CHAPTER 1

General Introduction

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

Mechanisms underlying species richness gradients

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

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

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

The importance of beta-diversity

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

Spatial autocorrelation

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

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

Human impacts on biodiversity

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

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

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

Objectives

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

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

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

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

Data and the rationale underlying its use

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

Data availability and reliability

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

Marked abiotic variation in the region

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

Human population density and conservation area data availability

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

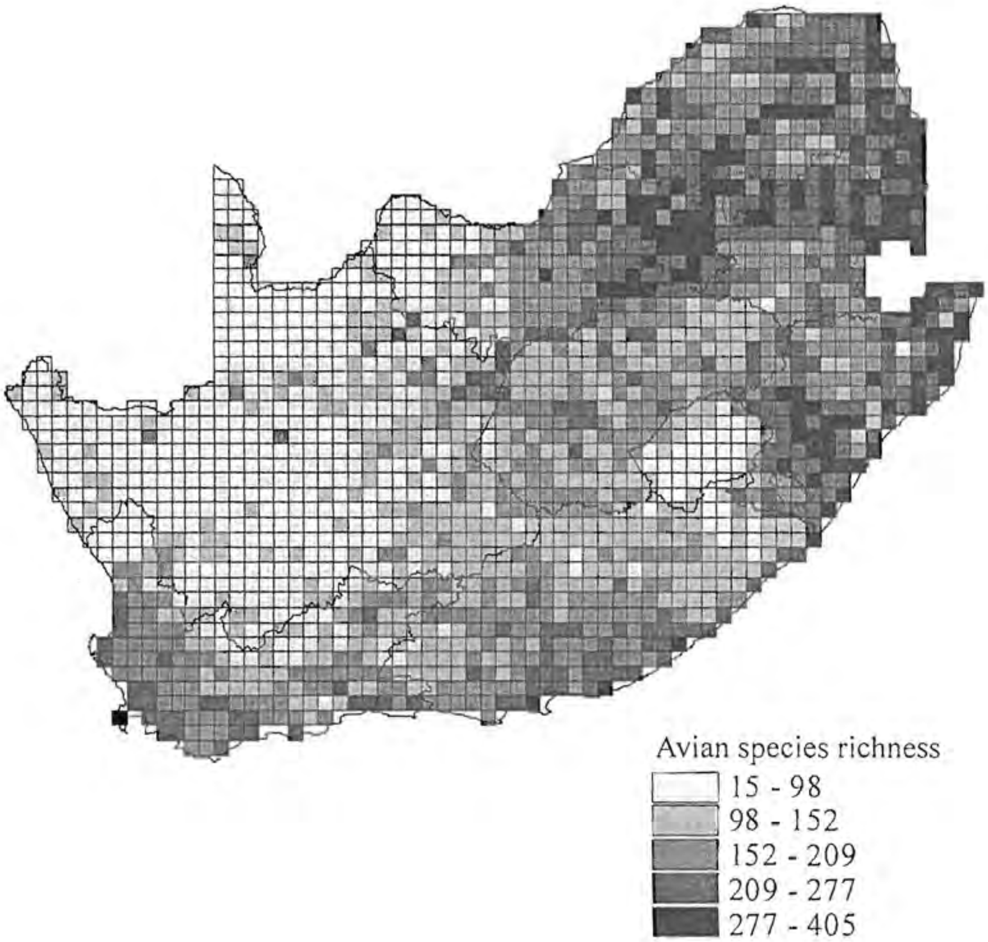


Figure 1 Avian species richness variation across South Africa.

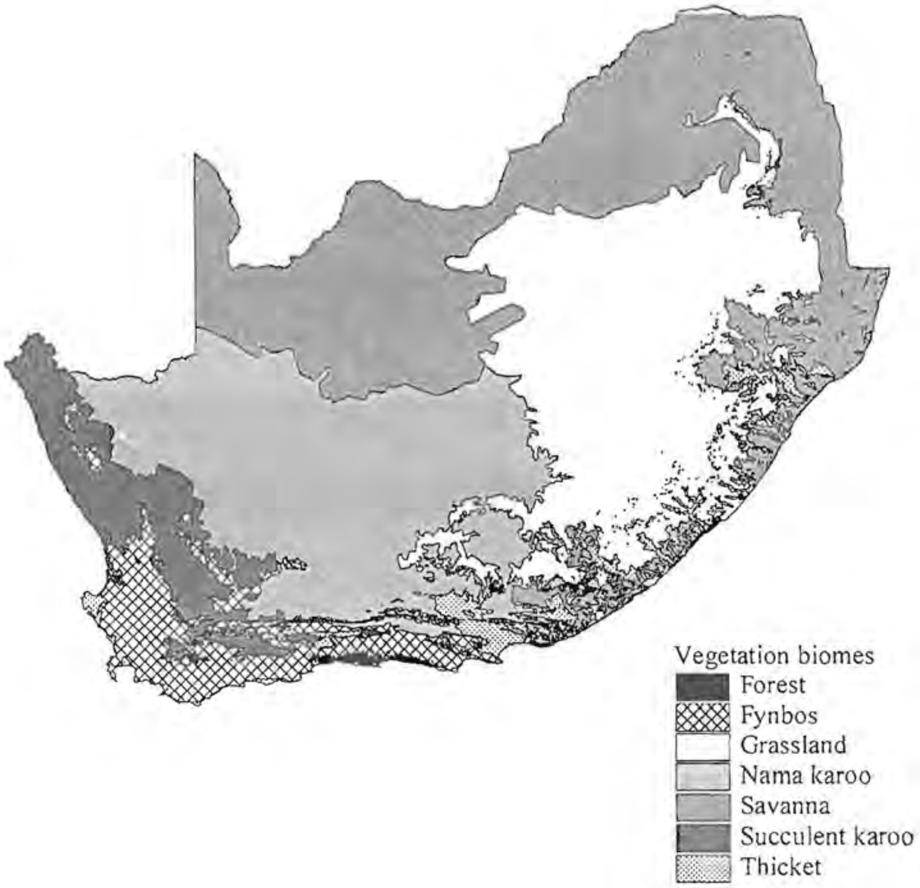


Figure 2 The vegetation biomes of South Africa and Lesotho based on Low & Rebelo (1996).

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

The availability of highly transformed areas

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

A scale relevant to conservation planning in times of change

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

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

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

References

Allan, D. G., Harrison, J. A., Navarro, R. A., van Wilgen, B. W. & Thompson, M. W. 1997. The impact of commercial afforestation on bird populations in Mpumalanga province, South Africa: insights from the bird atlas data. *Biological Conservation* 79: 173-185.

Andrews, P. & O'Brien, E. M. 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology* 251: 205-231.

Anonymous. 1997. *White paper on the conservation and sustainable use of South Africa's biological diversity.* Pretoria, Government Gazette no. 18163.

Araújo, M. B. & Williams, P. H. 2001. The bias of complementary hotspots towards marginal populations. *Conservation Biology* 15: 1710-1720.

Ashton, K. G. 2001. Are ecological and evolutionary rules being dismissed prematurely? *Diversity and Distributions* 7: 289-295.

Balmford, A. & Long, A. 1994. Avian endemism and forest loss. *Nature* 372: 623-624.

Balmford, A., Moore, J., Brooks, T., Burgess, N., Hansen, L. A., Lovett, J. C., Tokumine, S., Williams, P., Woodward, F. I. & Rahbek, C. 2001b. Response. *Science* 293: 1591-1592.

Balmford, A., Moore, J. L., Brooks, T., Burgess, N., Hansen, L. A., Williams, P. & Rahbek, C. 2001a. Conservation conflicts across Africa. *Science* 291: 2616-2619.

Bawa, K. S. & Dayanandan, S. 1997. Socioeconomic factors and tropical deforestation. *Nature* 386: 562-563.

Bestelmeyer, B. T. & Wiens, J. A. 2001. Local and regional-scale responses of ant diversity to a semiarid biome transition. *Ecography* 24: 381-392.

Bibby, C. J. 1995. Recent past and future extinctions in birds. *Extinction rates* (ed. by J. H. Lawton & R. M. May), pp. 98-110. Oxford University Press.

Blackburn, T. M. & Gaston, K. J. 1996a. Spatial patterns in the species richness of birds in the New World. *Ecography* 19: 369-376.

Blackburn, T. M. & Gaston, K. J. 1996b. Spatial patterns in the geographical range sizes of bird species in the New World. *Philosophical Transitions of the Royal Society, London B* 351: 897-912.

Blackburn, T. M. & Gaston, K. J. 2002. Scale in macroecology. *Global Ecology & Biogeography* 11: 185-189.

Böhning-Gaese, K. 1997. Determinants of avian species richness at different spatial scales. *Journal of Biogeography* 24: 49-60.

Bokma, F., Bokma, J. & Mönkkönen, M. 2001. Random processes and geographical species richness patterns: why so few species in the north? *Ecography* 24: 43-49.

Boone, R. B. & Krohn, W. B. 2000. Partitioning sources of variation in vertebrate species richness. *Journal of Biogeography* 27: 457-470.

Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.

Brooks, T. M., Pimm, S. L., Kapos, V. & Ravilious, C. 1999. Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. *Journal of Animal Ecology* 68: 1061-1078.

Brooks, T. & Thompson, H. S. 2001. Current bird conservation issues in Africa. *The Auk* 118: 575-582.

Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.

Brown, J. H. & Lomolino, M. V. 1998. *Biogeography* 2nd edn. Sinauer, Sunderland, MA.

Bruner, A. G., Gullison, R. E., Rice, R. E. & da Fonseca, G. A. B. 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* 291: 125-128.

Cabeza, M. & Moilanen, A. 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution* 16: 242-248.

Ceballos, G. & Ehrlich, P. R. 2002. Mammal population losses and the extinction crisis. *Science* 296: 904-907.

Chown, S. L. & Gaston, K. J. 1999. Patterns in procellariiform diversity as a test of species-energy theory in marine systems. *Evolutionary Ecology Research* 1: 365-373.

