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Capturing biodiversity: selecting priority areas for conservation using different criteria

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Abstract. International treaties call for the protection of biodiversity in all its manifestations, including ecosystem and species diversities. The selection of most priority area networks focuses, however, primarily on species richness and occurrence. The effectiveness of this approach in capturing higher order manifestations of biodiversity, that is ecosystem and environmental diversity patterns, remains poorly understood. Using a case study of birds and environmental data from South Africa and Lesotho, we test how complementary networks that maximise species diversity perform with regard to their representation of ecosystem and environmental diversity, and vice versa. We compare these results to the performance of the existing reserve network. We conclude that focusing on any single biodiversity component alone is insufficient to protect other components. We offer explanations for this in terms of the autocorrelation of species diversity in environmental space.

Introduction

Global biodiversity is being lost at an unprecedented rate, as a consequence of human induced environmental change (Pimm et al. 1995). In order to protect biodiversity in all its manifestations (Convention on Biological Diversity, IUCN 1992), priority areas for nature conservation are to be recognised and networks of protected areas established and maintained. But what should these protect? The Convention on Biological Diversity explicitly defines biodiversity as a hierarchical concept, with three principal organisation levels: genetic, species and ecosystem diversity. Ecosystems at the highest level form "interacting systems of biotic and abiotic components" (Glowka et al. 1994) and "... comprise both the communities of organisms within particular habitats and the physical conditions under which they live" (Wilson 1992). Therefore, it is important to protect not just genotypes and species, but also the non-living environment. Protected area networks should adequately represent environmental as well as species diversity (Noss 1990). Maximising environmental diversity within conservation networks, that is maximising the range of suitable living conditions for different species, should guarantee the representation of a diversity of species (Faith and Walker 1996), also of little known or mapped species. The protection of a wide span of environmental variation may also ensure the long-term persistence of species by allowing adaptive response to future change (Channell and Lomolino 2000; Smith et al. 2001; but see Araujo 2002).

Guidelines for the selection of priority areas for conservation, however, have focussed principally on species protection, and especially that of rare or endangered species (e.g., Bibby et al. 1992; Stattersfield et al. 1998; Myers et al. 2000). Indeed, the extensive literature on the development of methods for the selection of priority areas has focussed on finding the minimum set of areas that represent all species in occurrence locations (Williams 1998; Cabeza and Moilanen 2001), or, recently, on finding appropriate areas that maximise probabilities of species persistence (Rodrigues et al. 2000; Williams and Araujo 2000; Araujo et al. 2002; Bonn et al. 2002). This view has become so predominant, that the performance of existing protected area systems is commonly measured in terms of the proportion of the regional, threatened or endemic species pool that it encompasses (Siegfried 1989; Lombard 1995; Eeley et al. 2001; Moore et al. 2003). However, as complete representation of overall species diversity will not be achieved by areas selection based on indicator groups alone (see e.g. Moore et al. 2003), it may be wise to incorporate information on environmental diversity to capture also all rare or endemic species whose occurrence may correlate with special environmental characteristics of their habitat.

Arguments for conservation planning and evaluation to focus attention on ecosystems and environmental diversity have principally concerned the paucity of data on patterns of species occurrence in some of the most important regions for conservation. On the grounds that this is all that can be done and/or that environmental diversity should act as an effective surrogate for patterns of biodiversity at lower organisational levels (Belbin 1993; Folke et al. 1996; Noss 1996a, b; Cowling et al. 1999; Fairbanks and Benn 2000; Faith 2003), several area selection activities have been suggested. They have been discussed or conducted in terms of a variety of higher level organisational units, for example land facets (Wessels et al. 1999), land types (Pressey and Taffs 2001), geomorphological heterogeneity (Nichols et al. 1998), environmental diversity (Faith and Walker 1996), environmental units (Pressey et al. 1996), environmental classes (Woinarski et al. 1996) and ecosystems (Noss 1996a, b). However, the effectiveness of priority areas for conservation identified at one level of organisation in adequately capturing diversity at another level remains poorly understood. In this study, using birds of South Africa and Lesotho, we explore whether complementary networks aiming to maximise either species diversity (*SD*) or environmental diversity are successful in representing one another. For environmental diversity we employ three measures, using remotely sensed abiotic data (*ED*), and pre-classified environmental information on habitat diversity (vegetation types) and ecosystem diversity (biomes).

Data

Environmental data

South Africa and Lesotho incorporate a wide range of environmental conditions, including climate, topography and vegetation cover. They extend over 12° latitude

Table 1. Eigenvalues for the first four axes from principal component analysis (PCA) and intraset correlation coefficients of explanatory factors (see text) with axis scores.

