

CHAPTER 5

A multicriteria approach to reserve selection: addressing long-term biodiversity maintenance

A multicriteria approach to reserve selection: addressing long-term biodiversity maintenance

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Abstract

Existing reserve selection techniques concerned with maximal biodiversity representation within minimum land area, do not necessarily ensure the long-term maintenance of biodiversity. These traditional approaches ignore the maintenance of natural processes, turnover of feature diversity and the need to minimise threats within conservation areas. We address these three emergent issues in the identification of potential avian conservation areas in the Northern Province of South Africa, by combining ordination and spatial autocorrelation analyses, as well as land transformation data into traditional reserve selection techniques. Existing conservation areas are biased and inefficient and traditional methods do little to correct this skew. The inclusion of species assemblage structure as well as the underlying environmental gradients ensures a conservation area network that strives to maintain both biodiversity pattern and process. Spatial autocorrelation analysis allows for the identification of areas with high beta diversity, important areas for the long-term maintenance of biodiversity. The inclusion of land transformation data leads to viable conservation area networks and highlights areas of potential conflict between biodiversity conservation interests and human land-use issues. These improvements on the current generation of reserve selection techniques bring us a step closer to ensuring the long-term maintenance of biodiversity within conservation areas.

Introduction

Historic opportunistic methods for assigning land with low potential for economic and political conflict; or high potential for recreation and tourism to biodiversity conservation are inefficient and ultimately more costly means of conservation area allocation (for review see Pressey & Tully, 1994; Rodrigues *et al.*, 1999). This realisation has led to the development of a wide array of systematic reserve selection techniques designed to make conservation area selection more efficient. These techniques are concerned with the maximal coverage problem and include complementarity-based reserve selection and linear programming algorithms (for review see Church *et al.*, 1996; Csuti *et al.*, 1997; Williams, 1998; Margules & Pressey, 2000). However, the ultimate goal of conservation planning is to ensure the long-term security of the planet's biodiversity (Scott *et al.*, 1989) and the extent to which conservation areas fulfil this role depends only partly on this long established representation goal concerned mainly with sampling the biodiversity pattern in a complementary fashion.

Several authors have emphasised that current biodiversity representation within conservation areas is not equivalent to the ultimate goal of maintaining biodiversity in the long-term (Balmford *et al.*, 1998; Williams, 1998; Cowling *et al.*, 1999; Margules & Pressey, 2000; Rodrigues *et al.*, 2000). Many suggestions have been put forward as to how to ensure the long-term maintenance of biodiversity within conservation areas. Williams (1998) suggests promoting viability and reducing threat as vital components of the conservation area selection process. Margules and Pressey (2000) agree but add the maintenance of natural processes as an important component of conservation area selection. Cowling *et al.* (1999) separate these issues into retention goals, generally formulated in the context of threats to biodiversity, and long-term persistence goals, which concern the maintenance of natural processes. Rodrigues *et al.* (2000) argue that as species diversity distribution patterns change over time, the selection of conservation areas which are robust to turnover in feature diversity is a critical component of conservation area selection for ensuring the long-term maintenance of biodiversity. We address all three emergent issues of natural process maintenance, turnover of feature diversity and minimising threat in the present study as we identify potential avian conservation areas in the Northern Province of South Africa for the long-term maintenance of regional avian diversity.

Maintenance of natural processes

In order to ensure the long-term maintenance of biodiversity within conservation areas, these areas must conserve not only the biodiversity pattern, but also the natural processes that control and maintain that pattern (Balmford *et al.*, 1998). Conservation of ecosystem processes that sustain ecosystem structure and function, and evolutionary processes that sustain lineages and generate diversity, are essential for achieving the long-term maintenance of biodiversity in conservation areas (Nicholls, 1998). These processes include interspecific interactions, regular and nomadic faunal movements, disturbance regimes and climate change among many others (Balmford *et al.*, 1998; Cowling *et al.*, 1999). But, as Margules

and Pressey (2000) point out, because conservation area selection is often a spatial exercise, protection of these natural processes is often based on their spatial surrogates rather than on the processes themselves. These surrogates can include size, lack of roads, watershed boundaries, dispersal routes, land classes, landscapes and other geographic features (Cowling *et al.*, 1999; Margules & Pressey, 2000). There are numerous natural processes that need to be considered and, as is often the case, they have not been adequately documented for a region such as the Northern Province. However, as Noss (1996) points out, by ensuring that conservation areas are large and span substantial environmental gradients it should be possible to accommodate, at least partially, many of these processes.

We aim therefore to investigate not only the avian diversity pattern within the region but also the processes responsible for that pattern by identifying broad avian communities in the study area, as well as the environmental gradients that drive this emergent community structure. In pursuit of identifying these environmental gradients responsible for the biodiversity pattern, ordination (gradient) analyses have illustrated tremendous potential (Taggart, 1994; Faith, 1995; Faith & Walker, 1996a). This analytical approach has a long history in community ecology and is used for identifying key processes responsible for the control and maintenance of biodiversity patterns by integrating multiple environmental effects across a landscape (Bray & Curtis, 1957; Whittaker & Niering, 1965; Jongman *et al.*, 1995). In addition to this, ordination explores biodiversity patterns by interpreting entire species assemblages of sample sites, rather than through species-by-species relations, offering community level results and responses to often complex environmental gradients (Jongman *et al.*, 1995).

Turnover in feature diversity

Despite the importance of beta diversity in determining regional species richness patterns, little attention has been paid to this component of diversity within conservation area selection (Whittaker, 1977; Cowling *et al.*, 1989). Alpha diversity refers to the number of species within a homogenous community (Whittaker, 1972; 1977); beta diversity on the other hand is concerned with species turnover or the rate at which species are replaced by others along habitat gradients (Whittaker, 1972). Conservation areas selected based on representation of alpha feature diversity patterns, without considering the turnover of features or beta diversity, may not necessarily continue to serve their purpose over a period of years. Several authors have found that traditional complementary-based approaches to conservation area selection may not be adequate if the role of a conservation areas is to maintain biodiversity in the long-term rather than simply represent current biodiversity patterns (Margules *et al.*, 1994; Virolainen *et al.*, 1999; Rodrigues *et al.*, 2000). In this study we aim to address this issue of beta diversity by identifying and focussing on areas with a high turnover in species along associated environmental gradients.

Minimising threat

The basic role of conservation areas is to protect elements of biodiversity from external processes and

factors that threaten their existence (Margules & Pressey, 2000). Very few of the existing methods for identifying conservation areas include measures of threat into the selection process (Balmford *et al.*, 1998; Faith & Walker, 1996b; Williams, 1998). Land-cover changes, caused mainly by agriculture and urban development, present the single most important threat to global biodiversity (Soulé, 1991; Dale *et al.*, 1994). As a result, signatories to the Convention on Biological Diversity are obligated to assess the impact of land transformation on biodiversity and to implement appropriate responses if necessary (DEAT, 1997).

Many areas identified as important areas for conservation based on historical species distribution data may in reality be largely transformed (Wessels *et al.*, 2000 (see Addendum II)). In addition, although transformed areas may currently harbour some species, these areas may not be able to sustain natural ecological processes and complete samples of non-target taxa (Baudry, 1993; Di Benedetto *et al.*, 1993; Freemark, 1995), thus precluding these areas from viable conservation area networks. Therefore the incorporation of land-cover (the suite of natural and human-made features that cover the earth's immediate surface) information into conservation planning is essential (Wessels *et al.*, 2000 (see Addendum II)). We include these data into conservation area selection techniques in the Northern Province of South Africa in order to identify and minimise threats within the proposed avian conservation area network.

Methods

Study area

The Northern Province of South Africa occupies about 10% (122305 km²) of the country and lies at the northeastern tip of South Africa bordering on the countries of Mozambique, Botswana and Zimbabwe (Figure 1). The province includes the northern end of the Drakensberg escarpment which separates the low-lying, warm and humid Lowveld region on the east from the higher lying, drier and cooler Bushveld plateau region in the west (Figure 1). The Limpopo river forms the northern and northeastern boundary of the province where it borders on the neighbouring states of Botswana and Zimbabwe. This Limpopo river valley is separated from the Lowveld and central Bushveld plateau by the Soutpansberg and Blouberg mountain ranges. The Waterberg mountain range falls within the central Bushveld plateau region and together with the escarpment encircles the Springbok flats, a clay substrate basin within the Bushveld plateau with a long history of dry land cultivation (Figure 1).

