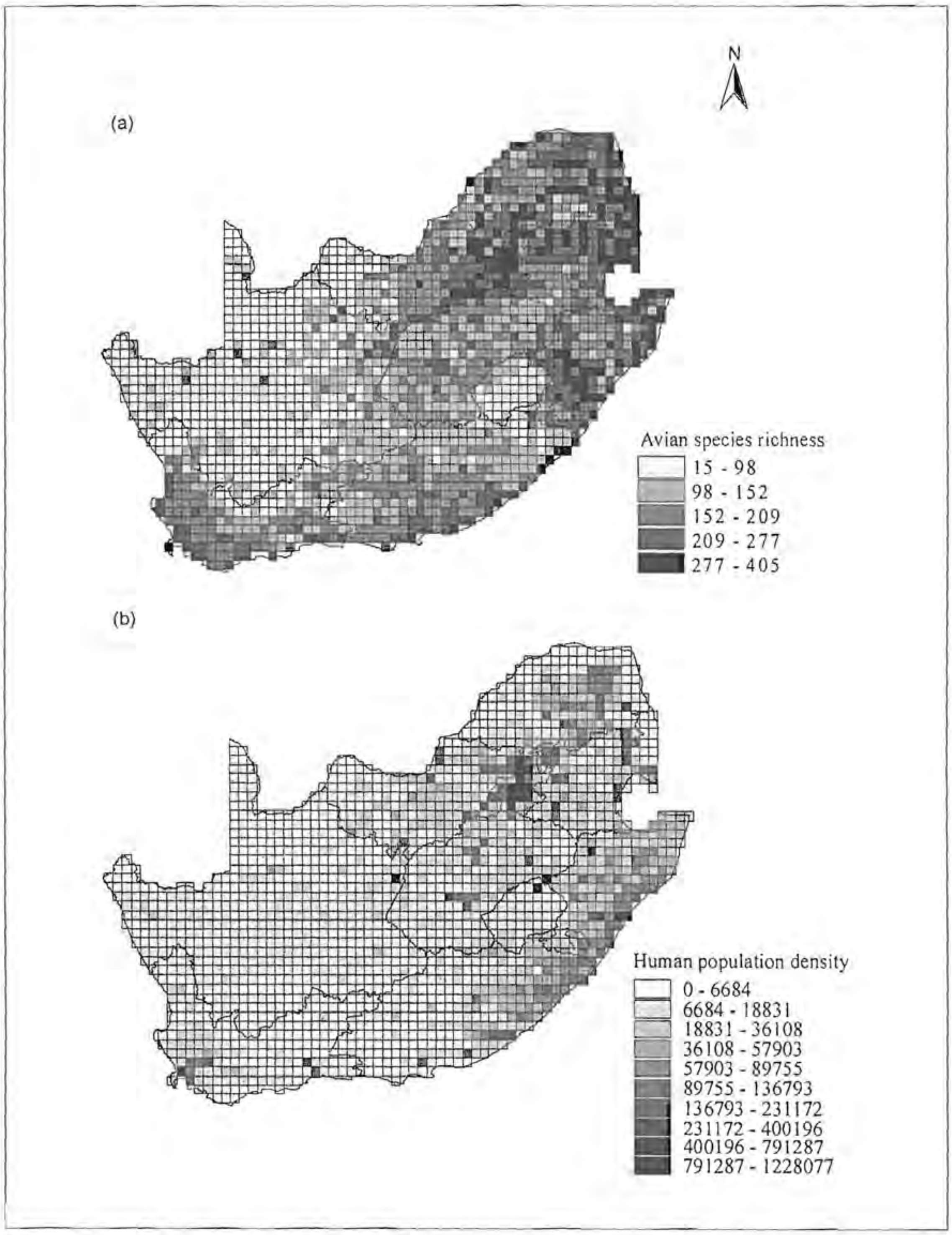

Fig. 1. Avian species richness (a) and human population size (b) variation across South Africa.

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:

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

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.