Chown, S. L. & Gaston, K. J. 2000a. Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution* 15: 311-315.

Chown, S. L. & Gaston, K. J. 2000b. Response. *Trends in Ecology & Evolution* 15: 514-515.

Clark, I. 1982. *Practical geostatistics*. Applied Science, London.

Clifford, P., Richardson, S. & Hemon, D. 1989. Assessing the significance of the correlation between two spatial processes. *Biometrics* 45: 123-134.

Cody, M. L. 1975. Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. *Ecology and evolution of communities* (ed. by M. L. Cody & J. M. Diamond), pp. 214-257. Harvard University Press, Cambridge, Massachusetts.

Colwell, R. K. & Hurtt, G. C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist* 144: 570-595.

Colwell, R. K. & Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution* 15: 70-76.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* 137: 27-49.

Desrochers, A. & Fortin, M. J. 2000. Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. *Oikos* 91: 376-384.

Dunn, P. O. & Winkler, D. W. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London B* 266: 2487-2490.

Easterling, W. E., Brandle, J. R., Hays, C. J., Guo, Q. & Guertin, D. S. 2001. Simulating the impact of human land use change on forest composition in the Great Plains agroecosystems with the *Seedscape* model. *Ecological Modelling* 140: 163-176.

Erasmus, L. & van Jaarsveld, A. S. 2002. Exploring policy interventions for sustainable development in South Africa: a modeling approach. *South African Journal of Science* 98: 3-8.

Erasmus, B. F. N., van Jaarsveld, A. S., Chown, S. L., Kshatriya, M. & Wessels, K. J. 2002. Vulnerability of South African animal taxa to climate change. *Global Change Biology* 8: 679-693.

Everett, R. A. 2000. Patterns and pathways of biological invasions. *Trends in Ecology & Evolution* 15: 177-178.

Fairbanks, D. H. K., Kshatriya, M., van Jaarsveld, A. S. & Underhill, L. G. 2002. Scales and consequences of human land transformation on South African avian diversity and structure. *Animal Conservation* 5: 61-74.

Fairbanks, D. H. K., Reyers, B. & van Jaarsveld, A. S. 2001. Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. *Biological Conservation* 98: 365-379.

Fairbanks, D. H. K., Thompson, M. W., Vink, D. E., Newby, T., van den Berg, H. M. & Everard, D. A. 2000. The South-African land-cover characteristics database: a synopsis of the landscape. *South African Journal of Science* 96: 69-86.

Faith, D. P. 2001. Overlap of species richness and development-opportunity does not imply conflict. Science 293: http//www.sciencemag.org/cgi/letters/ 293/5535/1591.

Fjeldså, J. & Rahbek, C. 1998. Continent-wide conservation priorities and diversification processes. *Conservation in a changing world* (ed. by G. M. Mace, A. Balmford & J. R. Ginsberg), pp. 139-160. Cambridge Univ. Press, Cambridge.

Fraser, R. H. 1998. Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. *Global Ecology and Biogeography Letters* 7: 215-220.

Freitag, S., Nicholls, A. O. & van Jaarsveld, A. S. 1998. Dealing with established reserve networks and incomplete distribution data sets in conservation planning. *South African Journal of Science* 94: 79-86.

Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405: 220-227.

Gaston, K. J. & Blackburn, T. M. 1995. Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proceedings of the Royal Society of London B* 262: 335-341.

Gaston, K. J. & Blackburn, T. M. 2000. *Patterns and process in macroecology*. Blackwell Science, United Kingdom.

Gaston, K. J., Blackburn, T. M. & Spicer, J. I. 1998. Rapoport's rule: time for an epitaph? *Trends in Ecology & Evolution* 13: 70-74.

Gaston, K. J. & Rodrigues, A. S. L. in press. Reserve selection in regions with poor biological data. *Conservation Biology*.

Gosz, J. R. 1993. Ecotone hierarchies. *Ecological Applications* 3: 369-376.

Gotelli, N. J. & Graves, G. R. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, DC.

Hannah, L., Midgley, G. F., Lovejoy, T., Bond, W. J., Bush, M., Lovett, J. C., Scott, D. & Woodward, F. I. 2002. Conservation of biodiversity in a changing climate. *Conservation Biology* 16: 264-268.

Hanski, I. & Gyllenberg, M. 1997. Uniting two general patterns in the distribution of species. *Science* 275: 397-400.

Harcourt, A. H., Parks, S. A. & Woodroffe, R. 2001. Human density as an influence on species/area relationships: double jeopardy for small African reserves? *Biodiversity and Conservation* 10: 1011-1026.

Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V. & Brown, C. J. 1997. *The atlas of southern African birds*, vols. 1 and 2. BirdLife South Africa, Johannesburg.

Harrison, J. A. & Martinez, P. 1995. Measurement and mapping of avian diversity in southern Africa: implications for conservation planning. *Ibis* 137: 410-417.

Huston, M. A. 1993. Biological diversity, soils, and economics. *Science* 262: 1676-1680.

Huston, M. A. 2001. People and biodiversity in Africa. *Science* 293: 1591.

James, A., Gaston, K. J. & Balmford, A. 2001. Can we afford to conserve biodiversity? *BioScience* 51: 43-52.

Jetz, W. & Rahbek, C. 2001. Geometric constraints explain much of the species richness patterns in African birds. *Proceedings of the National Academy of Sciences, USA* 98: 5661-5666.

Kaspari, M., Alonso, L. & O'Donnell, S. 2000a. Three energy variables predict ant abundance at a geographical scale. *Proceedings of the Royal Society of London B* 267: 485-489.

Kaspari, M., O'Donnell, S. & Kercher, J. 2000b. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *American Naturalist* 155: 280-293.

Kendal, M. A. & Aschan, M. 1993. Latitudinal gradients in the structure of macrobentic communities: a comparison of Arctic, temperate and tropical sites. *Journal of Experimental Marine Biology and Ecology* 172: 157-169.

Kerr, J. T. & Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385: 252-254.

Kiker, G. 2000. *Climate change impacts in southern Africa. Report to the National Climate Change Committee.* Department of Environmental Affairs and Tourism, Pretoria, South Africa.

Koleff, P. & Gaston, K. J. 2001. Latitudinal gradients in diversity: real patterns and random models. *Ecography* 24: 341-351.

Krasnov, B. R. & Shenbrot, G. I. 1998. Structure of communities of ground-dwelling animals at the junction of two phytogeographic zones. *Journal of Biogeography* 25: 1115-1131.

Laurance, W. F., Cochrane, M. A., Bergen, S., Fearnside, P. M., Delamonica, P., Barber, C., D'Angelo, S. & Fernandes, T. 2001. The future of the Brazilian Amazon. *Science* 291: 438-439.

Laurance, W. F., Gascon, C. & Rankindemerona, J. M. 1999. Predicting effects of habitat destruction on plant-communities: a test of a model using Amazonian trees. *Ecological Applications* 9: 548-554.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*, 2nd English edition. Elsevier Science BV, Amsterdam.

Lennon, J. J. 2000. Red-shifts and red herrings in geographical ecology. *Ecography* 23: 101-113.

Lennon, J. J., Greenwood, J. J. D. & Turner, J. R. G. 2000. Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. *Journal of Animal Ecology* 69: 581-598.

Lennon, J. J., Koleff, P., Greenwood, J. J. D. & Gaston, K. J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70: 966-979.

Levine, J. M. 2000. Species-diversity and biological invasions: relating local-process to community pattern. *Science* 288: 852-854.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology & Evolution* 8: 133-137.

Lombard, A. T. 1995a. The problems with multi-species conservation: do hotspots, ideal reserves and existing reserve coincide? *South African Journal of Zoology* 30: 145-163.

Lombard, A. T. 1995b. Introduction to an evaluation of the protection status of South Africa's vertebrates. *South African Journal of Zoology* 30: 63-70.

Lombard, A. T., Nicholls, A. O. & August, P. V. 1995. Where should nature reserves be located in South Africa? A snake's perspective. *Conservation Biology* 9: 363-372.

Low, A. B. & Rebelo, A. G. 1996. *Vegetation of South Africa, Lesotho, and Swaziland.* Department of Environmental Affairs and Tourism, Pretoria, South Africa.

Macdonald, I. A. W. 1989. Man's role in changing the face of southern Africa. *Biotic diversity in southern Africa. Concepts and conservation* (ed. by B. J. Huntley), pp. 51-77. Oxford University Press, Cape Town.

Mack, M. C. & Dantonio, C. M. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution* 13: 195-198.

Margules, C. R., Nicholls, A. O. & Usher, M. B. 1994. Apparent species turnover, probability of extinction and the selection of nature reserves: a case study of the Ingleborough Limestone Pavements. *Conservation Biology* 8: 398-409.

McLaughlin, J. F., Hellmann, J. J., Boggs, C. L. & Ehrlich, P. R. 2002. Climate change hastens population extinctions. *Proceedings of the National Academic of Science, USA* 99: 6070-6074.

McNeely, J. A. 1994. Protected areas for the 21st century: working to provide benefits to society. *Biodiversity and Conservation* 3: 390-405.

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I. & Gough, L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381-2396.

Nicholls, A. O. & Margules, C. R. 1993. An upgraded reserve selection algorithm. *Biological Conservation* 64: 165-169.

O'Brien, E. M. 1993. Climate gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography* 20: 181-198.

O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography* 25: 379-398.

O'Brien, E. M., Whittaker, R. J. & Field, R. 1998. Climate and woody plant diversity in southern Africa: relationships at species, genus and family levels. *Ecography* 21: 495-509.

O'Brien, E. M., Field, R. & Whittaker, R. J. 2000. Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. *Oikos* 89: 588-600.

Økland, B., Bakke, A., Hagvar, S. & Kvamme, T. 1996. What factors influences the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity and Conservation* 5: 75-100.