The study area consists primarily of the savanna biome, with small areas on the escarpment covered by grassland and forest biomes (Low & Rebelo, 1996). The province includes extensive areas of arable land and as a result 14% of the province has been transformed by cultivation. Urbanisation (1.6%) and forestry plantations (0.8%) account for the remaining land transformations (Thompson, 1996; Fairbanks *et al.*, 2000). However the study area has not been excessively degraded and transformed since 73% is still covered by natural vegetation (Table 1; Figure 2) and 11.36% is under formal protection in

provincial and national protected areas.

Avian distribution data

Information on avian distribution at a quarter degree grid cell (15' x 15'; ~700 km² hereafter referred to as a grid cell) resolution was collated from the South African Bird Atlas Project (Harrison, 1992; Harrison *et al.*, 1997). The presence/absence of 565 avian species, comprising 60% of the bird diversity recorded in the Southern African sub-region (South Africa, Lesotho, Swaziland, Namibia, Botswana, Zimbabwe and southern Mozambique), was recorded from 1980–1992. The Northern Province contains 48803 unique distribution records for these bird species within 214 grid cells (Figure 3).

Environmental data

Among the factors and processes that have been hypothesised to account for spatial patterns of species diversity are climatic extremes, climatic stability, productivity, and habitat heterogeneity (Brown, 1995; Wickham *et al.*, 1997). Data were compiled from existing sources to represent these factors (Table 2), including interpolated weather stations (Schulze, 1998) and topographic contours (SA Surveyor General, 1993) mapped in a geographic information system (GIS; ESRI, 1998) using Albers equal area projection. This GIS database had a grid cell resolution of 1km x 1km, which was determined by the cell size of existing rasterised data sets and a logical cell size for future integrative work.

Land-cover data

Land-cover data were mapped from 1:250000 scale geo-rectified space-maps, based on seasonally standardised Landsat TM satellite imagery captured primarily during 1994-95 (Thompson, 1996; Fairbanks *et al.*, 2000). For the purpose of the present study the 31 land-cover classes were reclassified into three categories, namely natural vegetation, modified vegetation and transformed (Table 1; Figure 2) (based on Wessels *et al.*, 2000 (see Addendum II)). Natural vegetation included all untransformed vegetation, e.g. forest, woodland, thicket and grassland. The modified vegetation category was dominated by degraded classes of land-cover. These areas have a very low vegetation cover in comparison with the surrounding natural vegetation cover and were typically associated rural population centres and subsistence level farming, where fuel-wood removal, over-grazing and subsequent soil erosion were excessive (Thompson, 1996).

The transformed category consisted of areas where the structure and species composition were completely or almost completely altered (Poore, 1978) and includes cultivated, afforested or urbanised areas, as well as mines and quarries. The average thematic mapping accuracy for the province was 73%, with much of the error being attributed to misclassification in bushland-woodland transition zones, not in identifying human land-use impacts (Fairbanks & Thompson, 1996; Fairbanks *et al.*, 2000).