	Axis 1	Axis 2	Axis 3	Axis 4
Energy related variables				
PET	−0.92	−0.17	−0.15	−0.09
SRAD	−0.77	0.11	−0.49	−0.03
Climate				
Mean annual temperature	−0.22	−0.96	0.00	−0.02
MAX_ temperature	−0.47	−0.82	−0.15	−0.03
MIN_temperature	0.07	−0.97	0.15	−0.01
Seasonal temperature variation	−0.79	0.25	−0.38	−0.07
Mean annual precipitation (PPT)	0.94	−0.05	−0.19	−0.07
MAX_PPT	0.86	−0.06	−0.41	0.00
MIN_PPT	0.17	0.05	0.81	−0.22
Seasonal PPT variation	0.68	−0.10	−0.69	0.04
Topography				
Elevation_Mean	0.14	0.73	−0.63	−0.03
Elevation_Range	0.59	0.38	0.46	−0.01
Slope_Mean	0.62	0.42	0.42	−0.03
Aspect_Mean	−0.25	0.10	−0.16	−0.92
Vegetation				
NPP (half degree)	0.84	−0.29	−0.35	−0.04
LAI (half degree)	0.83	−0.24	−0.34	−0.10
NDVI_July	0.73	−0.27	0.39	−0.19
NDVI_January	0.91	−0.18	−0.24	−0.05
Eigenvalues (cumulative)	0.45	0.66	0.83	0.88

and 16° longitude. The resolution of the data used for analysis was at a quarter degree ($15' \times 15' \approx 676\,\mathrm{km}^2$) for a total of 1858 grid cells. For each grid cell, data were obtained for 19 environmental variables relating to topography, climate and energy availability (Table 1). Selection of variables was based on those shown previously to be biologically meaningful in relation to species distributions (e.g., Currie 1991; Fairbanks et al. 2001; van Rensburg et al. 2002).

Climate and energy related data were taken from monthly time series for the last 30–50 years supplied by the South African Computing Centre for Water Research (Schulze 1997), based on interpolated climate surfaces. These were mean annual potential evapotranspiration (PET; an unscreened A-Pan equivalent; mm yr^{-1}) and mean annual solar radiation (SRAD; $\mathrm{MJ\,m^{-2}\,yr^{-1}}$). For temperature (°C) and precipitation (PPT; $\mathrm{mm\,yr^{-1}}$) we included: mean annual measurements, mean absolute monthly minimum (MIN_) and mean absolute monthly maximum (MAX_) and the seasonal variation as the difference between the former values. The HYDRO1k database, developed at the U.S. Geological Survey's (USGS) EROS Data Center, was used as a digital elevation model (DEM) to calculate the topography variables, elevation, slope and aspect. As a measure of primary productivity, data were used on mean annual Net Primary Productivity (NPP; $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) and

Leaf Area Index (LAI, total one-sided leaf area per unit area of ground) based on model simulations by Woodward et al. (2001). These data were available only at a half degree grid resolution. At quarter degree resolution, a 9-year mean index of primary production based on satellite data, Normalised Difference Vegetation Index (NDVI), was obtained from the African Real Time Environmental Monitoring using Meteorological Satellites program (ARTEMIS) of the Food and Agriculture Organisation (FAO). Here, information for the first decade in January and the first decade in July was compiled.

Information was also used on the cover of 68 vegetation types (Low and Rebelo 1996), as vegetation type is a prime determinant of ecosystem type (Peters 1992), driving patterns of the associated fauna and soil microbiota. The vegetation types are classed into seven biomes. Within these biomes, Low and Rebelo (1996) included a 'Thicket biome' as a separate classification, although it is not formally recognised in scientific literature, they regarded it to be distinct from 'Forest' and 'Savanna'.

Bird data

Birds have been shown to be the most representative taxon to predict complementary patterns of occurrence in other vertebrate taxa within the study region (Lombard 1995). Therefore, to assess the representation of species diversity within hypothetical priority area networks, we considered a total of 651 native species excluding marine, vagrant, marginal and introduced or escaped species from the analysis. Information was derived from the Southern African Bird Atlas Project (SABAP; Harrison et al. 1997) which provides the most comprehensive and detailed information 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 this analysis we used presence/absence data and peaks of abundance based on reporting rates. Reporting rates were calculated for each species in each cell as the proportion of check lists submitted for that cell on which the species was recorded. Peaks of reporting rates for each species were defined as cells with reporting rates of $\geq$80% of the maximum value observed for that species. We assumed these peaks to correspond to peaks of abundance (Robertson et al. 1995; see also Gaston and Rodrigues 2003). Grid cells containing these peaks of abundance correspond on average to 5.8% of the total number of records for each species.