O'Riordan, T. 1998. Sustainability for survival in South Africa. *Global Environmental Change* 8: 99-108.

Parks, S. A. & Harcourt, H. 2002. Reserve size, local human density, and mammalian extinctions in U.S. protected areas. *Conservation Biology* 16: 800-808.

Parmesan, C. 1996. Climate and species' range. *Nature* 382: 765-766.

Parmesan, C., Ryrholm, N., Steganescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. & Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Pennisi, E. 2001. Climate change: early birds may miss the worms. *Science* 291: 2532-2532.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100: 65-75.

Pounds, J. A., Fogden, M. P. L. & Campbell, J. H. 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611-615.

Qian, H. & Ricklefs, R. E. 2000. Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature* 407: 180-182.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist* 149: 875-902.

Rahbek, C. & Graves, G. R. 2000. Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proceedings of the Royal Society of London B* 267: 2259-2265.

Rahbek, C. & Graves, G. R. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academic of Science, USA* 98: 4534-4539.

Reyers, B., Fairbanks, D. H. K., Wessels, K. J. & van Jaarsveld, A. S. 2002. A multicriteria approach to reserve selection: addressing long-term biodiversity maintenance. *Biodiversity and Conservation* 11: 769-793.

Richardson, D. M., van Wilgen, B. W., Higgins, S. I., Trinder-Smith, T. H., Cowling, R. M. & McKell, D. H. 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity and Conservation* 5: 607-647.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 167-171.

Ricklefs, R. E., Latham, R. E. & Qian, H. 1999. Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos* 86: 369-373.

Rodrigues, A. S. L., Cerdeira, J. O. & Gaston, K. J. 2000a. Flexibility, efficiency, and accountability: adapting reserve selection algorithms to more complex conservation problems. *Ecography* 23: 565-574.

Rodrigues, A. S. L. & Gaston, K. J. 2002. Rarity and conservation planning across geopolitical units. *Conservation Biology* 16: 674-682.

Rodrigues, A. S. L., Gregory, R. D. & Gaston, K. J. 2000b. Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society of London B* 267: 49-55.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65: 514-527.

Rohde, K. 1998. Latitudinal gradients in species diversity. Areas matters, but how much? *Oikos* 82: 184-190.

Rohde, K. 1999. Latitudinal gradients in species diversity and Rapoport's revisited: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography* 22: 593-613.

Rosenzweig, M. L. 1992. Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy* 73: 715-730.

Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, United Kingdom.

Rosenzweig, M. L. & Sandlin, E. A. 1997. Species diversity and latitudes: listening to area's signal. *Oikos* 80: 172-176.

Roy, K., Jablonski, D. & Martien, K. K. 2000a. Invariant size frequency distributions along a latitudinal gradient in marine bivalves. *Proceedings of the National Academic of Science, USA* 97: 13150-13155.

Roy, K., Jablonski, D. & Valentine, J. W. 2000b. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proceedings of the Royal Society of London B* 267: 293-299.

Roy, K., Jablonski, D., Valentine, J. W. & Rosenberg, G. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academic of Science, USA* 95: 3699-3702.

Rutherford, M. C., Powrie, L. W. & Schulze, R. E. 1999. Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Diversity and Distributions* 5: 253-262.

Rutherford, M. C. & Westfall, R. H. 1994. Biomes of southern Africa: an objective categorization. *Memoirs of the Botanical Survey of South Africa* 63: 1-94.

Ryti, R. T. & Gilpin, M. E. 1987. The comparative analysis of species occurrence patterns on archipelagos. *Oecologia* 73: 282-287.

Scheiner, S. M., Cox, S. B., Willig, M., Mittelbach, G. G., Osenberg, C. & Kaspari, M. 2000. Species richness, species-area curves and Simpson's paradox. *Evolutionary Ecology Research* 2: 791-802.

Scholtz, C. H. & Chown, S. L. 1993. Insect conservation and extensive agriculture: the savanna of southern Africa. *Perspectives on insect conservation* (ed. by K. J. Gaston, T. R. New & M. J. Samways), pp. 75-95. Intercept, Andover.

Schulze, R. E. 1997a. Climate. *Vegetation of southern Africa* (ed. by R. M. Cowling, D. M. Richardson & S. M. Pierce), pp. 21-41. Cambridge University Press, Cambridge.

Schulze, R. E. 1997b. *South African atlas of agrohydrology and climatology*. Water Research Commission, Pretoria, Report TT82/96.

Shannon, D. A. 2000. *Land surface response to climate change forcing over southern Africa*. Ph.D. thesis, Department of Environmental and Geographic Science, University of Cape Town.

Sillett, T. S., Holmes, R. T. & Sherry, T. W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288: 2040-2042.

Smith, P. A. 1994. Autocorrelation in logistic regression modeling of species distribution. *Global Ecology and Biogeography Letters* 4: 47-61.

Soulé, M. E. & Sanjayan, M. A. 1998. Conservation targets: do they help? *Science* 279: 2060-2061.

South African Integrated Spatial Information System. 2001. http://www.sa-isis.co.za/.

Statistics South Africa. 1996. *Population Census 1996*. Pretoria, Report no. 03-01-30.

Stevens, G. C. 1989. The latitudinal gradient in geographic range: how so many species coexist in the tropics. *American Naturalist* 133: 24-256.

Stone, L. 1995. Biodiversity and habitat destruction: a comparative-study of model forest and coral-reef ecosystems. *Proceedings of the Royal Society of London B* 261: 381-388.

Taylor, P. H. & Gaines, S. D. 1999. Can Rapoport's rule be rescued? Modelling causes of the latitudinal gradient of species richness. *Ecology* 80: 2474-2482.

Terborgh, J. 1999. *Requiem for nature*. Washington D. C., Island Press.

Thomas, C. D. & Lennon, J. J. 1999. Birds extend their ranges northwards. *Nature* 399: 213-213.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D. & Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. *Science* 292: 281-284.

Tilman, D., Lehman, C. L. & Yin, C. J. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. *American Naturalist* 149: 407-435.

Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65-66.

Van Jaarsveld, A. S. & Chown, S. L. 2001. Climate change and its impacts in South Africa. *Trends in Ecology & Evolution* 16: 13-14.

Van Jaarsveld, A. S., Freitag, S., Chown, S. L., Muller, C., Koch, S. O., Hull, H. E., Bellamy, C. L., Krüger, M., Endrödy-Younga, S., Mansell, M. W. & Scholtz, C. H. 1998. Biodiversity assessment and conservation strategies. *Science* 279: 2106-2108.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P. & Parmenter, R. 1999. The relationship between productivity and species richness. *Annual Review of Ecological Systematic* 30: 257-300.

Walther, G-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.

Warren, M. S., Hill, J. K., Thomas, J. A. Asher, J., Fox, R., Huntley, B., Roy, D. B., Teifer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, B., Willis, S. G., Greatorex-Davies, J. N., Moss, D. & Thomas, C. D. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65-69.

Whitehead, D. R. & Jones, C. E. 1969. Small islands and the equilibrium theory of insular biogeography. *Evolution* 23: 171-179.

Whittaker, R. J. 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs* 30: 279-338.

Whittaker, R. J. 1977. Evolution of species diversity in land communities. *Evolutionary biology*, vol. 10 (ed. by M. K. Hecht, W. C. Steere & B. Wallace), pp. 250-268. Plenum Press, New York.

Whittaker, R. J., Willis, K. J. & Field, R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28: 453-470.

Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.

Williams, P. H. 1996. Mapping variations in the strength and breath of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London B* 263: 579-588.

Williams, P. H., de Klerk, H. M. & Crowe, T. M. 1999. Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography* 26: 459-474.

Williamson, M. 1988. Relationship of species number to area, distance and other variables. *Analytical biogeography: an integrated approach to the study of animal and plant distributions* (ed. by A. A. Myers & P. S. Giller), pp. 92-115. Chapman & Hall, London.

Willis, K. J. & Whittaker, R. J. 2000. The refugial debate. *Science* 287: 1406-1407.

Wilson, M. V. & Shmida, A. 1984. Measuring beta-diversity with presence-absence data. *Journal of Ecology* 72: 1055-1064.

Woodward, F. I., Lomas, M. R. & Lee, S. E. 2001. Predicting the future production and distribution of global terrestrial vegetation. *Terrestrial global productivity* (ed. by J. Roy, B. Saugier & H. Mooney), pp. 519-539. Academic Press.

World Development Report. 2000/2001. http://www.worldbank.org/poverty/wdrpoverty/ report/toc.pdf.

WCMC. 1997. World conservation monitoring centre. United Nations list of protected areas for South Africa. Http://www.wcmc.org.ukindexshock.html.

Wright, D. H., Currie, D. J. & Maurer, B. A. 1993. Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R. E. Ricklefs & D. Schluter), pp. 66-74. University of Chicago Press, Chicago.

CHAPTER 2

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

B. J. van Rensburg[1], S. L. Chown[1,2*], and K. J. Gaston[3]

1 Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

2 Current address: Department of Zoology, University of Stellenbosch, Private Bag X1, Matieland, 7602, South Africa

3 Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K.