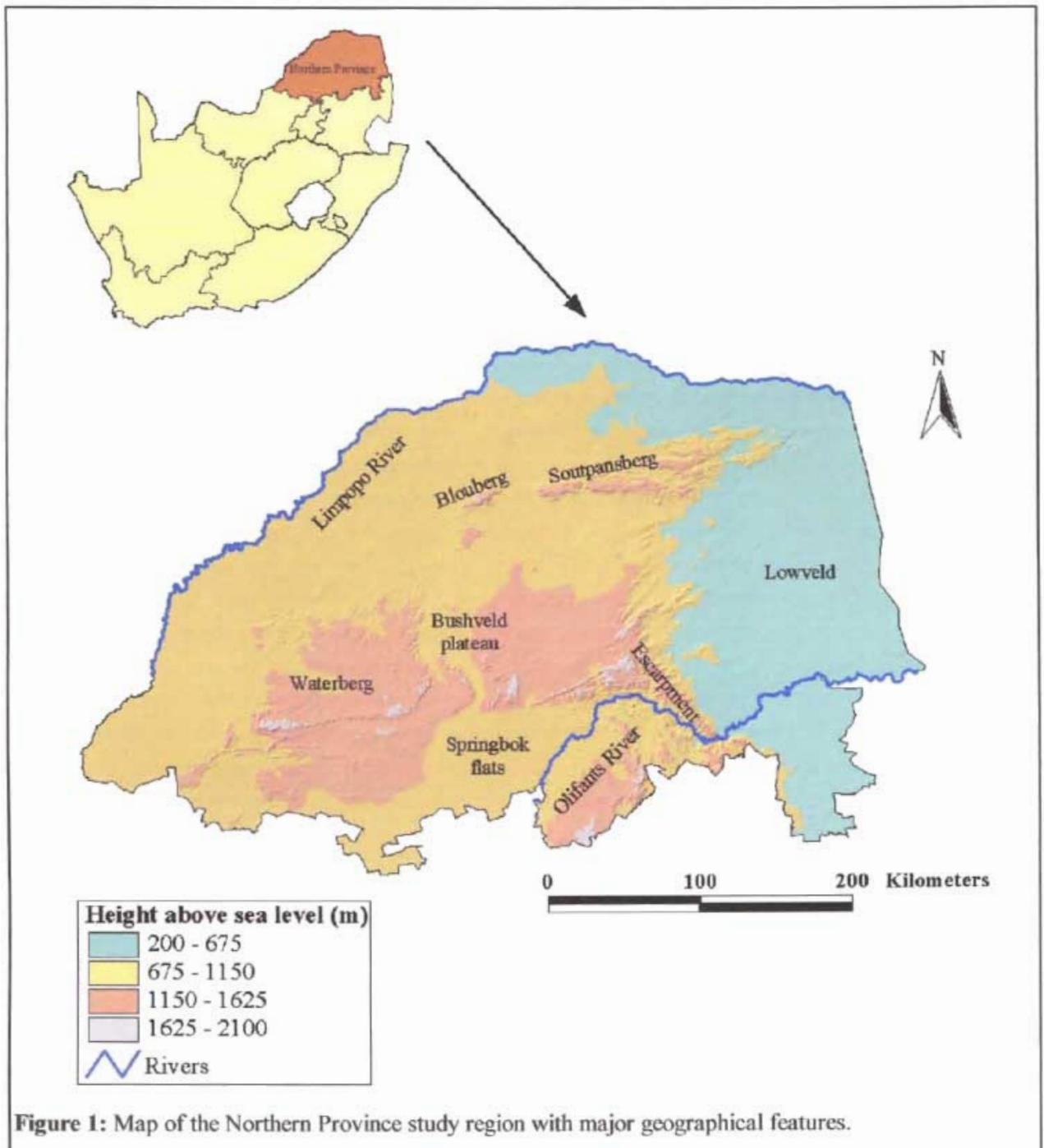


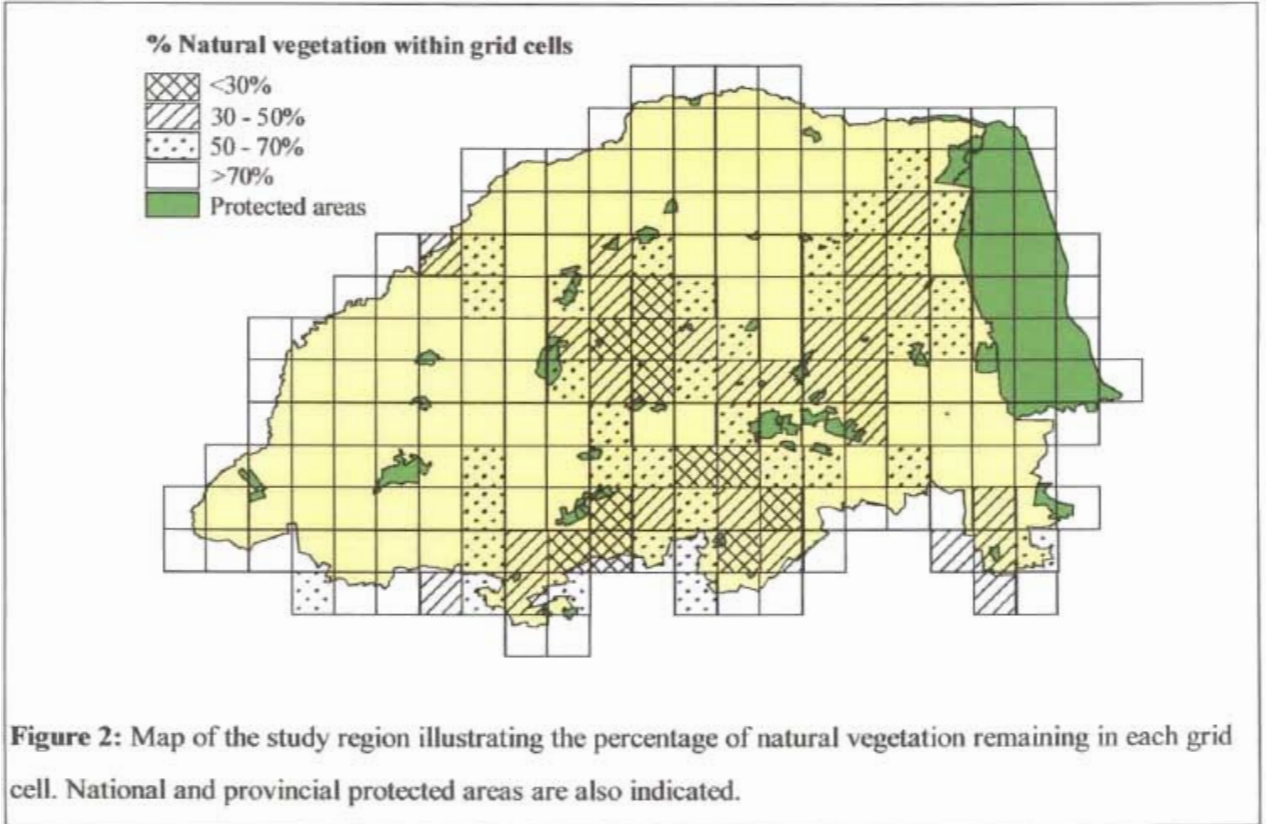
Figure 1: Map of the Northern Province study region with major geographical features.

Table 1: Land-cover classes reclassified into transformation categories (after Wessels *et al.*, 2000 (see Addendum II)).

Transformation category	% area	Land-cover class
Natural vegetation	73.4%	Wetlands, grassland, shrubland, bushland, thicket, woodland, forest
Modified vegetation	10.1%	Degraded land (9.9%), erosion scars (0.1%), waterbodies (0.1%)
Transformed	16.5%	Cultivated lands (14%), urban/built-up areas (1.6%), mines and quarries (0.01%), forestry plantations (0.8%)

Table 2: Codes and definitions of explanatory variables used in canonical correspondence analysis.

Code	Definition
Topography	
DEMMEAN	Elevation (m)
DEMSTD	Elevation heterogeneity (std. Deviation)
Climate	
GDMEAN	Number of days per annum on which sufficient water is available for plant growth
MAP	Mean annual precipitation (mm)
GTMEAN	Annual mean of the monthly mean temperature (°C) weighted by the monthly GD
NGTMEAN	Mean temperature (°C) during negative water balance
MAT	Mean annual temperature (°C)
MAXMNTHMN	Mean temperature of the hottest month, usually January (°C)
MINMNTHMN	Mean temperature of the coldest month, usually July (°C)
EVANNMN	Total annual pan evapotranspiration (mm)
PSEAS_MN	Precipitation seasonality from the difference between the January and July means
TSEAS_MN	Temperature seasonality from the difference between the January and July means
MXSEAS_MN	Maximum temperature seasonality from the difference between January and July



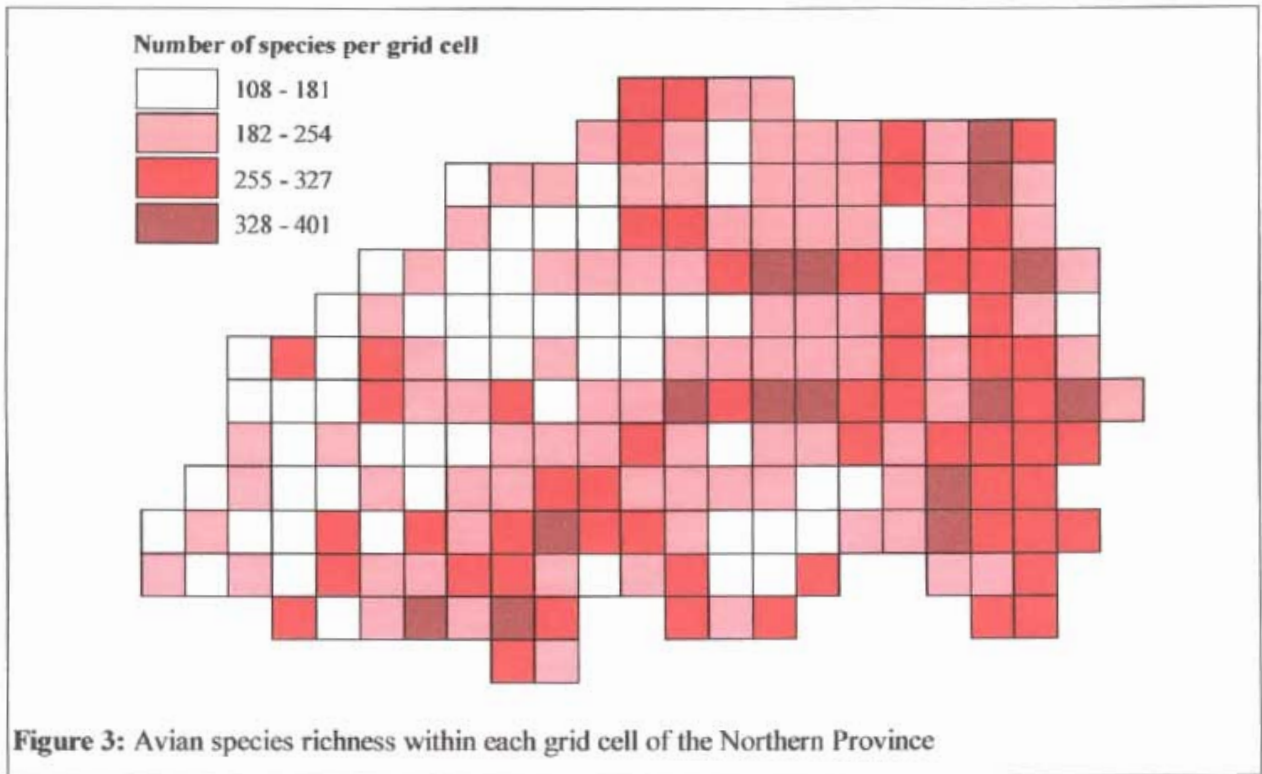


Figure 3: Avian species richness within each grid cell of the Northern Province

GIS analysis

The environmental and land-cover data were overlaid with the 15' x 15' grid. Each grid cell had an aggregated mean statistic recorded of the environmental and topographical features found within that grid cell, with the addition of the standard deviation of the elevation also being recorded. The extent of land-cover classes, as well as national and provincial protected areas within each grid cell were calculated using ArcInfo (Figure 2) (Albers equal area projection).

Ordination analysis

Our primary analytical tool was canonical correspondence analysis (CCA; ter Braak & Prentice, 1988), a direct gradient analysis method used widely in community ecology (Palmer, 1993), and detrended correspondence analysis (DCA), an indirect gradient analysis method (Gauch, 1982). The program CANOCO, version 4.0 (ter Braak & Smilauer, 1998) was used to conduct all gradient analyses. DCA was used to determine the dominant avian species communities within the Northern Province. Environmental data (e.g. the 12 environmental parameters found under topography and climate in Table 2) were entered with the species data using stepwise CCA to investigate which environmental variables explained the patterns in observed avian diversity (ter Braak & Smilauer, 1998).

Spatial autocorrelation analysis

In order to combine this information on species patterns and the environmental gradients responsible for those patterns into practical conservation planning techniques, we employed spatial autocorrelation analyses. This form of analysis identifies areas with high levels of species and associated environmental gradient turnover. Using Moran's I analysis based on the information gained from the previous ordination analyses we identified local spatial clusters of integrated species composition and their associated environmental gradients (Fairbanks *et al.*, In Press). A grid cell with a high positive Moran I value is highly autocorrelated, or similar, to neighbouring grid cells in terms of the avian species it contains i.e. its species assemblage structure as well as environmental characteristics responsible for the presence of those species. A grid cell with a negative Moran I value shows a low level of autocorrelation and is thus very different from surrounding grid cells in terms of its species assemblage composition and the environmental variables associated with those assemblages. Thus those grid cells with low levels of spatial autocorrelation are indicative of areas with high turnover in species diversity as well as the environmental gradients responsible, and should be included into conservation area selection procedures.