Methods

Networks

Complementary networks (Pressey et al. 1993; Margules and Pressey 2000) were identified to address the following management goals: (i) representation of all native bird species, preferably in grid cells with large local population sizes (species diversity, *SD*), (ii) representation of environmental diversity (*ED*), and

(iii) representation of all native habitats (*HD*). In addition, for comparison with real-world applications, we evaluated the performance of (iv) the existing reserve network within the study region. Using the 117 grid cells of the existing reserve network as a yard stick (6.3% of total area, see below), representation targets were set to aim for a similar number of grid cells in each network.

(i) *Complementary networks for species diversity (SD).* For maximising species diversity, complementary networks were obtained representing all bird species in the minimum possible number of grid cells. We evaluate two scenarios: (a) SD_{occ} and (b) SD_{peak}. Using presence/absence data, SD_{occ} networks were selected to represent all bird species within at least six occurrences (or the maximum possible) locations (see Rodrigues et al. 2000). This approach may imply an overly optimistic representation of species diversity, as some species might only be represented in sites inadequate to ensure their persistence, for example in marginal sites of their distribution (Gaston et al. 2001). Therefore, taking viability concerns into account, SD_{peak} networks were selected that represent all bird species in at least one peak abundance location.

(ii) *Complementary network for environmental diversity (ED).* To maximise the representation of environmental diversity (*ED*) within a network, representative sites from an environmental space matrix were chosen. First, variation of the 19 environmental variables was summarised in an environmental space matrix using Principal Component Analysis (PCA), after standardisation of data to zero means and unit variances (Table 1). Axes were weighted by their respective eigenvalues to take into account the different contribution to sampling variation in environmental space. In this way, the importance of the first axis was increased in relation to the other axes, since distance in space was increased. Second, a *k*-means cluster analysis was employed to identify homogeneous groups of cases within the space matrix. This non-hierarchial clustering algorithm can handle a large number of cases within a short time span (SPSS v.10.0. software). It forms a specified number of clusters of sites in environmental space (999 iterations), minimising the Euclidean distances between all points in the matrix, and then defines centroids, that is the means of the clusters. For the *ED* network selection, the closest site to each centroid was taken as representative of each cluster.

(iii) *Complementary networks for habitat diversity (HD).* As a contrasting approach to (ii), which uses solely remote sensing data, we based network selection on information on pre-classified environment units, that is vegetation types. Complementary networks were calculated to include at least two representative grid cells for each vegetation type which exhibited a coverage of $\geq$50% (or the maximum possible) of this vegetation type.

(iv) *Existing reserve network.* Size and location details were available for 264 reserves, based on the 1997 United Nations list of protected areas for South Africa (WCMC 1997, see http://www.wcmc.org.ukindexshock.html). The 264 reserves are located within 485 quarter-degree grid cells, each covering 0.1–99% of the respective grid cell areas. As information on all environmental variables as well as species records were not available on a site-specific basis, we focussed our analyses on those 117 grid cells that had reserve cover of $\geq$20%. For these grid cells, we assumed the reserves to have the same characteristics as the entire grid cell in which they reside. Throughout this paper, the term existing reserve network will refer to these 117 grid cells.

For the *SD* networks and the *HD* network, several optimal solutions are possible. Therefore, 10 randomly selected optimal solutions were attained using C-PLEX software (ILOG 2001). As a null-model, 1000 randomly selected networks of 117 grid cells were chosen.

Evaluation of network performance

To evaluate the effectiveness of each network we employed four measures: environmental, habitat, ecosystem and species diversity.

(i) *Environmental diversity.* The effectiveness of each network in representing *ED* was evaluated by comparing the frequency distribution of the network areas to that of all grid cells (1858) within environmental space, that is along the first four PCA axes. Because the number of grid cells along the PCA axes were non-normally distributed, random draws were accomplished. From the distribution of all grid cells random samples of size n were drawn without replacement ($n =$ number of sites tested, e.g., 117 for the existing reserve network). For 10,000 permutations, the 95% confidence intervals for the mean values of the mean, minimum, maximum and the range of the PCA scores were calculated and compared to the corresponding values of the tested networks.

(ii) *Habitat diversity.* We assessed how effective networks represent habitat diversity by their incorporation of grid cells for each vegetation type, with a respective coverage of (a) $\geq$50% or (b) $\geq$25% (or the maximum possible).

(iii) *Ecosystem diversity.* The effectiveness of each network in representing ecosystem diversity was evaluated by comparison of the proportional size representation of biomes within each network with their actual cover in South Africa and Lesotho.

(iv) *Species diversity.* To assess how effective networks represent *SD*, we used the proportion of bird species (out of 651) represented in each network using presence/absence data. As a second measure, we used the number of birds represented in peak abundance locations.