Berndt J. van Rensburg: Telephone: (+2712) 420-4611; Fax: (+2712) 362-5242;
E-mail: bjvanrensburg@zoology.up.ac.za

Steven L. Chown: Telephone: (+2721) 808-3236; Fax: (+2712) 808-2405
E-mail: slchown@maties.sun.ac.za

Kevin J. Gaston: Telephone: (0114) 222 0030; Fax: (0114) 222 0002
E-mail: K.J.Gaston@Sheffield.ac.uk

Keywords: energy availability, habitat heterogeneity, primary productivity, potential evapotranspiration, grain

Running title: Environmental correlates and avian species richness

Published in: *American Naturalist (2002), 159, 566-577.*

---

[*] corresponding author

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

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

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

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

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

Methods

Data

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

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

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

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

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

Regression analysis

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

Spatial data analysis

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

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

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

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

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

Results

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

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

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

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

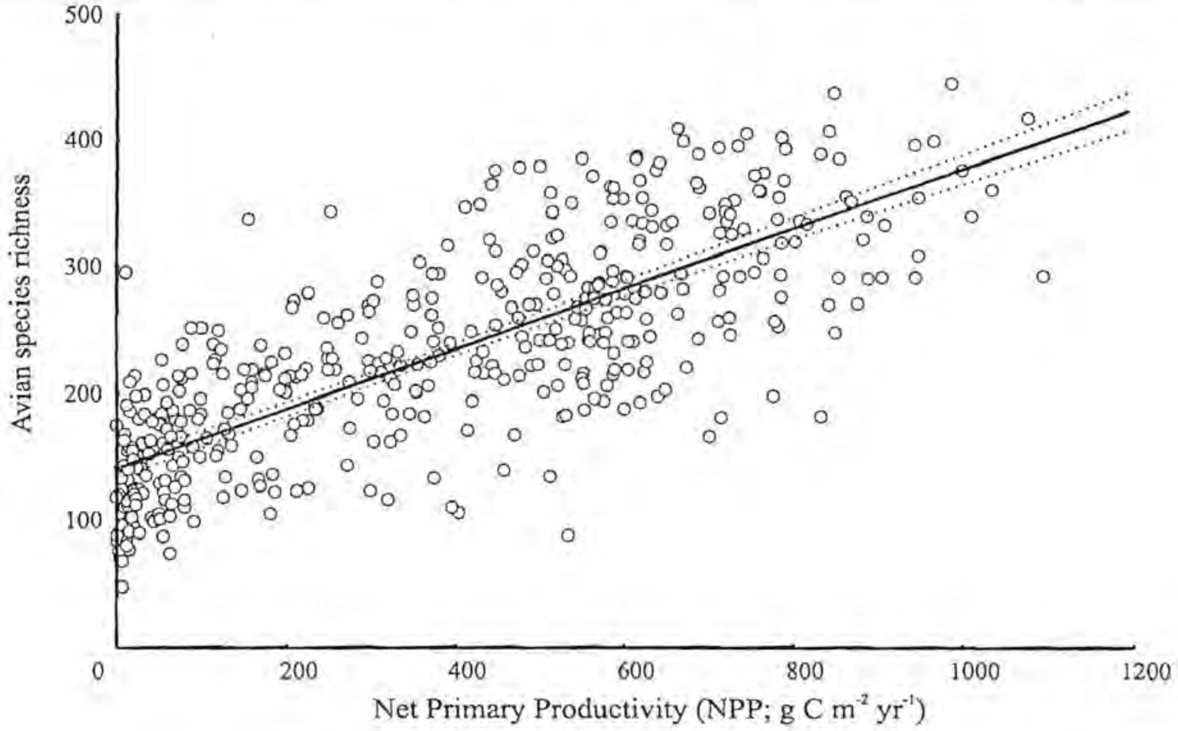
	Avian species richness		
Environmental variables	Quarter degree r	Half degree r	One degree r
PET	-.52***	-.64***	-.71***
MAX	.02 NS	.02 NS	-.25*
MIN	.39***	.42***	.27**
PPT	.65***	.77***	.82***
MAXMO	-.12***	-.13**	-.28**
MINMO	.42***	.45***	.29**
SRAD	-.47***	-.49***	-.60***
VEG	.32***	.43***	.70***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

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

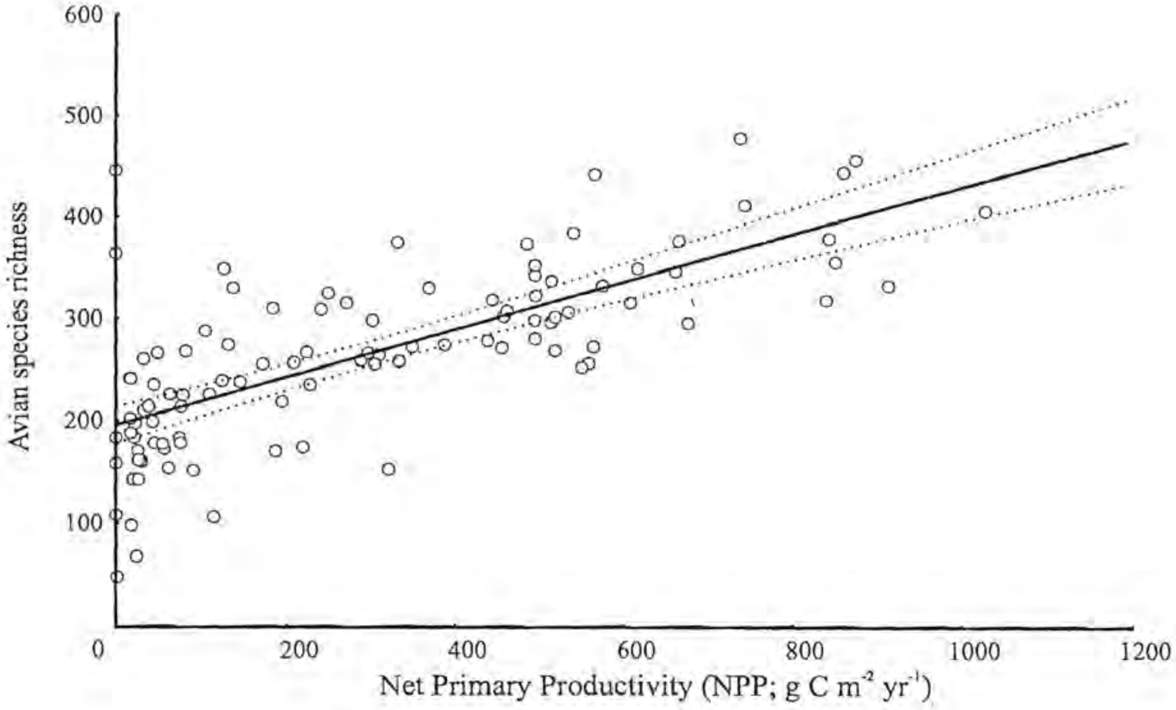
* $P < .05$.

** $P < .01$.

*** $P < .001$.



(*A*)



(*B*)

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

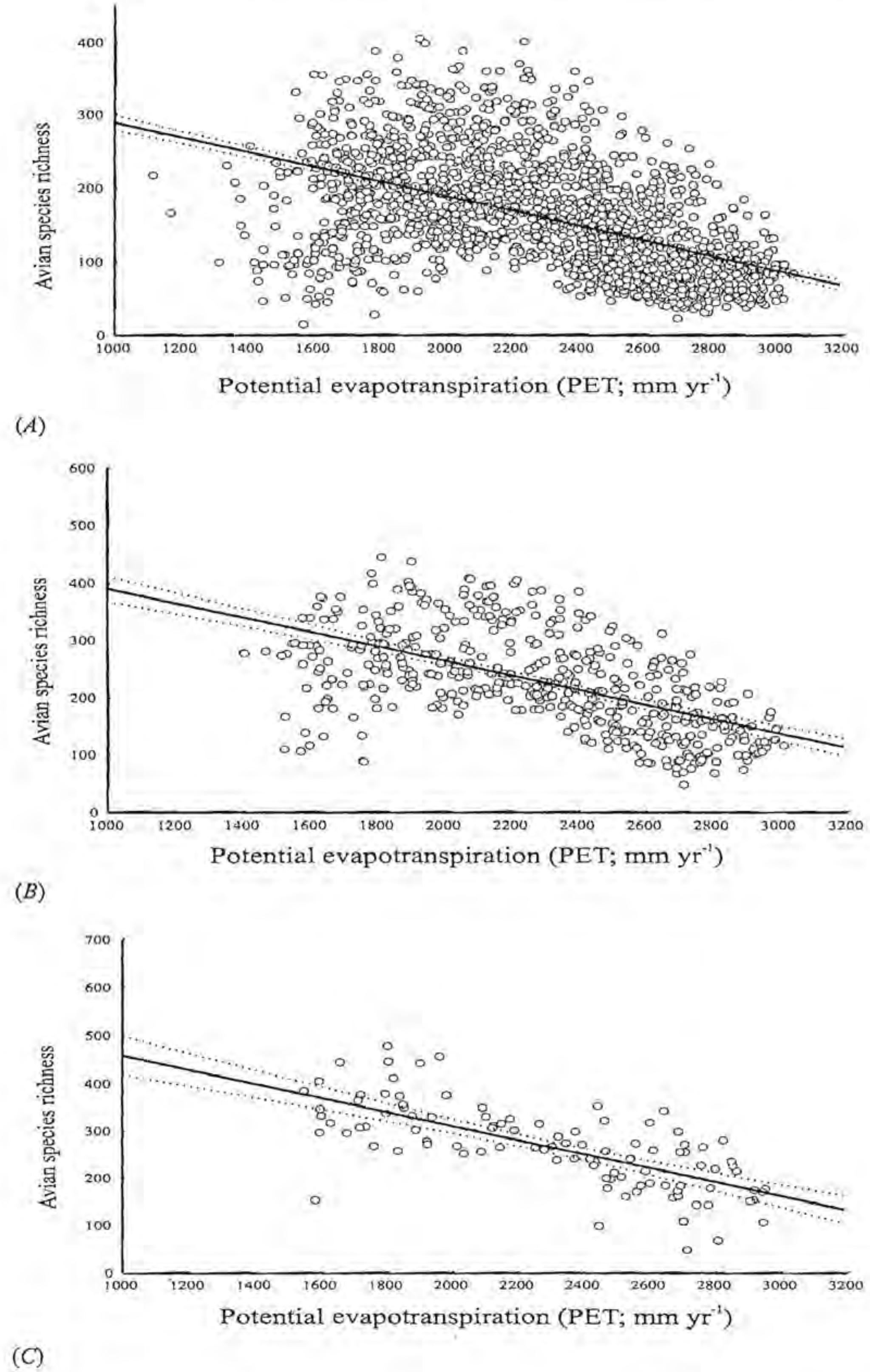


Figure 2: Relationships between avian species richness and PET (potential evapotranspiration). *A*, Quarter-degree resolution (avian species richness = 389.97 - 0.1009 x PET; $r = -0.52$). *B*, Half-degree resolution (avian species richness = 516.10 - 0.1261 x PET; $r = -0.64$). *C*, One-degree resolution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