Conservation area selection

Richness-based complementary algorithms (Kirkpatrick, 1983; Howard *et al.*, 1998; Chapters 2 & 3) were initially run on the bird species distribution data. However, as mentioned previously and as evidenced by the results, species-based conservation area selection does not successfully select areas for

the representation of natural processes responsible for generating biodiversity patterns. Nor does it target areas of high beta diversity i.e. areas with a high turnover in feature diversity. Thus, the traditional techniques of complementarity based algorithms were adapted to include steps that select areas important to the representation of alpha species diversity patterns, as well as beta species diversity and their associated environmental gradients or processes.

The spatial analysis results enabled the addition of not only species assemblage structure and turnover into reserve selection procedures, it also allowed for the inclusion of those environmental characteristics responsible for assemblages and assemblage turnover. Moran's I values were used as indicators of the importance of a grid cell in terms of species and environmental turnover with respect to neighbouring grid cells. This was done by employing Moran I values as an indication of the uniqueness of the species assemblages contained in that grid cell, as well as the uniqueness of the underlying environmental factors, with respect to the neighbouring cells (Fairbanks *et al.*, In Press). This then made it possible to include the representation of not only alpha diversity patterns, but also beta diversity patterns and the underlying environmental gradients of these patterns into a conservation area selection procedure. Thus the traditional complementarity-based algorithm was reprogrammed to select areas that were high in complementary species richness and low in spatial autocorrelation.

This was done by categorising Moran I values of each grid cell into four groups: negative autocorrelation, weak positive autocorrelation, moderate positive autocorrelation and strong positive autocorrelation. The algorithm started by selecting grid cells with a low level of spatial autocorrelation (i.e. grid cells in the first category of negative autocorrelation), if there was more than one grid cell within the category then complementary species richness of the grid cells was used to resolve ties. The algorithm then proceeded through all spatial autocorrelation categories until all species were represented at least once. In this way grid cells were selected with a high complementary species richness (high alpha diversity), but also with highly dissimilar species compositions and related environmental characteristics from neighbouring and previously selected grid cells (high beta diversity). This beta diversity (BD) algorithm, therefore, selects a network that not only represents all species in the area, but also the unique species assemblages, heterogeneous areas, transition zones, and environmental gradients, i.e. it samples both biodiversity pattern and process in a representative manner.

To identify a conservation area network that reduces conflict with other land-uses and avoids areas that are largely modified and transformed, the algorithms were then modified to successively exclude from selection grid cells that were more than 10, 20 ... 90% transformed and modified (Lombard *et al.*, 1997; Wessels *et al.*, 2000 (see Addendum II)). In essence, this land-use constrained (LUC) algorithm was initially limited to select only grid cells that contained more than 90% natural vegetation until no new species could be added to the system. After that it proceeded in a step-wise fashion to select grid cells that contained less than 90, 80 ... 10% natural vegetation, until all species were represented. The LUC algorithm was therefore based on a trade-off between the primary objective

of avoiding transformed land and a secondary objective of representing all species, including unique species assemblages and heterogeneous transition zones. This land-use constraint option was included into a traditional species richness-based reserve selection algorithm, and was also included into the BD algorithm. This BD algorithm first invoked the LUC before using Moran I values to select grid cells. Grid cells where there was a conflict between biodiversity conservation and alternative land-uses could be identified and local scale issues highlighted for further investigation. In all conservation area selection procedures species recorded in grid cells with more than 25% currently protected were assumed to be already represented and were excluded from the reserve selection algorithms.

Results

Ordination analysis

Geographic patterns of DCA scores are indicated in Figure 4 illustrating the four dominant avian assemblages present in the province. The Lowveld community in the east, the central Bushveld plateau community, the Limpopo river basin community forming the northern and western borders of the province and the Escarpment community at the northern tip of the Drakensberg escarpment all containing unique combinations of species. Eigenvalues and gradient lengths were slightly higher for DCA than for the detrended canonical correspondence analysis (DCCA) for the first two axes (Table 3). This fact together with the strong and significant correlations between the DCA for axis 1 and 2 and the explanatory variables (Table 4) suggested that much of the variation in avian diversity distribution is related to the measured environmental variables. The stepwise CCA reduced the number of significant variables required to explain the variation in species gradients (Table 5). The majority (94%) of the species variation in the Northern Province was accounted for by the explanatory environmental variables of mean growth days, mean minimum monthly temperatures and mean height above sea level.

The CCA results are graphed as a biplot, in which arrow length and direction indicate correlations between explanatory variables and CCA axes, smaller angles between arrows indicate stronger correlations between variables (ter Braak & Smilauer, 1998) (Figure 5). The dominant compositional gradient (axis 1) reflected an altitudinal gradient, which was primarily represented by mean temperature of the coldest month and mean elevation, from the tropical climate of the low lying savanna of the Lowveld to the subtropical savanna of the bushveld plateau. These two variables are moderately correlated with each other, but reflected low inflation factors in the CCA analysis therefore each was able to provide explanation for the species compositional gradients. With minor exceptions, the axis 1 gradient was generally longitudinal from the low lying Lowveld with mild winter temperatures up to the high lying Bushveld plateau areas with colder winter temperatures region (Figure 5).

The second CCA axis was a gradient in growing season moisture stress, from the areas of warm, dry growing seasons at lower elevations to areas of cooler, wet growing seasons (Figure 5).

Table 3: Eigenvalues and gradient lengths (1 Standard Deviation) for the first two axes from DCA and CCA of all bird species for the Northern Province.

	Axis 1		Axis 2	
	DCA	CCA	DCA	CCA
Eigenvalue	0.13	0.11	0.07	0.08
Gradient length	1.62		1.42	

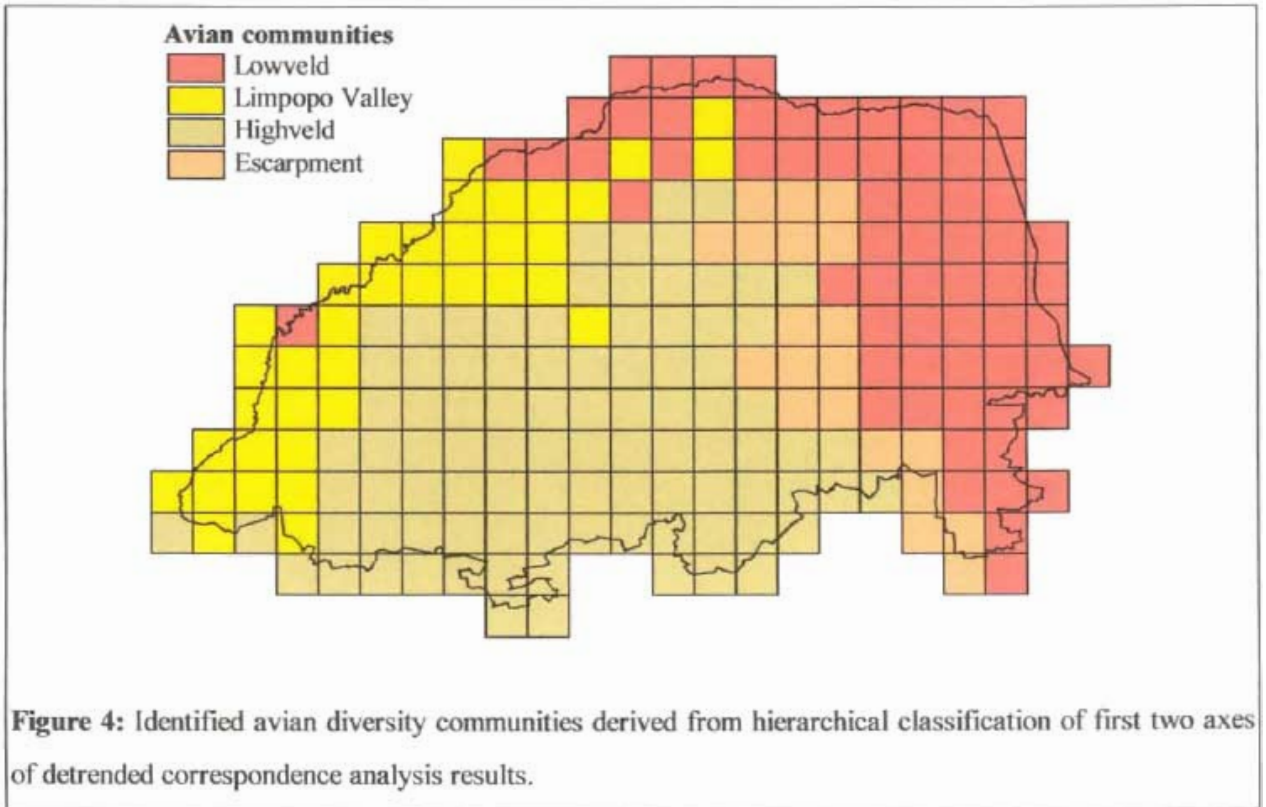
Table 4: Spearman's rank correlations of explanatory factors with axis scores from DCA and intraset correlation coefficients from CCA that included all explanatory variables.