Results

Ordination analysis – environmental space

The first four PCA axes summarise the variation in environmental diversity of our data set (total eigenvalue of 0.88, Table 1). The first dominant compositional

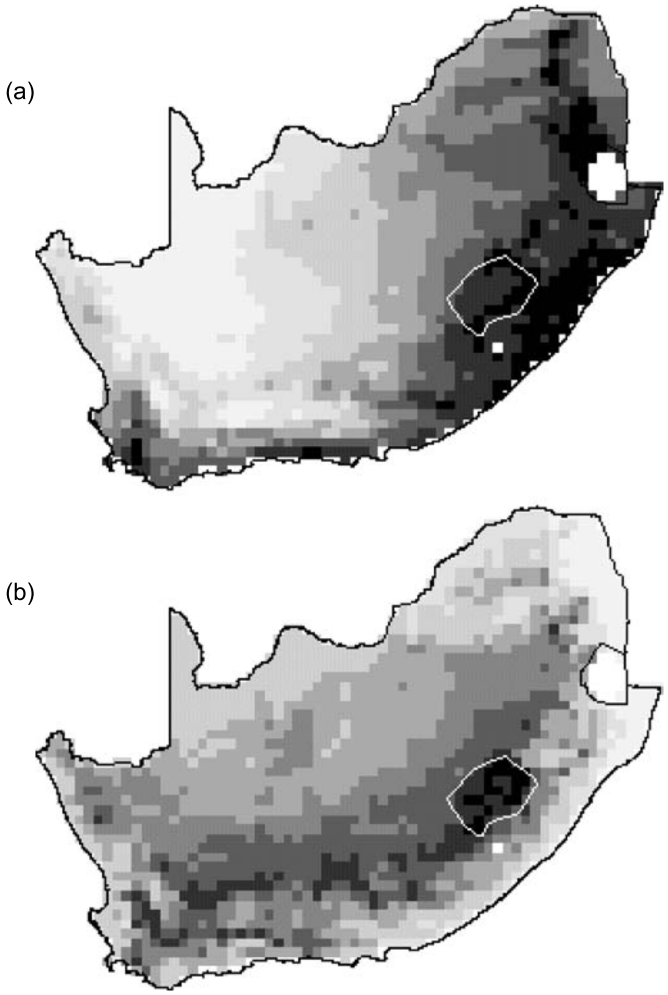

Figure 1. Geographic patterns of the PCA scores (see Table 1) within the study area for the first two principal component axes, reflecting (a) gradients of aridity and productivity, and (b) temperature and elevation. Darker shades of grey indicate higher values (eight equal interval classes).

gradient reflects a strong east–west gradient in aridity and oceanity in South Africa and Lesotho. This shows the transition from the Succulent Karoo and Nama Karoo biomes in the east with elevated solar energy input levels, indicated by potential evapotranspiration (PET) and solar radiation (SRAD), towards Grassland and Savanna habitats in the west with rising precipitation and primary productivity and less pronounced climatic extremes expressed by seasonal temperature variation (Figure 1a). The second PCA axis reflects a gradient in temperature that is in reverse to an altitudinal gradient (Figure 1b).

Table 2. Comparison of distributions of networks in relation to the 95% confidence intervals of corresponding random draws from all grid cells along the first two PCA axes. Complementary networks: SD_{occ} and SD_{peak} selected for maximising bird species diversity within at least six occurrences or 1 peak abundance location, respectively and *HD* for maximising habitat diversity (vegetation types). Departures of distribution parameters: + bigger than upper 2.5% tail; −smaller than lower 2.5% tail; ns non-significant; actual value given only for means.

Networks	PCA axis 1			PCA axis 2		
	Mean	Variance	Range	Mean	Variance	Range
SD_{occ}	+(0.58)	ns	ns	−(−0.18)	−	+
SD_{peak}	+(0.57)	ns	ns	−(−0.64)	+	ns
HD	+(0.31)	ns	ns	−(−0.27)	ns	ns
Existing reserves	+(0.43)	ns	ns	−(−0.62)	−	ns

Representation of environmental diversity

The complementary networks maximising species diversity, SD_{occ} and SD_{peak}, do not share the same distribution pattern as the community of all grid cells in environmental space (Table 2, Figure 2a, b). The same is true for the *HD* network and the existing reserve network (Figure 2c, d). For all four networks the means of the distributions are significantly shifted towards more positive values along PCA axis 1 and towards more negative values along PCA axis 2 (Table 2).

Nevertheless, all networks cover the whole range of environmental conditions along all four composite gradients, and also have the same variance, at least for PCA axis 1 (Table 2). Thus, the networks are well dispersed in environmental space and at least some network grid cells are always located at the maximum and minimum of the composite environmental gradients.