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

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

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

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

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

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

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

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

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

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

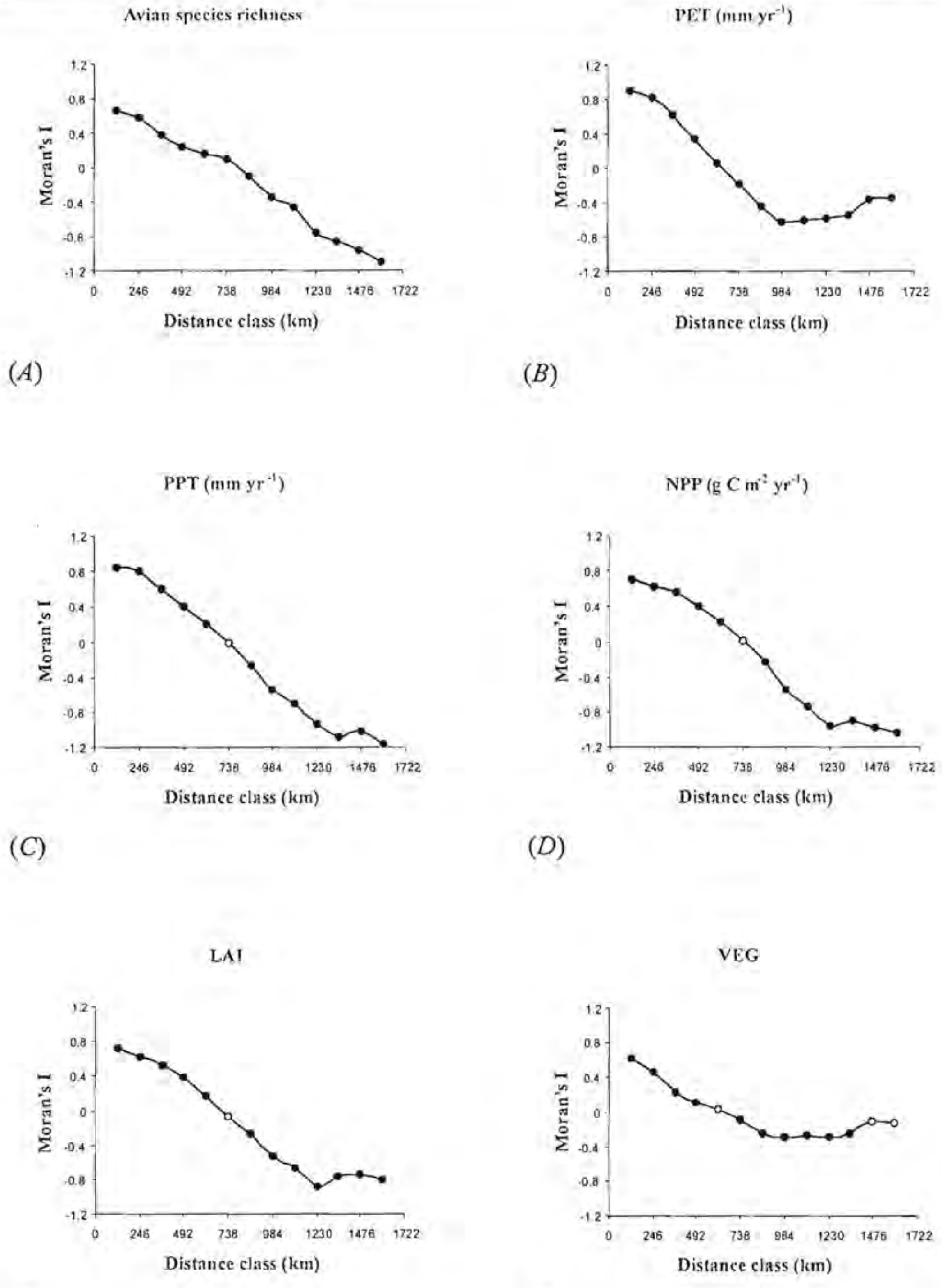
*** $P < .05$.

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

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

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

*** $P < .05$.



(*A*) (*B*)

(*C*) (*D*)

(*E*) (*F*)

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

Discussion

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

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

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

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

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

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

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

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

Acknowledgments

The Avian Demography Unit, University of Cape Town, and particularly Prof. L.G. Underhill, are thanked for providing access to the South African Bird Atlas Project data. N.J.M. Gremmen and M.A. McGeoch are thanked for discussion, and R.J Whittaker and two anonymous reviewers for their helpful comments on an earlier version of the ms. The Mellon Foundation Mentoring Scheme at the University of Pretoria and the National Research Foundation provided financial support, and Geographical Information Management Systems (Pty) Ltd supplied the Geographical Information System software. K.J. Gaston is a Royal Society University Research Fellow.

Literature Cited

Allan, D. G., J. A. Harrison, M. Herremans, R. A. Navarro, and L. G. Underhill. 1997. Southern African geography: its relevance to birds. Pages lxv-ci *in* J. A. Harrison, D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker and, C. J. Brown, eds. The atlas of southern African birds. Birdlife South Africa, Johannesburg.

Andrews, P., and E. M. O'Brien. 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. Journal of Zoology 251:205-231.

Blackburn, T. M., J. H. Lawton, and R. Gregory. 1996. Relationships between abundances and life histories of British birds. Journal of Animal Ecology 65:52-62.

Boone, R. B., and W. B. Krohn. 2000*a*. Partitioning sources of variation in vertebrate species richness. Journal of Biogeography 27:457-470.

———. 2000*b*. Relationship between avian range limits and plant transition zones in Maine. Journal of Biogeography 27:471-482.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045-1055.

Chown, S. L., and K. J. Gaston. 1999. Patterns in procellariiform diversity as a test of species-energy theory in marine systems. Evolutionary Ecology Research 1:365-373.

Clark, I. 1982. Practical geostatistics. Applied Science, London.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137:27-49.

———. 1993. What shape is the relationship between body size and population density? Oikos 66:353-358.

Currie, D. J., A. P. Francis, and J. T. Kerr. 1999. Some general propositions about the study of spatial patterns of species richness. Ecoscience 6:392-399.

Fraser, R. H. 1998. Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. Global Ecology and Biogeography Letters 7:215-220.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220-227.

Hanski, I. M., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747-762.

Harrison, J. A., D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker, and C. J. Brown. 1997. The atlas of southern African birds. Birdlife South Africa, Johannesburg.

Hulme, M., D. Conway, A. Joyce, and H. Mulenga. 1996. A 1961-90 climatology for Africa south of the Equator and a composition of potential evapotranspiration estimates. South African Journal of Science 92: 334-343.

James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's Box. Annual Review of Ecology and Systematics 21:129-166.

Jetz, W., and C. Rahbek. 2001. Geometric constraints explain much of the species richness patterns in African birds. Proceedings of the National Academy of Sciences of the United States of America 98: 5661-5666.

Kaspari, M., S. O'Donnell, and J. Kercher. 2000*a*. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. American Naturalist 155:280-293.

Kaspari, M., L. Alonso, and S. O'Donnell. 2000*b*. Three energy variables predict ant abundance at a geographical scale. Proceedings of the Royal Society of London B. 267:485-489.

Kerr, J. T., and D. J. Currie. 1999. The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. Ecoscience 6:329-337.

Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252-254.

Kerr, J. T., R. Vincent, and D. J. Currie. 1998. Lepidopteran richness patterns in North America. Ecoscience 5:448-453.

Kohn, D. D., and D. M. Walsh. 1994. Plant species richness – the effect of island size and habitat diversity. Journal of Ecology 82:367-377.

Krebs, C. J. 1999. Ecological methodology. 2d ed. Addison-Wesley, Boston.

Legendre, P. 1990. Quantitave methods and biogeographic analysis. Pages 9-34 *in* D. J. Garbary and, G. R. South, eds. Evolutionary biogeography of the marine algae of the North Atlantic. NATO ASI Series, vol. G 22. Springer, Berlin.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80:107-138.

Legendre, L., and P. Legendre. 1998. Interpretation of ecological structures. *In* Numerical ecology. 2d ed. Elsevier, Amsterdam.

Low, A. B., and A. G. Rebelo. 1996. Vegetation of South Africa, Lesotho, and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

MacArthur, R. H. 1964. Environmental factors effecting bird species diversity. American Naturalist 98:387-397.

Machtans, C. S., M.-A. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology 10:1366-1379.

Morin, P. J. 2000. Biodiversity's ups and downs. Nature 406:463-464.

O'Connor, R. J., M. T. Jones, D. White, C. Hunsaker, T. Loveland, B. Jones, and E. Preston. 1996. Spatial partitioning of environmental correlates of avian biodiversity in the coterminous United States. Biodiversity Letters 3:97-110.

O'Brien, E. M. 1993. Climate gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. Journal of Biogeography 20:181-198.

———. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography 25:379-398.

O'Brien, E. M., R. J. Whittaker, and R. Field. 1998. Climate and woody plant diversity in southern Africa: relationships at species, genus and family levels. Ecography 21: 495-509.

O'Brien, E. M., R. Field, and R. J. Whittaker. 2000. Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. Oikos 89: 588-600.

Osborne, P. E., and B. J. Tigar. 1992. Interpreting bird atlas data using logistic models: an example from Lesotho, southern Africa. Journal of Applied Ecology 29:55-62.

Reed, T. 1981. The number of breeding landbird species on British Islands. Journal of Animal Ecology 50:613-624.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Ricklefs, R. E., and I. J. Lovette. 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology 68:1142-1160.