	Axis 1		Axis 2	
	DCA	CCA	DCA	CCA
DEMMEAN	-0.4247	-0.6798	0.7551	0.6142
DEMSTD	0.1985	0.1187	0.6620	0.7095
GDMEAN	0.3270	0.231	0.6264	0.7783
MAP	0.2855	0.2178	0.5636	0.7313
GTMEAN	0.2302	0.4541	-0.8602	-0.7517
NGTMEAN	0.3445	0.5649	-0.8145	-0.7029
MAT	0.3945	0.6238	-0.7992	-0.6525
MAXMNTHMN	0.2317	0.4421	-0.8601	-0.7477
MINMNTHMN	0.5982	0.8155	-0.6034	-0.4416
EVANNMN	-0.6531	-0.581	-0.3561	-0.4908
PSEAS_MN	0.1677	0.0671	0.6040	0.7319
TSEAS_MN	-0.7629	-0.7482	-0.1321	-0.3065
MXSEAS_MN	-0.7907	-0.8054	0.0319	-0.1538

Table 5: Inter set correlations of environmental variables for step-wise CCA for first two axes

Variable	Axis 1	Axis 2
GDMEAN	0.1765	-0.6896
MINMNTHMN	0.8504	0.3393
DEMMEAN	-0.7279	-0.5627

Note: Sign reflects arbitrary selection of gradient direction by CANOCO. $P < 0.01$



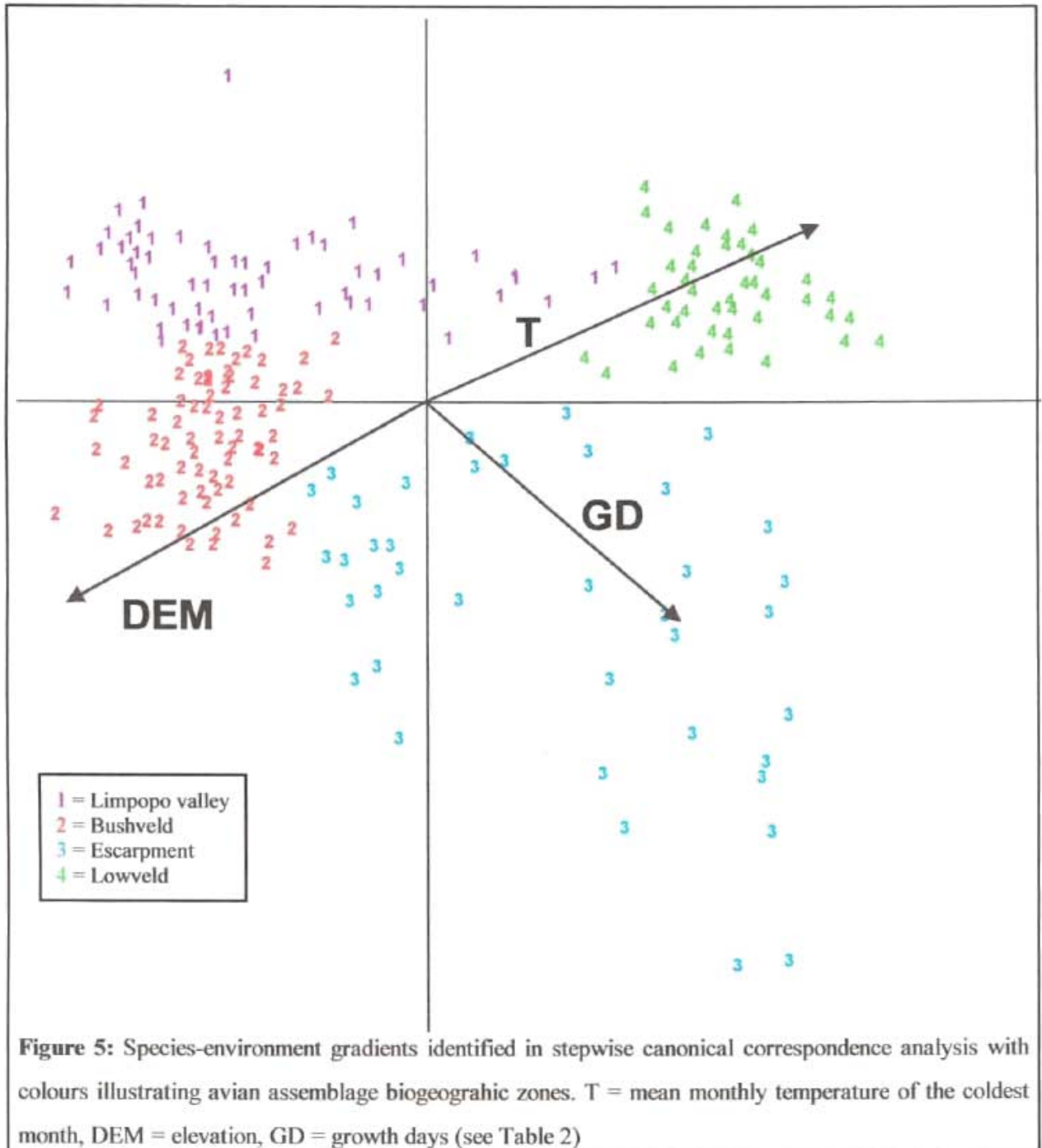
Areas of low summer precipitation and high summer temperature include the Limpopo river valley and the low lying Lowveld of the Kruger National Park. The Drakensberg escarpment represents the cool, high summer precipitation, with low evaporation leading to the longer positive water balance.

Spatial autocorrelation analysis

This form of analysis was performed on axis 1 and axis 2 of the CCA analysis (Figure 5). The resultant Moran I values for both axes were then combined for each grid cell, allowing for the analysis of the species-environment gradient spatial structure. This revealed strong positive autocorrelated clusters of similar species-environment composition in the Lowveld and western Limpopo river valley regions (Figure 6). The Lowveld region is a well-protected region as a result of the Kruger National Park (Figure 4). Negative and weak positive spatial autocorrelated clusters were found in the central Bushveld plateau region representing the Waterberg mountains and the Springbok flats, as well as the northwestern areas representing the Blouberg and Soutpansberg mountain ranges (Figures 1 & 6). These grid cells identify dissimilar species-environment compositions from their immediate neighbours and therefore represent areas of high species turnover of species along the identified environmental gradients. These areas also tended to have poor levels of protection.

Conservation area selection

The study region of 214 grid cells included 27 (12.6%) grid cells that were more than 25% protected. These fell mostly within the Lowveld region in the Kruger National Park, and represented 89.73% of the bird species recorded within the province. In order to represent the remaining species, 8.56, 12.83, 15.51 and 18.18% of the province was required by the richness-based, BD, richness-based with LUC and BD with LUC algorithms respectively (Table 6; Figure 7). The traditional richness-based algorithm, although the most efficient in that it represents all species in the least amount of land area possible, because of its selection criteria, concentrates on the areas of high species richness (Figure 3). By selecting these species rich areas mostly in the southern Escarpment and Bushveld plateau regions the richness algorithm tends to avoid areas of negative and weak positive autocorrelation in the northern and western Bushveld plateau (Figure 7). While the BD algorithm, although selecting similar grid cells to the richness algorithm, also selects areas of high turnover in species and environmental variables in these north and northwestern regions of the province (Figure 7). The selection orders of the grid cells by the two algorithms, illustrated in Figures 7a and 7b, demonstrate the different values accorded to each grid cell by the two different approaches. The traditional richness algorithm placing higher precedence on areas with high species richness in the southern regions of the province, while the BD algorithm gives priority to the grid cells in the northern and northwestern regions with high levels of species-environment turnover.