Representation of habitat diversity

The two complementary *SD* networks and the existing reserve network represent only half or less of the vegetation types in grid cells with a respective vegetation cover of $\geq$50% (Table 3). Even for less strict representation goals ($\geq$25% grid cell cover), all three networks do not perform better than a random selection of grid cells. The *ED* network performs best in representing the variety of habitats. Nonetheless, it represents only 60% of all vegetation types in grid cells with a respective cover of $\geq$50%, but up to 78% in grid cells with a respective cover of $\geq$25%, although the performance does not differ significantly from a selection by chance ($p < 0.05$, Table 3). The ED network mainly misses some rare vegetation types but also a few dominant types, for example 'Great Nama Karoo' or 'Rocky Highveld Grassland'.

Representation of ecosystem diversity

Within the two *SD* networks and the existing reserve network the proportional size representation of biomes differs from their actual distribution in the study area

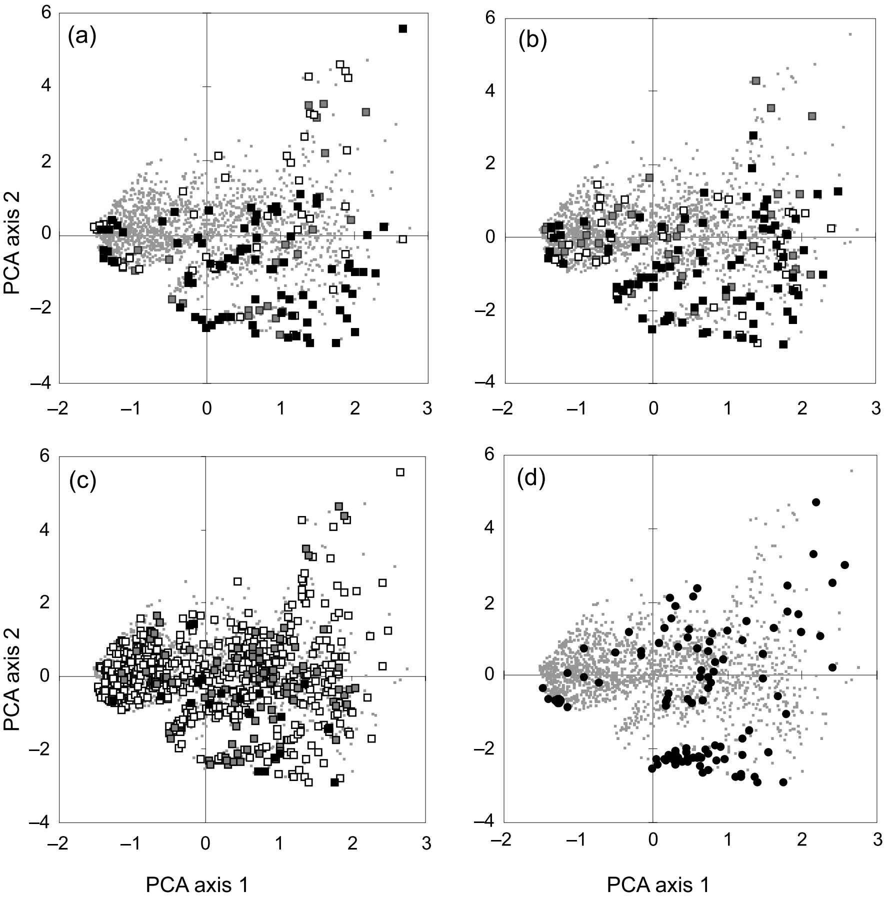

Figure 2. Location of networks within environmental space described by the first two PCA axes. Small grey points mark all 1858 grid cells. For the complementary networks (a) SD_{occ}, (b) SD_{peak} and (c) HD different coloured squares indicate the frequency of the respective grid cells within the 10 replicate selections of complementary networks (white: 1–4×; grey: 5–9×, black: 10×). This illustrates the flexibility of sites within the networks, with black squares representing the least replaceable cells. For (d) the existing reserve network, black circles indicate the 117 grid cells with a reserve cover $\geq$20%.

(Figure 3). This effect is also true but less pronounced within the *HD* network and the *ED* network. Within the existing reserve network, the biomes Grassland and Nama Karoo are underrepresented. Both *SD* networks, the *ED* network and the *HD* network, however, suggest a higher necessary cover in order to represent species as well as environmental diversity adequately.

There was a marked difference between the performance of the complementary networks: For Savanna, for example, the SD_{occ} and SD_{peak} networks select more grid cells than expected by chance, the *ED* network, however, selects fewer grid cells (light grey columns, Figure 3). The opposite is true for the Fynbos biome

Table 3. Proportional representation of 68 vegetation types and 651 bird species within different networks and areas selected at random. Representation of vegetation types was tested for grid cells containing each vegetation type with a respective cover of ≥50% or ≥25% (or the maximum possible). Representation of birds was tested for occurrence and peak abundance locations (grid cells = number of grid cells per network; *n* = number of solutions per network; means are given for each network with standard deviation in brackets, upper 5% tail is given for 1000 permutations of random selection).