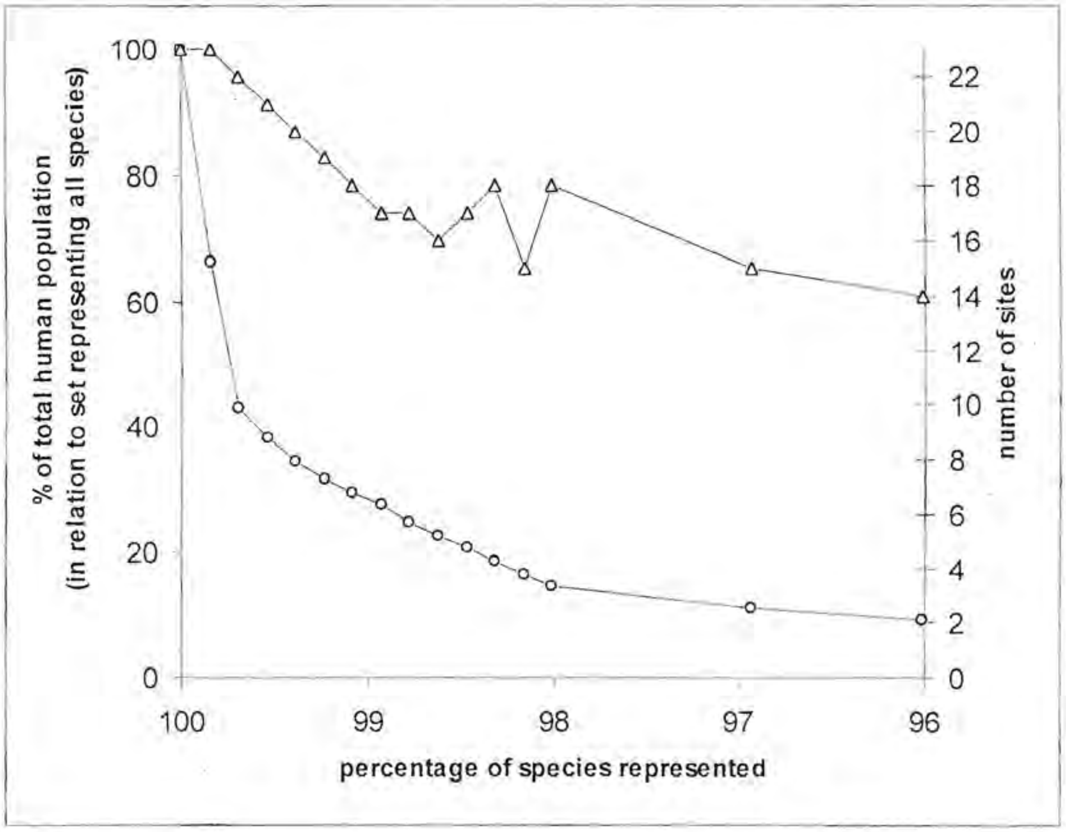

Fig. 2. Trade-off between species represented and total human population included in complementary reserve networks. Circles represent the minimum total population (as a percentage of the population in the set of 23 cells representing all 651 species) that is represented in selected sites (cells) while 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).