Root, T. 1988. Energy constraints on avian distributions and abundances. Ecology 69:330-339.

Rosenberg, N. J., B. L. Blad, and S. B. Verma. 1979. Microclimate: the biological environment. Wiley, New York.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages 52-65 *in* R. E. Ricklefs, and D. Schluter, eds. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.

Schulze, R. E. 1997*a*. Climate. Pages 21-41 *in* R. M. Cowling, D. M. Richardson, and S. M. Pierce, eds. Vegetation of southern Africa. Cambridge University Press, Cambridge.

———. 1997*b*. South African atlas of agrohydrology and climatology. Report TT82/96. Water Research Commission, Pretoria.

Smith, P. A. 1994. Autocorrelation in logistic regression modeling of species distribution. Global Ecology and Biogeography Letters 4:47-61.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. American Naturalist 152:510-529.

Verboom, J., A. Schotman, P. Opdam, and J. A. J. Metz. 1991. European Nuthatch metapopulations in a fragmented agricultural landscape. Oikos 61:149-156.

Verner, J., and T. A. Larson. 1989. Richness of breeding bird species in mixed-conifer forests of the Sierra Nevada, California. The Auk 106:447-463.

Villard, M.-A., G. Merriam, and B. A. Maurer. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a temperate fragmented forest. Ecology 76:27-40.

Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. Annual Review of Ecological Systematic 30:257-300.

Wartenberg, D. 1989. SAAP – a spatial autocorrelation analysis program. Robert Wood Johnson Medical School, Piscataway, N.J.

Wegner, J. F., and G. Merriam. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. Journal of Applied Ecology 16:349-357.

Wiebe, K. L., and K. Martin. 1998. Seasonal use by birds of stream-side riparian habitat in coniferous forest of northcentral British Columbia. Ecography 21:124-134.

Winterbottom, J. M. 1978. Birds. Pages 949-979 *in* M. J. A. Werger, ed. Biogeography and ecology of southern Africa. Junk, The Hague.

Woodward, F. I., M. R. Lomas, and S. E. Lee. 2001. Predicting the future production and distribution of global terrestrial vegetation. Pages 519-539 *in* J. Roy, B. Saugier, and H. Mooney, eds. Terrestrial global productivity. Academic Press, San Diego, Calif.

Wright, D. H., D. J. Currie, and B. A. Maurer. 1993. Energy supply and patterns of species richness on local and regional scales. Pages 66-74 *in* R. E. Ricklefs, and D. Schluter, eds. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.

Wylie, J. L., and D. J. Currie. 1993. Species-energy theory and patterns of species richness. II. Predicting mammal species richness on isolated nature reserves. Biological Conservation 63:145-148.

CHAPTER 3

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

Running title: Spatial congruence of ecological transition

In review: *Journal of Biogeography*

Abstract

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

Location South Africa and Lesotho.

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

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

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

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

INTRODUCTION

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

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

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

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

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

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

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

METHODS

Data

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

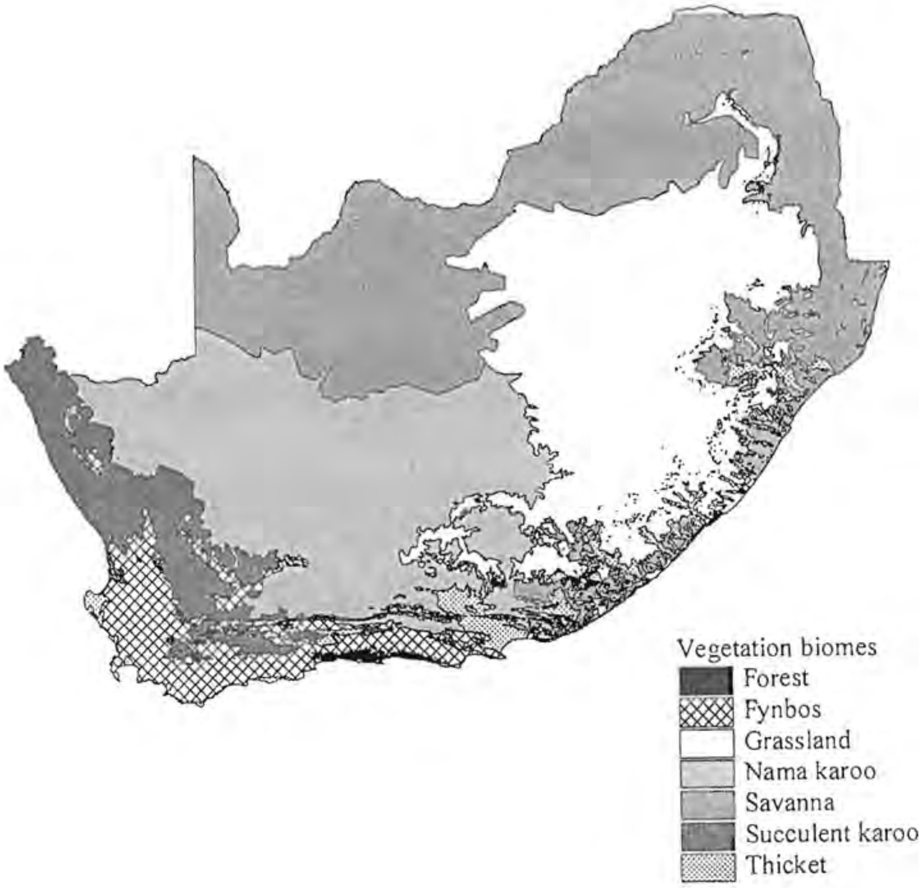


Figure 1 The vegetation biomes of South Africa and Lesotho based on Low & Rebelo (1996).

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

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

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

Spatial turnover in avian assemblages

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

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

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

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

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

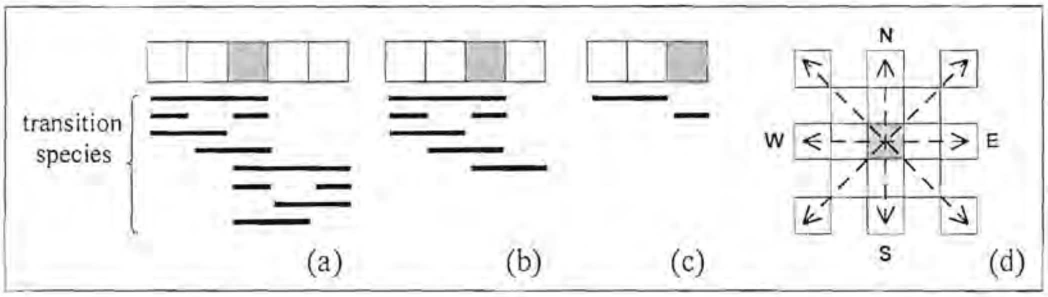


Figure 2 Illustration of the concept and measurement of β diversity based on multidirectional gradients (β_g). This measure highlights regions that have a high proportion of species that are on the edge of their ranges ('transition species'). (a) Considering a linear sequence of five adjacent cells centred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

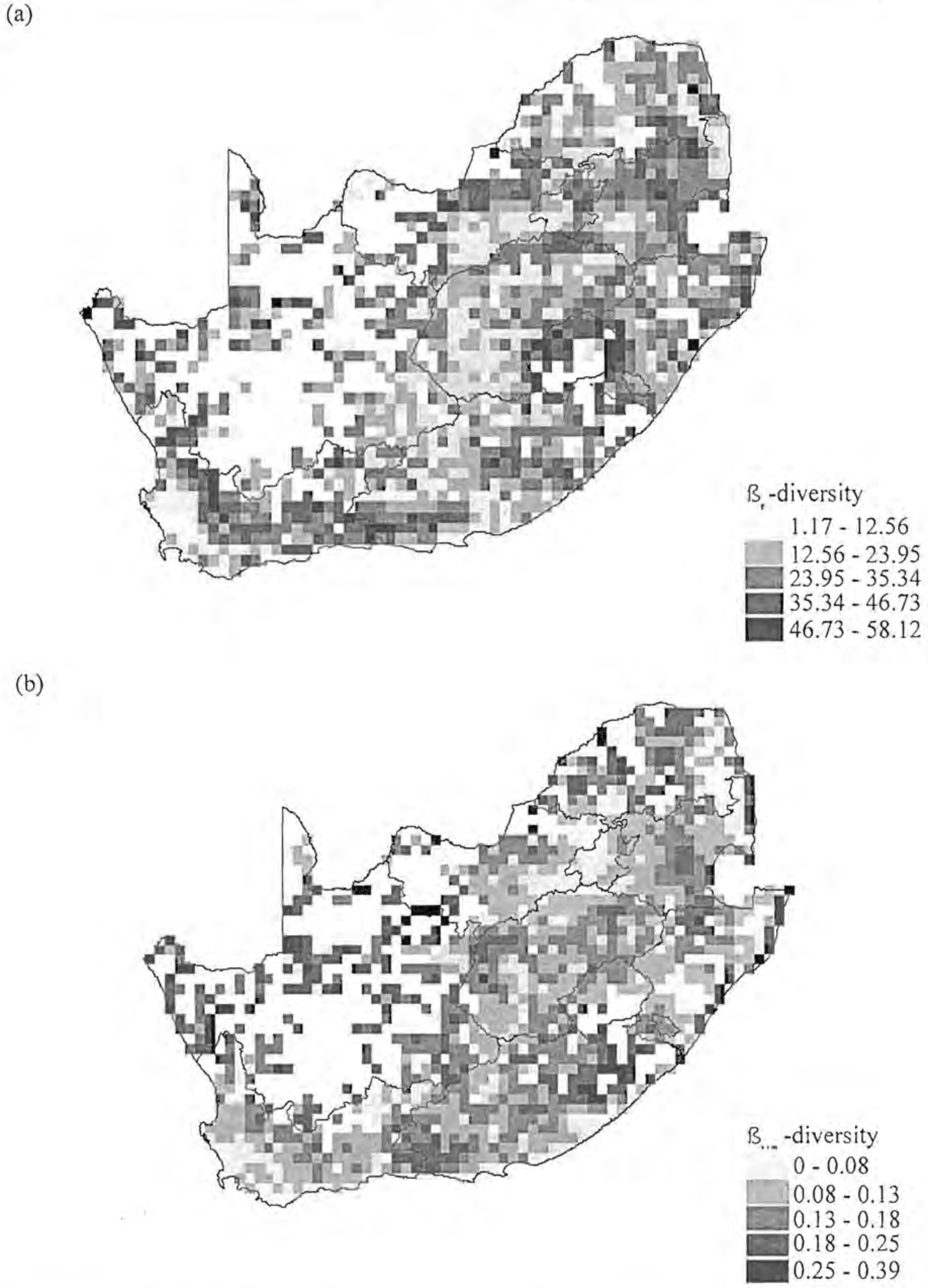


Figure 3 Patterns of: (a) β_g-diversity and (b) β_{sim}-diversity. The β-diversity values recorded ranged between 1.2% and 58.1%; 0% and 39.3% for the two β-measures respectively. Darker colours correspond to higher values of β-diversity and colour gradients represent 5 equal-interval classes. White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