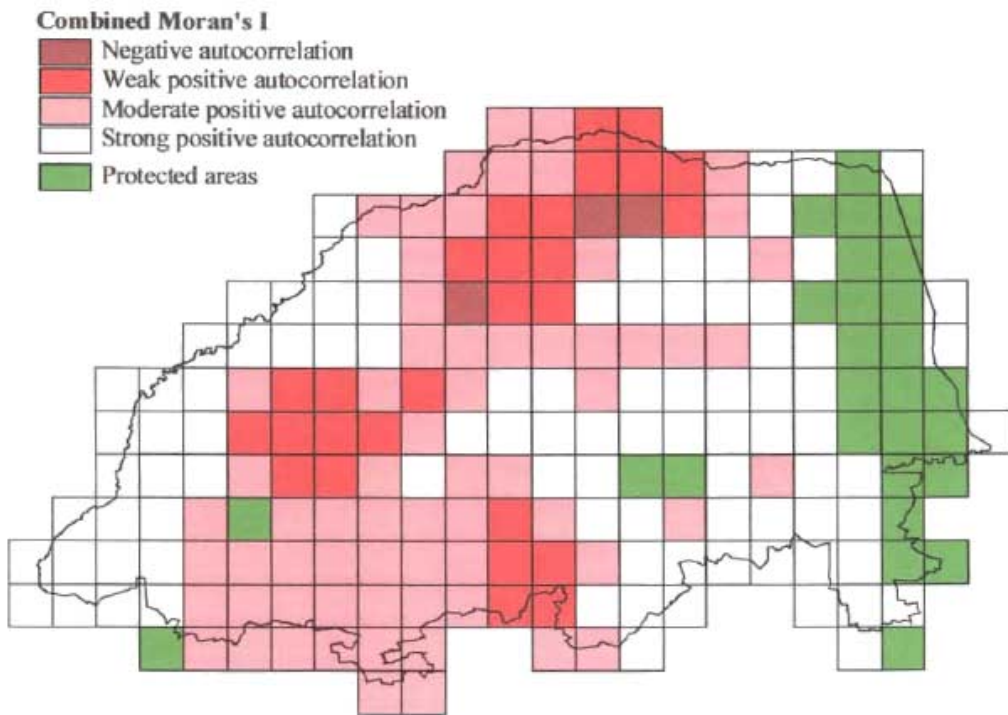


Figure 6: Moran's I spatial autocorrelation results for combined Moran's I axes 1 and 2.

Table 6: Results of reserve selection algorithms.

Algorithm type	Number and percentage grid cells selected (with 25% preselection)
Richness-based complementary	16 (8.56%)
Beta diversity (BD)	24 (12.83%)
Richness-based complementary with land-use constraint	29 (15.51%)
BD algorithm with land-use constraint	34 (18.18%)

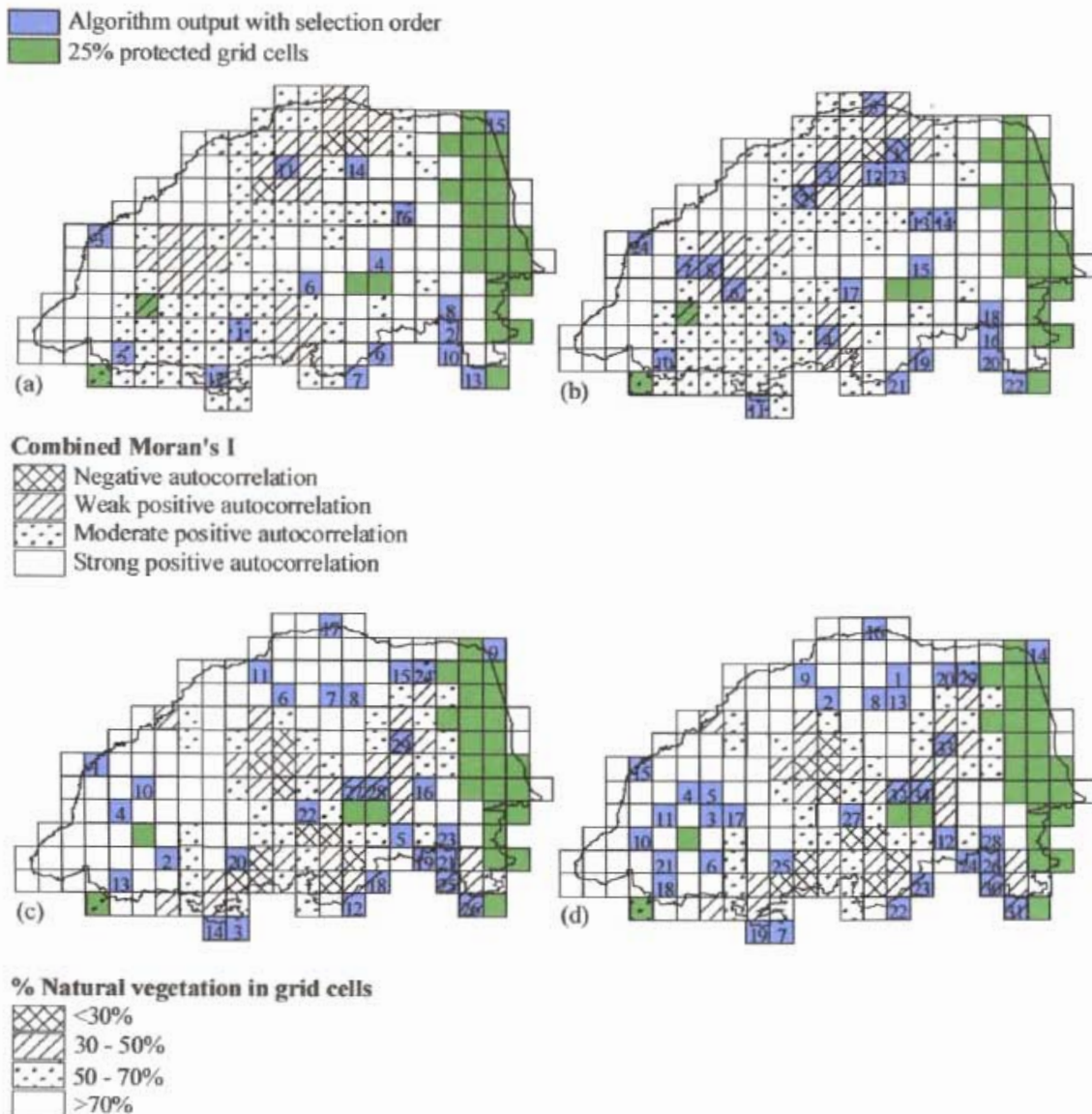


Figure 7: Output results for: (a) traditional richness-based complementary algorithm, (b) beta diversity algorithm, (c) traditional richness-based complementary algorithm with land-use constraint, and (d) beta diversity algorithm with land-use constraint. Illustrating degree of spatial autocorrelation within selected conservation area networks (a, b), and percentage of natural vegetation remaining in selected conservation area networks (c, d). Numbers in grid cells indicate selection order of grid cells by algorithms.

Once the land-use constraint is included, the level of efficiency decreases, but the amount of natural vegetation within the conservation area networks increases from 71.3 to 78.92% for the richness-based algorithm and from 74.53 to 80.7% for the BD algorithm (Figures 7 & 8). Although the difference may not seem large, the selection orders of the grid cells within the various networks demonstrate the different values accorded to the grid cells once the land-use constraint is included (Figure 7). The land-use constraint placing higher values on grid cells with low levels of land transformation in the northern and northwestern regions (Figures 7c & 7d)). There is therefore a trade off between land-use efficiency and the representation of species compositional and environmental turnover, as well as a trade off between this efficiency and the avoidance of largely modified and transformed areas.

Discussion

Traditional complementary approaches to conservation focus primarily on maximising the conservation of contemporary alpha diversity patterns using measures of species or feature richness (Pressey *et al.*, 1993, Margules & Pressey 2000). But as evidenced by the results of the present study, the use of traditional principles such as complementarity, flexibility and irreplaceability are not sufficient. Although they successfully represent existing biodiversity patterns, they do not guarantee the long-term maintenance of these patterns through conservation of governing natural processes, feature diversity turnover and the reduction of human driven threats on these patterns (Cowling *et al.*, 1999; Balmford *et al.*, 1998; Rodrigues *et al.*, 2000).

Maintenance of natural processes

Species, although an important component of the biodiversity hierarchy and a popular focus of many conservation efforts, should not be the only representation goal of conservation area selection (Faith & Walker, 1996a; Maddock & du Plessis, 1999; Noss, 1990; Pressey, 1994a; Wessels *et al.*, 1999). By focussing on only the species level many avian species communities and species-environment gradients important to avian diversity in the Northern Province are potentially ignored or left underrepresented. This underrepresentation results in an inefficient representation of overall regional biodiversity pattern and process.