Networks	Grid cells	*n*	Representation goals			
			Vegetation types		Species	
			>50% (%)	>25% (%)	Occurrence (%)	Peaks (%)
SD_{occ}	109	10	48.7 (1.3)	66.5 (0.9)	100	55.5 (2.1)
SD_{peak}	119	10	53.7 (2.1)	68.8 (1.9)	100	100
ED	117	1	60.3	77.9	95.7	31.2
HD	121	10	100	100	97.3 (0.1)	47.2 (0.1)
Existing reserves	117	1	44.1	58.8	98.3	44.9
Random	117	1000	61.8	77.9	96.8	43.9

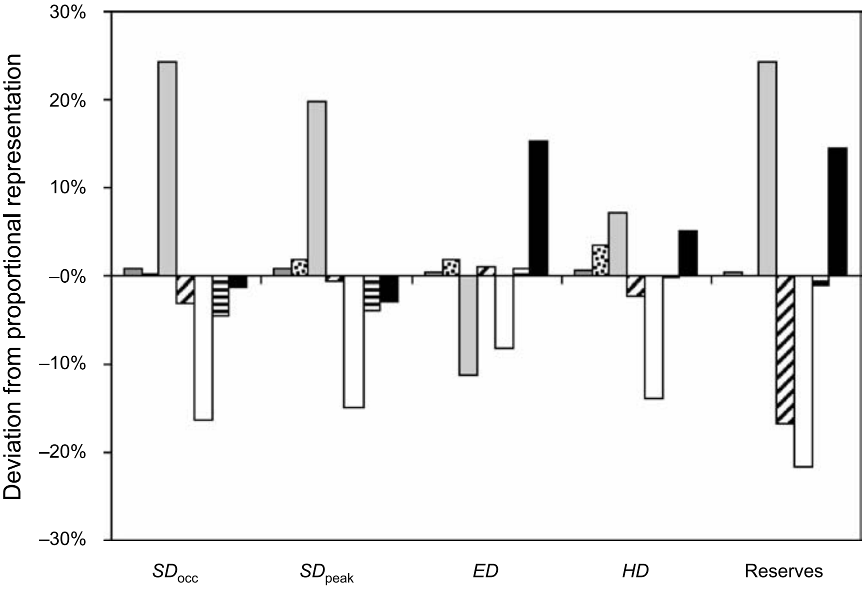

Figure 3. Deviation of the networks from a proportional size representation of the biomes. Different columns indicate the biomes: Forest (dark grey), Thicket (dotted), Savanna (light grey), Grassland (horizontally hatched), Nama Karoo (white), Succulent Karoo (hatched), Fynbos (black). Positive values indicate that a biome is overrepresented within a network, negative values indicate a proportional underrepresentation. As we consider only part of the existing reserves, proportions given might slightly differ in detail (for more concise data on biome coverage see e.g., Siegfried 1989; Lombard 1995; Barnes 1998).

(black columns, Figure 3). Within this biome, the environmental diversity needs to be represented by more sites than the proportional equivalent, while, at least, bird species diversity seems adequately covered by a proportional representation. Therefore, the number of sites necessary to sufficiently represent either species diversity or environmental diversity may differ for different biomes and deviate from a proportional allocation.

Representation of species diversity

The networks based on information other than species records represent species diversity in occurrence locations reasonably well (Table 3). However, even a random selection of 117 grid cells, that is 6.3% of the study area, achieves a mean representation of 95% of all species in occurrence locations. Therefore, *ED* areas do not represent significantly more species than expected by chance ($p < 0.05$).

Taking viability concerns into account, the performance of all networks is little satisfactory as peak abundance locations of species are poorly represented (Table 3). Even the SD_{occ} network represents peak abundance locations for only little more than 50% of all birds. Performance of the *HD* network and the existing reserve network are comparable, both capturing peak abundance locations for less than 50% of all birds. These results are, however, significantly better than a random selection of grid cells ($p < 0.05$), which is not true for the *ED* network performance.

Discussion

Complementary patterns of species diversity cannot act as complete surrogates for environmental diversity, and vice versa. Therefore, designing protected area networks using surrogate information on species, habitats or environmental data alone will not guarantee the full maintenance of other biodiversity features. However, there are differences in the success of different hierarchical levels of biodiversity in predicting others, that is species or environmental diversity.

Species diversity as surrogate for environmental diversity

Complementary networks designed for species sampled environmental space (*ED*) reasonably well. However, they exhibited a bias towards regions with higher rainfall and higher values of primary productivity, that is higher values along PCA axis 1. Furthermore, more *SD* network grid cells are located in regions with higher mean annual temperatures and higher absolute minimum temperatures outside mountain ranges than expected from a random choice of grid cells.