Biome and land transformation transitions

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

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

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

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

Environmental heterogeneity

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

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

Identifying spatial congruence in turnover

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

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

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

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

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

Highly transformed area

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

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

RESULTS

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

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

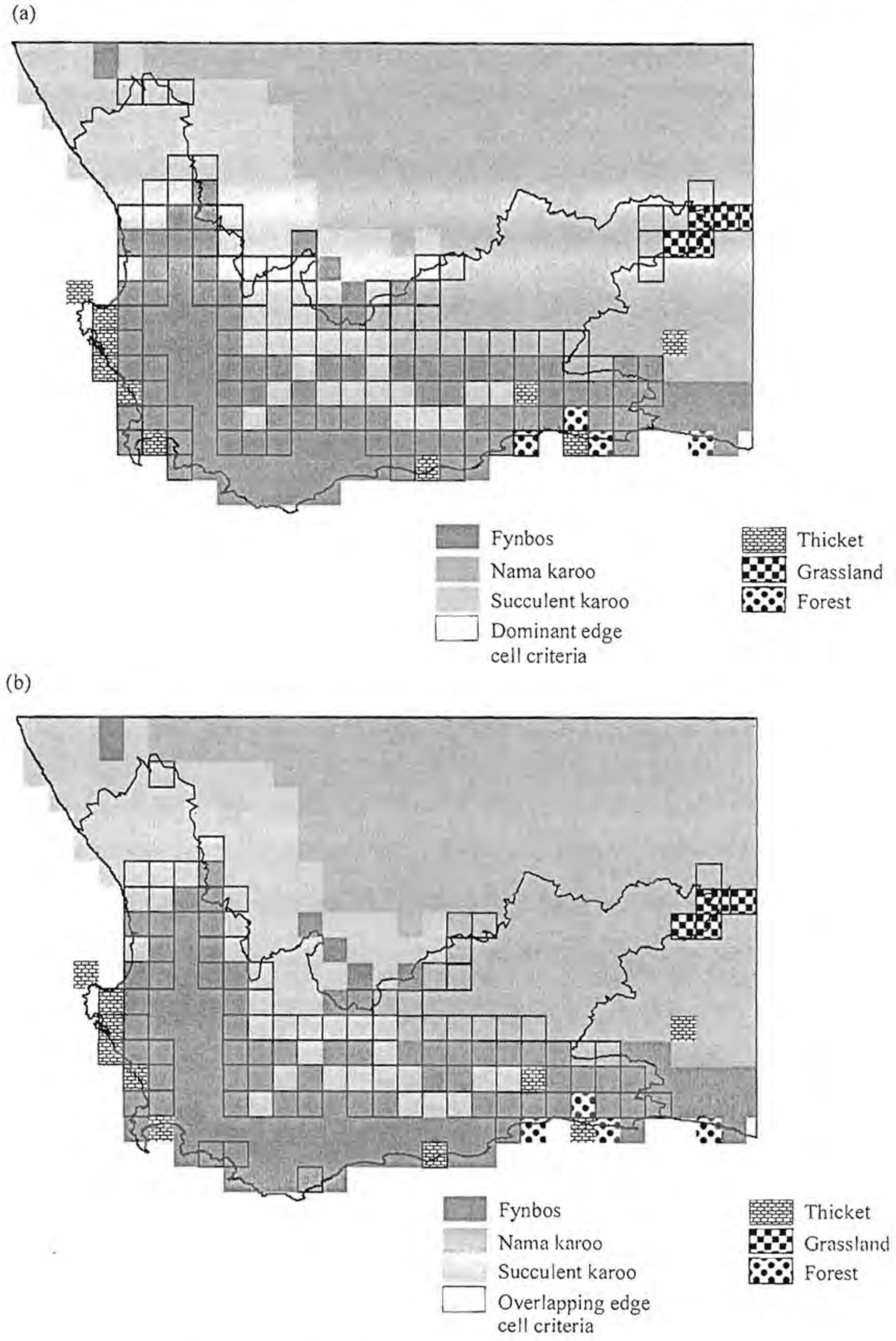


Figure 4 Biome edge cells for the Western Cape region based on the two different criteria used to detect edge cells namely, (a) the dominant edge criteria, and (b) the overlapping edge criteria.

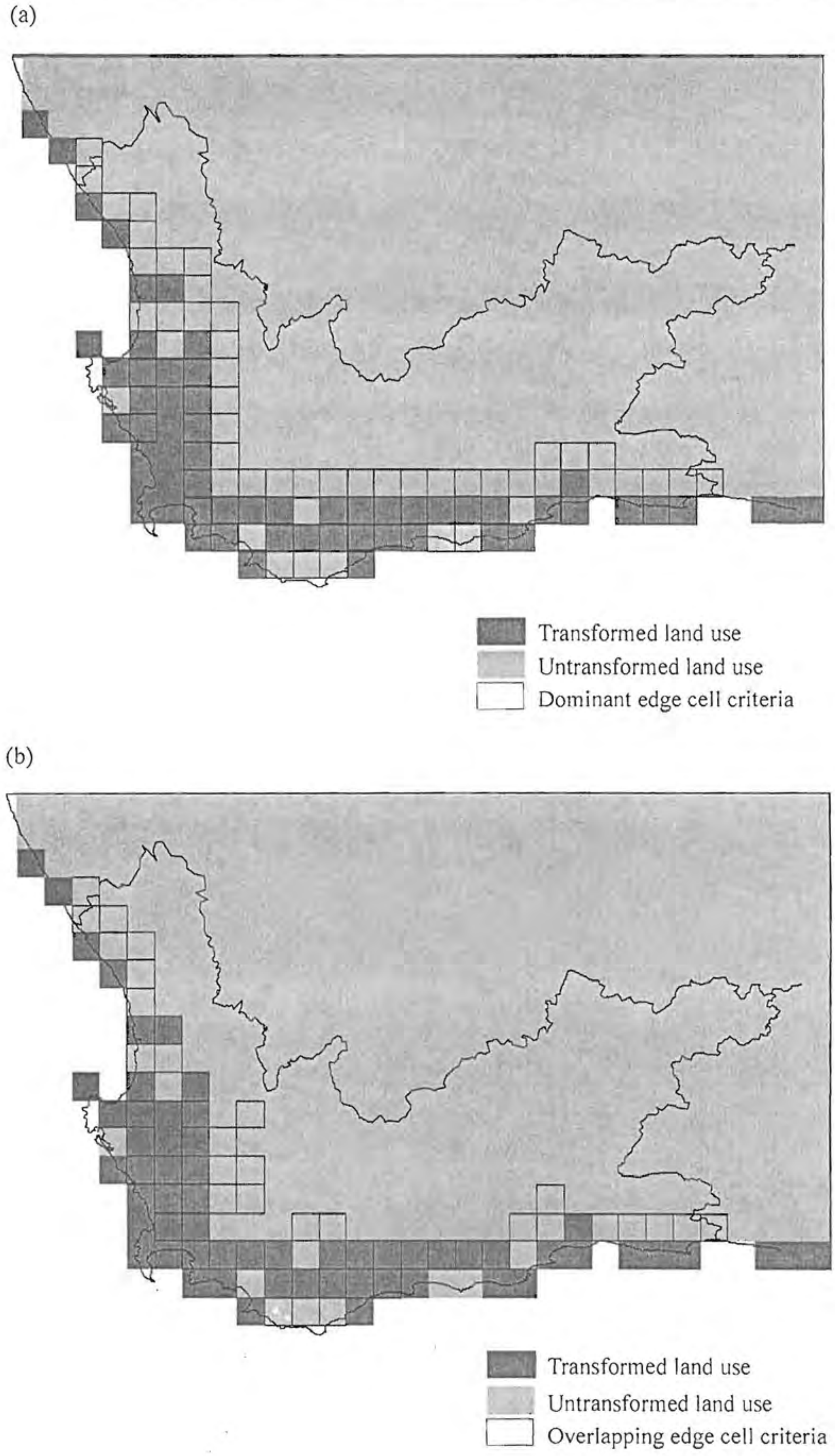


Figure 5 Land transformation edge cells for the Western Cape region based on the two different criteria used to detect edge cells namely, (a) the dominant edge criteria, and (b) the overlapping edge criteria.

areas of transition.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

ACKNOWLEDGMENTS

The Avian Demography Unit (University of Cape Town) and especially L.G. Underhill kindly provided access to the SABAP data, and the Computing Centre for Water Research (University of Natal) provided the climatic data. F. Zapata provided useful comments on an earlier version of this manuscript. B.J.V.R. and S.L.C. were supported by the South African National Research Foundation and the Andrew W. Mellon Foundation, and P.K. is supported by CONACyT (51822/122128).