Existing protected areas within the study area are concentrated mostly within the Lowveld region, most of which is made up by the Kruger National Park. This leaves the other avian communities largely unrepresented. The traditional complementarity based algorithm, does little to correct this representation bias selecting additional grid cells in the relatively homogenous southern Bushveld plateau regions, leaving the northern Bushveld plateau, Escarpment and Limpopo valley avian communities largely unprotected. This is due mostly to the fact that the Lowveld and southern Bushveld plateau regions are highly species rich areas (Figure 3) containing over 90% of the avian species recorded within the province.

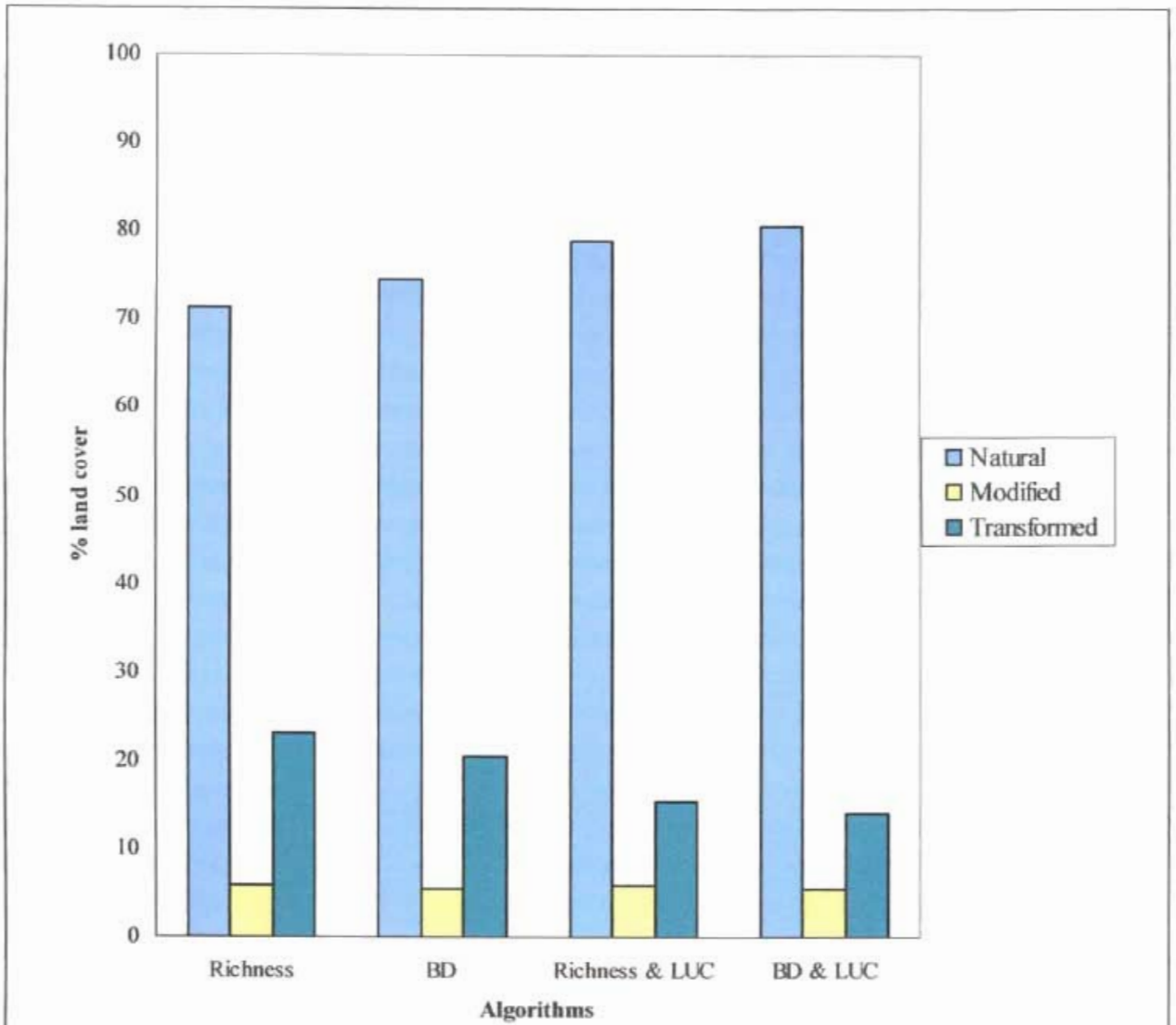


Figure 8: Graph of percentage land-cover categories included in conservation area networks selected by richness-based complementary algorithm and beta diversity (BD) algorithm (with and without land-use constraint (LUC)).

Thus, once these areas are represented, almost all of the avian diversity within the province is represented and from a species representation point of view there is no need for additional grid cells.

This makes the investigation and identification of the species community structure as well as the environmental gradients responsible for controlling and maintaining that structure an essential part of conservation area selection procedures. By attempting to protect not only the biodiversity pattern but also the processes responsible for that pattern, we come closer to guaranteeing the representation as well as the long-term maintenance of regional biodiversity. The grid cells selected by the new BD algorithm, although similar to those selected by the traditional algorithm, differ in that some grid cells fall within the other avian communities, particularly the highly heterogeneous areas in the northwestern and central Bushveld plateau community. These areas fall mostly within the Blouberg, Soutpansberg and Waterberg mountain ranges, as well as the Springbok flats region (Figure 1).

In addition to the underrepresentation of many of the avian species-environment communities by the traditional reserve selection procedures, it is obvious from the CCA analyses that they succeed in representing only one extreme of the CCA species-environment gradients. By focusing on species representation alone the low lying, moist, warm Lowveld region is well represented, but the dryer, higher lying, cooler areas with their unique species assemblages are excluded as well as the areas lying between these extremes. The role of the environment as a generator of species distribution patterns has long been a recognised fact (e.g. Whittaker, 1977; Wiens, 1989; Brown, 1995; Maurer, 1998). Fairbanks *et al.* (1996) presented evidence showing that the end points of species-environment gradients, areas where the climate is more stressful for life (overly cold, hot, or dry) (Jongman *et al.*, 1995), were found to be more strongly affected by climate change and therefore resulted in a possible species composition change. A South African climate change study conducted on invertebrate and vertebrate taxa estimated that 66% of all species found within the Kruger National Park, one extreme of the species-environment gradients, will have a less than 50% chance of being found there after a doubling of CO₂ levels (van Jaarsveld *et al.*, 2000). An issue often discussed but rarely applied in conservation biology regards the effect of climate change on current conservation areas and future conservation planning (Peters & Darling, 1985; Balmford *et al.*, 1998; Huntley, 1998).

Therefore, although the BD algorithm is less land-use efficient, requiring four percent more land area, it manages to represent high levels of species richness and avian communities, as well as the identified species-environmental gradients in the final proposed conservation area network. Thereby ensuring the representation of natural processes, and consequently the long-term maintenance of regional biodiversity in the face of less obvious human disturbances (e.g. climate change and altered fire regimes) as well as longer-term evolutionary and ecological processes (Balmford *et al.*, 1998; Cowling *et al.*, 1999).

Turnover in feature diversity

Spatial autocorrelation analysis proved to be a valuable tool in the identification of areas of high beta diversity, as opposed to employing simple measures of alpha diversity traditionally used by reserve selection techniques. Moran I values for both the altitudinal-temperature species-environment gradient of axis 1 and the water balance species-environment gradient of axis 2 from the CCA analysis (Figure 4) enabled the identification of areas high in beta diversity. These areas highlighted by low Moran I values contained very different species assemblages from their neighbouring grid cells, as well as different environmental variables controlling these assemblages. By focussing on grid cells with low levels of spatial autocorrelation, the BD algorithm identified areas with highly dissimilar species, community, and environmental compositions from neighbouring grid cells in the Waterberg, Blouberg and Soutpansberg mountain ranges as well as the Springbok flats region. These areas contain unique environmental characteristics not found in surrounding areas. The northern mountain ranges of the Blouberg and Soutpansberg are the meeting point of the southern limit of the Zambezi flora and the northern limit of the South African faunal and floral species. The Springbok flats is a basin surrounded by the Waterberg and escarpment in the Northern Province and by the Magaliesberg, a mountain range in the Gauteng Province which lies to the south of the study area. Due to its clay substrate the basin has poor drainage and contains wetlands as well as part of the Olifant River in the east and is therefore considered a birding hotspot. Thus these regions identified by the spatial analysis are important areas with unique species assemblages and environmental characters and are sites of high turnover in species diversity along the identified environmental gradients.