Central to understanding of this mismatch is the fact that species are not evenly distributed within environmental space. Their habitat association is driven by environmental factors and so is their distribution. Subsequently, as species richness

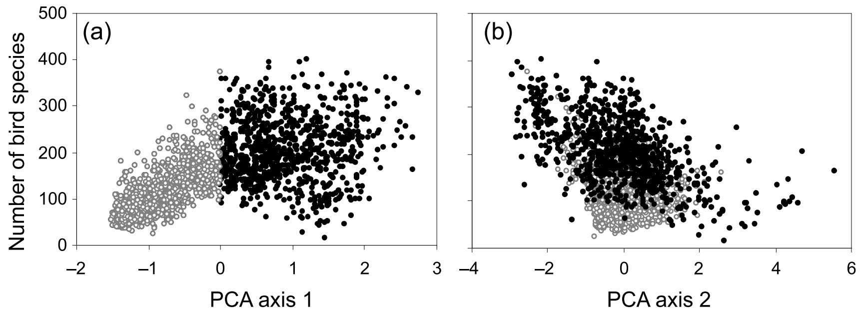

Figure 4. Correlation of bird species numbers with (a) PCA axis 1, and (b) PCA axis 2. Filled symbols indicate sites with positive scores for PCA axis 1.

determines reserve selection for complementary *SD* networks and to varying degrees also for existing reserves, these networks will follow the distribution pattern of species (see also Araujo et al. 2001, 2003).

In fact, species richness is highly correlated with the composite environmental gradient described by PCA axis 1 (Figure 4a). This relationship is, however, not significant when corrected for spatial autocorrelation (Spearman rho $= 0.64$, ess $= 5.78$, ns; ess – 'effective sample size', when redundancy produced by spatial autocorrelation is removed using the modified correlation test of Clifford et al. (1989)). The relationship becomes stronger when only negative values of the first axis are taken into account (Spearman rho $= 0.71$, ess $= 6.64$, $p < 0.05$), because variance spreads for positive values along PCA axis 1. This spread in variance may indicate two underlying relationships, that is a linear and a unimodal relationship, of species richness with productivity and related variables, such as energy and precipitation. Such patterns are common in other taxa and ecoregions (for reviews see Waide et al. 1999). For South Africa and Lesotho our results correspond to findings by van Rensburg et al. (2002) who report a positive linear correlation of bird species richness with mean annual precipitation and a unimodal relationship with respect to potential evapotranspiration (PET). Alternatively, the spread in variance along PCA axis 1 may be better explained by other principal components, for example PCA axis 2 (Figure 4b), a temperature and elevational gradient. In fact, the negative correlation of species richness with values of the second composite environmental gradient (Spearman rho $= -0.38$, ess $= 32.36$, ns) is strengthened, when considering only grid cells with positive values for PCA axis 1 (Spearman rho $= -0.57$, ess $= 15.64$, ns), although it is not significant when corrected for spatial autocorrelation. These underlying relationships of environmental correlation of species distribution may explain why the mean environmental conditions of the networks for SD_{occ}, SD_{peak}, habitats (*HD*) and existing reserves are shifted towards positive values for PCA axis 1 and towards negative values for PCA axis 2.

SD networks cover the range of the composite gradients, and some, even irreplaceable, grid cells are always located at the boundaries of environmental space (black squares in Figure 2a, b). This corresponds to the fact, that complementary area selection tends to select sites in environmental transition zones (Araujo and Williams 2001; Gaston et al. 2001). Therefore *SD* networks are likely to cover the extremes of the environmental gradients.

However, the *SD* networks do not sample the variety of habitats (*HD*) in representative areas very well, that is in grid cells with a respective vegetation type cover of $\geq$50%. This means that although networks maximising species diversity might capture the range of environmental conditions, they may not do so in uniform areas or core habitats but possibly in transition zones between habitats (Gaston et al. 2001).

Environmental diversity as surrogate for species diversity

Because of the spatial autocorrelation of species in environmental space, the suggestion that higher levels in the hierarchical organisation of biodiversity act as an effective surrogate for lower levels (Noss 1996; Nichols et al. 1998; Faith and Walker 1996) appears a too strong assumption. The *ED* network represents 95.6% of the database species in occurrence locations, which is a very high recovery rate, especially in comparison to other real-world case studies using species-surrogates for the representation of other taxa (e.g., Lombard 1995; Moore et al. 2003). This recovery rate is also higher than reported in the study by Araujo et al. (2001), who tested the performance of an *ED* network for the representation of different taxa in Europe. In Europe, however, species distributions may no longer directly correspond to favourable environmental conditions due to marked by human influence, and many species may have become restricted to remote, relatively pristine non-human populated areas, such as mountain ranges. But even for South Africa, a large ecoregion less affected by anthropogenic disturbance, selecting a network that maximises *ED* does not lead to significantly different results from a selection by chance. For this reason, *ED* cannot be strongly advocated as a surrogacy strategy (for debate see also Araujo et al. 2003; Faith 2003). More importantly, the *ED* network represents species peak abundance locations very poorly, so that *ED* seems no reliable surrogate to detect potentially viable locations for bird species.