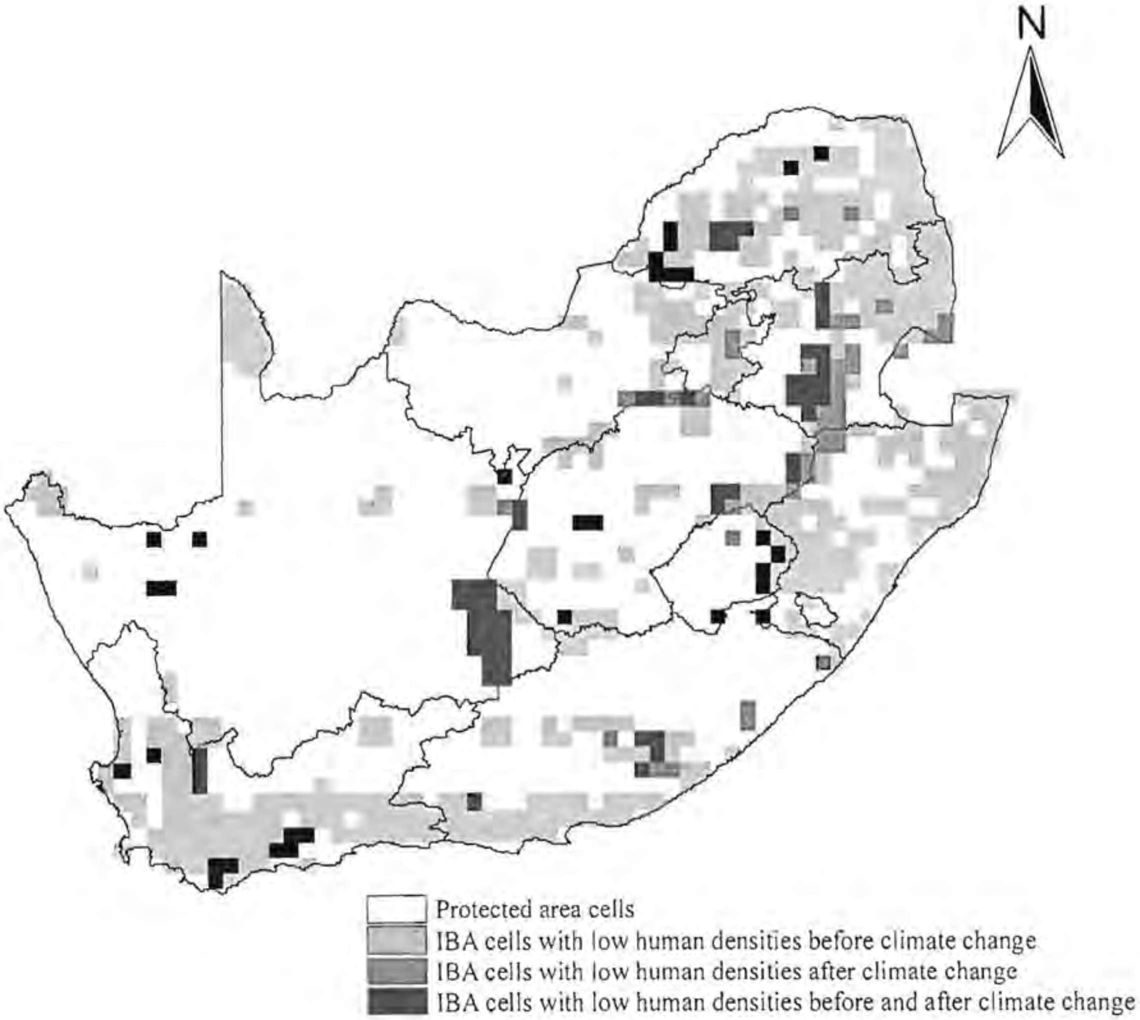

Fig. 1. The spatial distribution of protected area cells in relation to IBA (Important Bird Area) cells outside the current protected area network with lower than expected human density values prior to and after human population density responses to climate adjusted precipitation values across South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