The different selection orders (Figure 7) of the richness-based and BD algorithms illustrate the highly dissimilar approaches and values assigned to each grid cell by the two algorithms. The traditional richness method favouring areas of high species richness (Lowveld and southern Bushveld regions) and the BD method placing more importance on areas containing highly dissimilar species and environmental compositions from surrounding areas (northern and central Bushveld plateau). In order to identify conservation area networks that are robust to turnover in feature diversity, the identification of dominant environmental gradients controlling turnover in species composition using ordination techniques like CCA is important for understanding future environmental sensitivities and evolutionary potential (Cowling *et al.*, 1999; Noss, 1996). This spatial autocorrelation method allows for the incorporation of measures of beta diversity into what are traditionally alpha diversity based reserve selection techniques. The results of the present study illustrate the value of the inclusion of areas with high levels of alpha and also beta diversity. The mountain ranges and other regions highlighted by these analyses are areas of high turnover in avian diversity along unique environmental gradients, and under the existing protected area system are left largely unprotected.

Minimising threats

Since the early 1900's the area of cultivated land within South Africa has increased from 3 to 8% (Scotney *et al.*, 1988). Despite this increase the Northern Province remains largely untransformed and includes many land-uses considered to be more amenable with biodiversity conservation (Pressey, 1992), e.g. wildlife reserves, game ranching and livestock grazing. Including these largely untransformed areas into potential conservation areas and attempting to avoid conflict with other land-uses entails selecting a larger area. However, minimising land area requirements through efficient complementarity approaches often involves selecting highly transformed areas that may not be able to sustain species or ecological processes over the long-term (Freemark, 1995). These areas are therefore impractical conservation options and should be precluded from conservation area networks (Wessels *et al.*, 2000 (Addendum II)).

The present study does not demonstrate a large difference in the proportion of transformed land within conservation areas (seven percent difference) selected by techniques with or without the land-use constraint. This is probably due to the fact that the Northern Province, with over 70% natural land-cover, does not contain large areas of transformed and degraded land, thus the chances of selecting transformed land during reserve selection is rare. However, the selection order of the grid cells by the various algorithms illustrates how the land-use constraint gives preference to largely untransformed areas in the northern and western regions of the study area. It attempts to avoid the Springbok flats with high levels of commercial dryland cultivation, as well as the central, southwestern and escarpment regions with combinations of commercial and subsistence dryland cultivation and the associated erosion and degradation. The LUC algorithms select grid cells with less than 50% natural vegetation in these transformed and degraded regions only as a last resort if the species they contain are not present in any of the other less transformed grid cells.

This is similar to the finding by Nantel *et al.* (1998) and Wessels *et al.* (2000) (see Addendum II) that it is often the irreplaceable grid cells, containing some of the rarest species, which are more potentially conflicting than others, being closer to human populations, infrastructure and agriculture. This then enables one to investigate the potential conflict between conservation interests and land-uses within these irreplaceable grid cells at a local scale. Appendix 1 contains a list of the species found only within grid cells that are more than 50% transformed and is an example of how local scale potential conflict issues can be highlighted, specifically in the case of threatened and endangered species (Wessels *et al.*, 2000 (see Addendum II)). Fortunately in the case of the Northern Province it would appear that of the seven bird species found only within these transformed and irreplaceable cells in the study region, most do in fact occur elsewhere in southern Africa and often in the rest of Africa. The Ground Woodpecker, a globally threatened species, and the Caspian Tern, listed as rare in the South African Red Data Book are the only species of special conservation interest, but occur either widely in South Africa or else in the rest of the world. The Bluespotted Dove and Grey Waxbill require monitoring, but are not particularly threatened (Harrison *et al.*, 1997).

Conclusion

South Africa, ranked as one of the top 25 richest countries in the world in terms of its biodiversity (WCMC, 1992), faces large threats through human land-use and transformation (Macdonald, 1989; Fairbanks *et al.*, 2000). Existing conservation measures required to address and prevent these land-use changes are largely inadequate, with much of the country's biodiversity wealth lying outside of formal protected areas (Rebelo & Siegfried, 1992; Freitag *et al.*, 1998). This inadequacy of existing conservation measures is not unique to South Africa and is in fact a worldwide phenomenon. The techniques required to redress this issue are largely inadequate and seldom implemented. The issues of process and pattern maintenance, turnover and land transformation that we attempted to address proved to be important issues in reserve selection.

The benefits of the current generation of iterative complementarity based reserve selection algorithms are well-cited (Pressey *et al.*, 1993). These techniques do have their value and are an improvement on the largely *ad hoc* methods of the past. However the shortcomings associated with the use of these techniques alone are obvious and are a major contributor to their lack of implementation in conservation and land-use planning. The framework of complementarity analysis makes a large contribution to assessing the selection of important species assemblages for conservation, but extending this tool to capture the underlying processes ensures the maintenance of those assemblages.

The ordination and spatial structure additions to traditional complementarity based algorithms make several contributions to biodiversity conservation. These additions improve our knowledge on important environmental factors responsible for biodiversity patterns. They also identify species and environments that are currently underrepresented or threatened, as well as areas of high species turnover along the associated environmental gradients, areas which are often severely vulnerable to land transformation. By protecting these areas we can allow for possible changes in species turnover due to climate change, something which would not be possible using only species-based conservation area identification.

The benefit of maximising the area of natural habitat within a conservation area network carries with it the cost of higher land area requirements. However the inclusion of a land-use constraint makes for far more feasible conservation options by including largely untransformed areas into conservation networks. The identification of potential conflict within areas that are irreplaceable in terms of biodiversity conservation and also largely transformed is an important component of regional biodiversity assessments (Wessels *et al.*, 2000 (see Addendum II)). This enables the identification of crucial habitats within these areas required for the continued survival of specific species, as well as the investigation of land-use circumstances within the ranges of other important species.

However, it is unlikely that all the areas identified within these analyses can be formally protected. The future of conservation in South Africa, as in many other developing countries, is uncertain. The lack of resources for the expansion of current formal protected areas in an effort to

address the inadequate conservation efforts existing, evidenced by the largely biased current representation of the Lowveld region only in the Northern Province, is not the only problem facing South African conservation efforts. Land reform proposals and the redistribution of privately and state owned land to small-scale subsistence farmers could potentially conflict with conservation objectives. But, the development of effective and scientifically sound techniques for the identification of areas important to conservation need not only be limited to the expansion of existing formal protected areas, but also has an important role to play in the identification of conservation areas to be managed in the human matrix outside of formal protected area networks.

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Appendix I: Range and conservation status of avian species restricted to grid cells with less than 50% natural vegetation.

Common name	Species name	Grid cell % natural land- cover	Conservation status	Range
Bluespotted Dove	<i>Turtur afer</i>	2330AB (30-40%); 2330CC (30-40%)	Locally common. Population monitoring required	Restricted range in eastern Zimbabwe, adjacent Mozambique and northeastern South Africa.
Caspian Tern	<i>Hydroprogne caspia</i>	2330AD (30-40%)	Rare in the South African Red Data Book	Occurs throughout the holoartic, Australasian, Oriental and Afrotropical regions
Goldenrumped Tinker Barbet	<i>Pogoniulus bilineatus</i>	2531AA (40-50%)	Common in forest habitat. Not threatened	Widespread African species. Occurs in the eastern lowlands of South Africa, lowland forest of eastern Zimbabwe & Zimbabwe highlands, as well as Mozambique.
Grey Wagtail	<i>Motacilla cinerea</i>	2329DD (40-50%)	Regular occurrence in southern Africa.	Non-breeding African palaearctic migrant. Common in Africa as far south as northern Tanzania.
Grey Waxbill	<i>Estrilda perreini</i>	2230DA (50-60%)	Not particularly threatened but worth monitoring in southern Africa.	Occurs in Gabon, Angola and Zaire eastwards to Tanzania and Mozambique, and southwards to South Africa.
Ground Woodpecker	<i>Geocolaptes olivaceus</i>	2430DD (40-50%)	Globally near threatened. Wide range	South African endemic
Southern Tchagra	<i>Tchagra tchagra</i>	2430DD (40-50%)	Fairly common in its restricted range. Not of particular conservation concern.	Southern African endemic

Harrison *et al.*, (1997)