Environmental diversity: continuum versus classification

It seems, that pre-classified information on environment, for example habitats (*HD* network), performs as a better surrogate for species diversity (Table 3) than environmental diversity based on purely remote sensing data and continuous space (*ED* network). Especially for the representation of peak abundance locations the *HD* network has a much greater recovery rate of species than the *ED* network, although still not satisfactory. This is contrary to the concerns of Faith and Walker (1996), that initial classification of environment information might result in a loss of useful information. As shown above, species (as well as habitats) are autocorrelated and not continuously distributed in environmental space and therefore some *a priori* summarising of environmental conditions into broad classes, for example vegetation types, may be beneficial for area selection and across hierarchy representation goals.

Performance of existing reserves

The existing reserve network represented environmental diversity (*ED*) relatively evenly (Figure 2d). As the *SD* networks, they also covered the extremes of environmental conditions with grid cells for the two largest existing reserves, Kalahari Gemsbok National Park and Kruger National Park, situated at the lower end of PCA axis 1 and the minimum bound of PCA axis 2, respectively.

However, with regards to other measures of environmental diversity (*HD*, *ED*), the existing reserves exhibited a lower performance than the *SD* networks (Table 3), even though the latter focus only on species representation. This may indicate policies in priority setting for actual reserve designation, which may not have been the result of a national plan to protect all aspects of biodiversity, but of historical *ad hoc* decisions (Siegfried 1989). While historically, there was a bias toward placing reserves along the borders of South Africa (Siegfried 1989), today, reserves are increasingly designated within the vicinity of human settlements (Chown et al. 2003), possibly in order to protect pristine sites from development, cultivation or other land degradation.

Therefore, a proportional overrepresentation of biomes within the reserve network may be related to a special focus due to small area cover and/or threat by anthropogenic development, as for example the Forest biome. Also, special attention may have been given to those biomes that are either particularly species rich and/or represent touristic attractions, such as the Savanna for large mammals (Gelderblom and Bronner 1995) or the Fynbos for vascular plant species. Indeed, a greater number of grid cells is necessary to represent *SD* within the Savanna biome than would be accomplished by a proportional size representation (Figure 3). In contrast, *ED* and *HD* could be covered by proportionally less sites in this biome.

On the other hand, the proportional underrepresentation of some biomes, for example the Nama Karoo or Grassland biome, within the existing reserve network may be due to location in areas too remote or inhospitable for human development and therefore unfavourable for both tourism as well as conservation management. Nonetheless, to adequately protect *SD*, *ED* and *HD* of these biomes, a higher percentage cover is necessary.

Proportional representation goals

Neither the complementary *SD* networks nor the existing reserve network represent environmental or ecosystem diversity proportionally. However, they do sample the breadth of environmental conditions. It may be questionable whether the goal of representing all possible combinations of environmental diversity evenly or proportionally within a network is an effective approach for conserving biodiversity (as suggested 10% or 12% targets; IUCN 1992; Noss 1996b). This is because regions and habitats vary tremendously in terms of physical and biotic heterogeneity, area requirement of the extant fauna, land use and other factors (Noss 1996a,b). Representation target levels will differ for different regions, as visualised in Figure 3. For example, to ensure the protection of bird species diversity adequately, a minimum network requires a higher area proportion in the Savanna than in the Succulent Karoo. For other taxa, especially plants, or the entire representation of ecosystem properties (*HD*, *ED*), the situation will differ. Therefore, especially when taking into account the vulnerability or irreplaceability of different habitats (Pressey and Taffs 2001), different representation targets should be set for different environmental classes (see also Cowling and Heijnis 2001; Rodrigues and Gaston 2001).

Conclusions – conservation planning for persistence

Complementary networks designed for maximising species diversity (*SD*) and the existing reserve network represented a broad range of environmental conditions, albeit with a bias towards more productive areas outside mountain ranges. However, they sampled habitat diversity only in areas of high heterogeneity, as less than half of all vegetation types were represented in their core distribution areas. Networks aiming to maximise environmental diversity (*ED*, *HD*) as well as the existing reserve network represented bird species diversity quite satisfying regarding occurrence locations. However, the long-term efficiency of these networks is not guaranteed as less than half of all bird species were represented within their peak abundance locations.

Therefore, focusing on any single biodiversity component alone is insufficient to protect other components. This means, that information on species distribution, especially on peak abundance locations, as well as information on the location of rare vegetation types is necessary for sustainable conservation planning. Especially, when viability considerations are to be addressed, it is not enough to use surrogates.

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