*** $p < 0.001$.

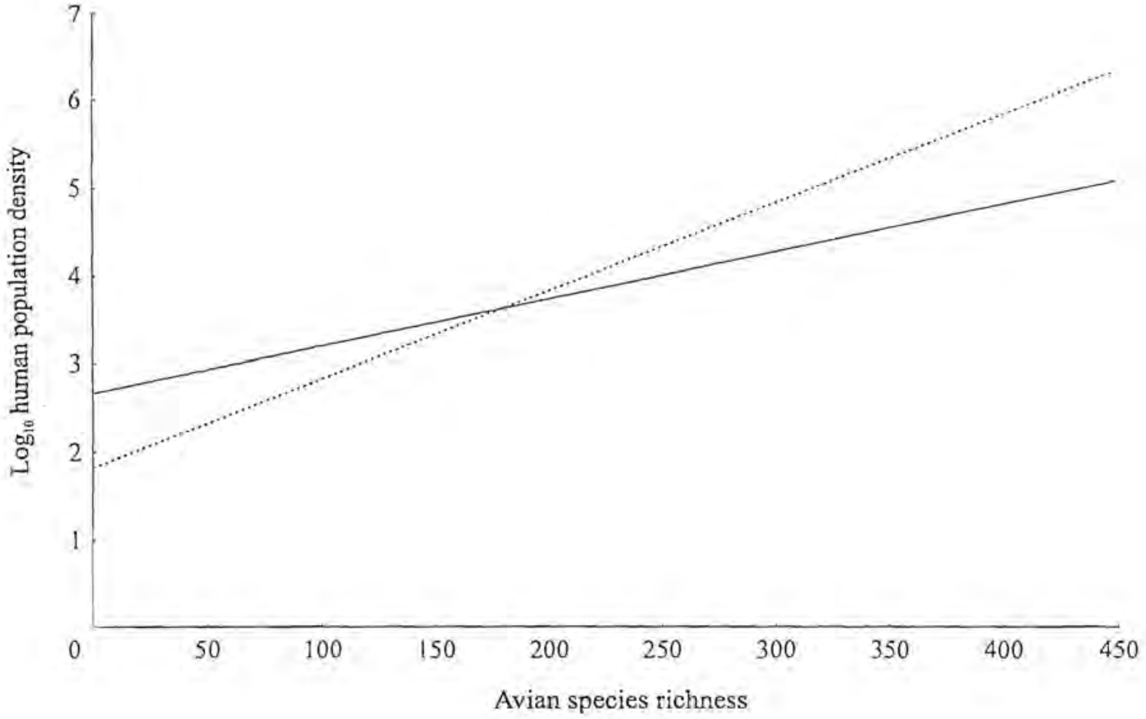

Fig. 2. The linear regressions between Log_{10} human population densities and avian species richness (——) before variable values were calculated based on climate adjusted PPT values (Log_{10} human density = 2.7235 + .006 X Avian species richness; r = .66), and (------) after variable values were calculated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

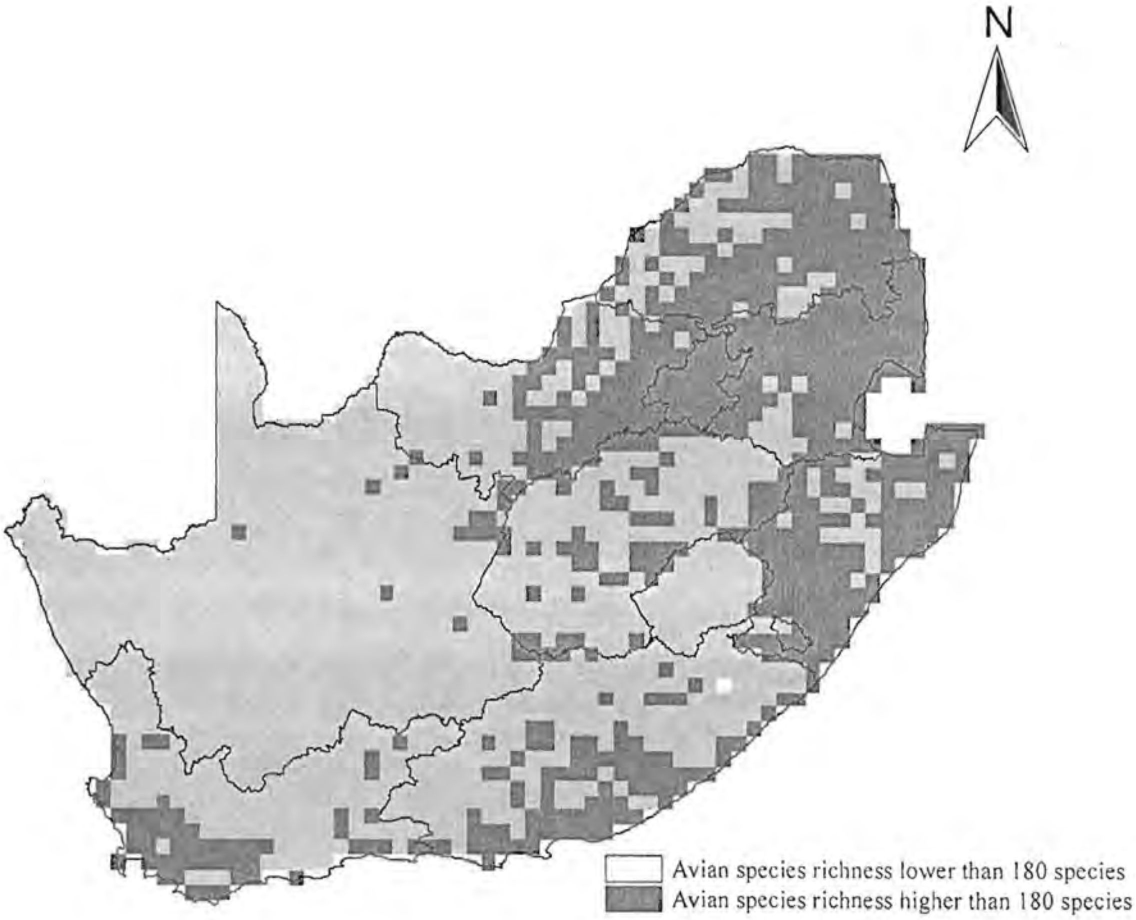

Fig. 3. The spatial distribution of quarter-degree grid cells with avian species richness values presently lower than 180 species per cell, and those grid cells with avian species richness values presently higher than 180 species per cell.

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]

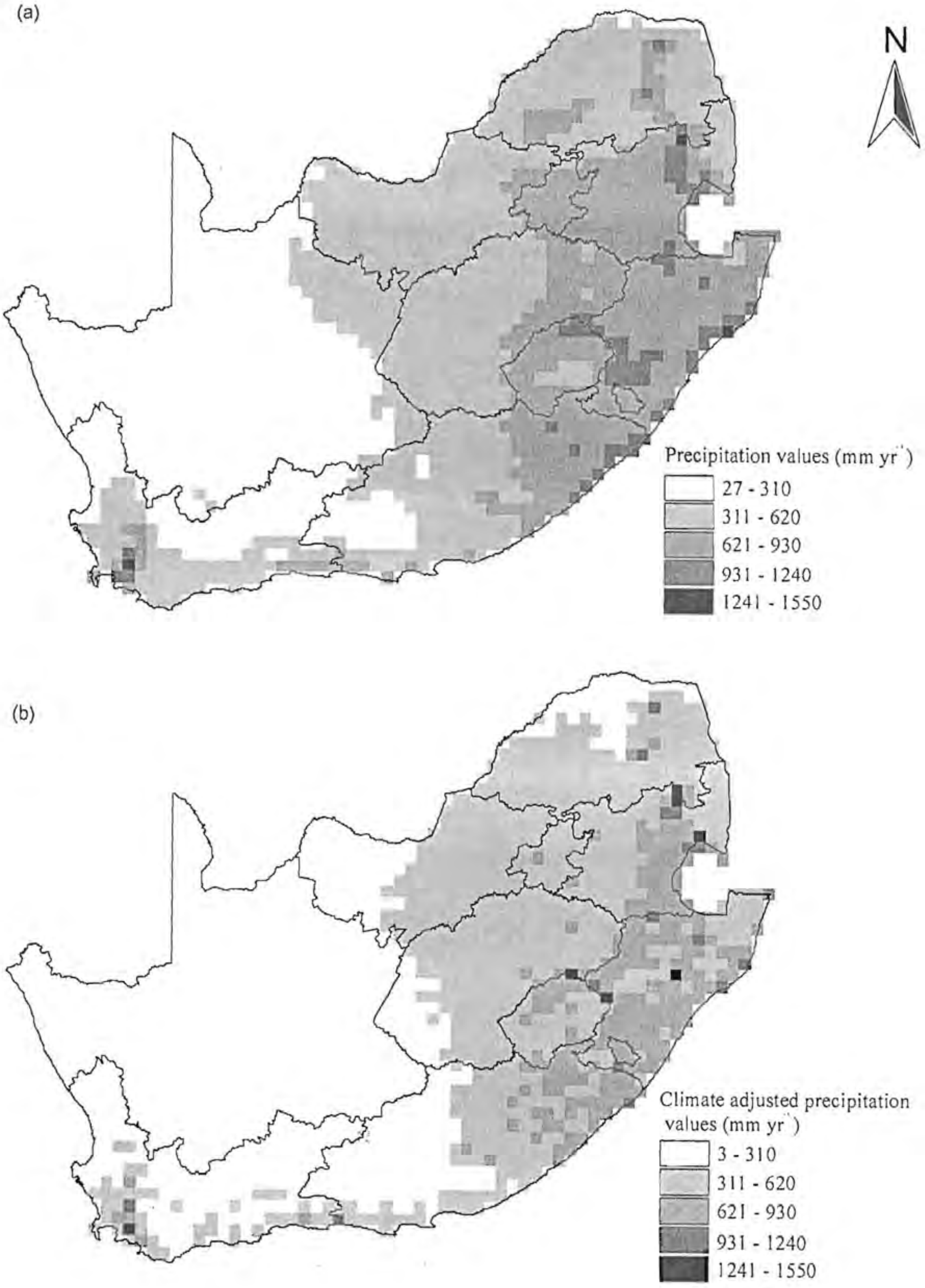

Fig. 4. Variation in precipitation (mm yr^{-1}) values across South Africa (a) before taking climate adjusted precipitation values into account and (b) after taking climate adjusted precipitation values into account as predicted by Shannon.[48]

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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