REFERENCES

Allan, D. G., Harrison, J. A., Herremans, M., Navarro, R. A. & Underhill, L. G. (1997a) Southern African geography: its relevance to birds. *The atlas of southern African birds* (ed. by J. A. Harrison, D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker and C. J. Brown), pp. lxv-ci. Birdlife South Africa, Johannesburg.

Allan, D. G., Harrison, J. A., Navarro, R. A., van Wilgen, B. W. & Thompson, M. W. (1997b) The impact of commercial afforestation on bird populations in Mpumalanga province, South Africa – insights from bird-atlas data. *Biological Conservation*, **79**, 173-185.

Andrews, P. & O'Brien, E. M. (2000) Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology*, **251**, 205-231.

Barnes, K. N. (1998) *The important bird areas of southern Africa*. BirdLife South Africa, Johannesburg.

Bell, G. (2001) Neutral macroecology. *Science*, **293**, 2413-2418.

Bellamy, P. E., Hinsley, S. A. & Newton, I. (1996) Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology*, **33**, 249-262.

Bestelmeyer, B. T. & Wiens, J. A. (2001) Local and regional-scale responses of ant diversity to a semiarid biome transition. *Ecography*, **24**, 381-392.

Blackburn, T. M. & Gaston, K. J. (2001) Local avian assemblages as random draws from regional pools. *Ecography*, **24**, 50-58.

Blondel, J. & Vigne, J. D. (1993) Space, time, and man as determinants of diversity of birds and mammals in the Mediterranean region. *Species diversity in ecological communities. Historical and geographical perspectives* (ed. by R. E. Ricklefs and D. Schluter), pp. 135-146. University of Chicago Press, Chicago.

Boone, R. B. & Krohn, W. B. (2000) Relationship between avian range limits and plant transition zones in Maine. *Journal of Biogeography*, **27**, 471-482.

Brooks, D. R. & McLennan, D. A. (1991) *Phylogeny, ecology and behaviour. A research programme in comparative biology*. University of Chicago Press, Chicago.

Brooks, D. R., van Veller, M. G. P. & McLennan, D. A. (2001) How to do BPA, really. *Journal of Biogeography*, **28**, 345-358.

Brooks, T. M., Pimm, S. L., Kapos, V. & Ravilious, C. (1999) Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. *Journal of Animal Ecology*, **68**, 1061-1078.

Brown, J. H. (1995) *Macroecology*. University of Chicago Press, Chicago.

Bruderer, B. & Bruderer, H. (1993) Distribution and habitat preferences of Redbacked Shrikes *Lanius collurio* in southern Africa. *Ostrich*, **64**, 141-147.

Caley, M. J. & Schluter, D. (1997) The relationship between local and regional diversity. *Ecology*, **78**, 70-80.

Catterall, C. P., Kingston, M. B., Park, K. & Sewell, S. (1998) Deforestation, urbanisation and seasonality: interacting effects on a regional bird assemblage. *Biological Conservation*, **84**, 65-81.

Ceballos, G. & Ehrlich, P. R. (2002) Mammal population losses and the extinction crisis. *Science*, **296**, 904-

907.

Channell, R. & Lomolino, M. V. (2000) Trajectories to extinction - spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography*, **27**, 169-179.

Clarke, K. R. (1993) Non-parametric multivariate analyses of change in community structure. *Australian Journal of Ecology*, **18**, 117-143.

Clarke, K. R. & Gorley, R. N. (2001) *PRIMER v5: User manual/tutorial*. PRIMER-E Ltd. Plymouth, United Kingdom.

Clarke, K. R. & Warwick, R. M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Natural Environmental Research Council, United Kingdom.

Clifford, P., Richardson, S. & Hemon, D. (1989) Assessing the significance of the correlation between two spatial processes. *Biometrics*, **45**, 123-134.

Cody, M. L. (1975) Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. *Ecology and evolution of communities* (ed. by M. L. Cody and J. M. Diamond), pp. 214-257. Harvard University Press, Cambridge, Massachusetts.

Cody, M. L. (1985) An introduction to habitat selection in birds. *Habitat selection in birds* (ed. by M. L. Cody), pp. 3-56. Academic press, London.

Cody, M. L. (1993) Bird diversity components within and between habitats in Australia. *Species diversity in ecological communities. Historical and geographical perspectives* (ed. by R. E. Ricklefs and D. Schluter), pp. 147-158. University of Chicago Press, Chicago.

Collar, N. J., Crosby, M. J. & Stattersfield, A. J. (1994) *Birds to watch 2. The world list of threatened birds*. Birdlife International, Cambridge.

Cornell, H. V. & Karlson, R. H. (1996) Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology*, **65**, 233-241.

Cornell, H. V. & Lawton, J. H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1-12.

Cowling, R. M. (1992) *The ecology of Fynbos. Nutrients, fire and diversity*. Oxford University Press, Cape Town.

Cowling, R. M. & Campbell, B. M. (1980) Convergence in vegetation structure in the Mediterranean communities of California, Chile and South Africa. *Vegetation*, **43**, 191-197.

Cowling, R. M., Gibbs Russell, G. E., Hoffman, M. T & Hilton-Taylor, C. (1989) Patterns of plant species diversity in southern Africa. *Biotic diversity in southern Africa. Concepts and conservation* (ed. by B. J. Huntley), pp. 19-50. Oxford University Press, Cape Town.

Cowling, R. M., Macdonald, I. A. W. & Simmons, M. T. (1996) The Cape Peninsula, South Africa: physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation*, **5**, 527-550.

Cox, C. B. (2001) The biogeographic regions reconsidered. *Journal of Biogeography*, **28**, 511-523.

Cox, C. B. & Moore, P. D. (1993) *Biogeography. An ecological and evolutionary approach*. Blackwell Science, Oxford.

Cracraft, J. & Prum, R. O. (1988) Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. *Evolution*, **42**, 603-620.

Darlington, P. J. (1957) *Zoogeography: The geographical distribution of animals*. John Wiley, New York.

Davis, A. L. V. (1997) Climatic and biogeographical associations of southern African dung beetles (Coleoptera: Scarabaeidae *s. str*). *African Journal of Ecology*, **35**, 10-38.

Davis, A. L. V. (2002) Dung beetle diversity in South Africa: influential factors, conservation status, data inadequacies and survey design. *African Entomology*, **10**, 53-65.

Davis, A. L. V., Scholtz, C. H. & Chown, S. L. (1999) Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *Journal of Biogeography*, **26**, 1039-1055.

Dean, W. R. J. (2000) Factors affecting bird diversity patterns in the Karoo, South Africa. *South African Journal of Science*, **96**, 609-616.

Desrochers, A. & Fortin, M. J. (2000) Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. *Oikos*, **91**, 376-384.

Endler, J. A. (1982) Problems in distinguishing historical from ecological factors in biogeography. *American Zoologist*, **22**, 441-452.

Erasmus, L. & van Jaarsveld, A. S. (2002) Exploring policy interventions for sustainable development in South Africa: a modeling approach. *South African Journal of Science*, **98**, 3-8.

ESRI Inc. (1998) *Environmental systems research institute*. Inc., Redlands, California.

Fairbanks, D. H. K., Kshatriya, M., van Jaarsveld, A. S. & Underhill, L. G. (2002) Scales and consequences of human land transformation on South African avian diversity and structure. *Animal Conservation*, **5**, 61-73.

Fairbanks, D. H. K., Thompson, M.W., Vink, D.E., Newby, T., van den Berg, H.M. & Everard, D.A. (2000) The South-African land-cover characteristics database: a synopsis of the landscape. *South African Journal of Science*, **96**, 69-86.

Gaston, K. J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220-227.

Gaston, K. J. & T. M. Blackburn. (2000) *Patterns and process in macroecology*. Blackwell Science, United Kingdom.

Gaston, K. J. & A. S. L. Rodrigues. (2002) Reserve selection in regions with poor biological data. *Conservation Biology*, in press.

Gaston, K. J., Rodrigues, A. S. L., van Rensburg, B. J., Koleff, P. & Chown, S. L. (2001) Complementary representation and zones of ecological transition. *Ecology Letters*, **4**, 4-9.

Gentilli, J. (1992) Numerical clines and escarpments in the geographical occurrence of avian species; and a search for relevant environmental factors. *Emu*, **92**, 129-140.

Gosz, J. R. (1992) Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. Landscape boundaries: consequences for biotic diversity and ecological flows (ed. by A. J.

Hansen and F. di Castri), pp. 55-75. Springer.

Gosz, J. R. (1993) Ecotone hierarchies. *Ecological Applications*, **3**, 369-376.

Gosz, J. R. & Sharpe, P. J. H. (1989) Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. *Landscape Ecology*, **3**, 229-243.

Hanski, I., & Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, **275**, 397-400.

Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V. & C Brown, C. J. (1997) *The atlas of southern African birds*, vols. 1 and 2. BirdLife South Africa, Johannesburg.

Hattersley, A.F. (1969) *An illustrated social history of South Africa*. A. A. Balkema, Cape Town.

Hengeveld, R. (1990) *Dynamic biogeography*. Cambridge University Press, Cambridge.

Hockey, P. A. R., Allan, D. G., Rebelo, A. G. & Dean, W. R. J. (1988) The distribution, habitat requirements and conservation status of Rudd's Lark *Heteromirafra ruddi* in South Africa. *Biological Conservation*, **45**, 255-266.

Holm, E. & Scholtz, C. H. (1985) A zoogeographical delimitation of the Kalahari subregion based on excluded species. *Journal of Arid Environment*, **8**, 165-169.

Huntley, B. J. (1989) *Biotic diversity in southern Africa. Concepts and conservation*. Oxford University Press, Cape Town.

Jeannel, R. (1964) Biogéographie des terres Australes de l'Océan Indien. *Revue Francaise d'Entomologie*, **31**, 319-417.

Krasnov, B. R. & Shenbrot, G. I. (1998) Structure of communities of ground-dwelling animals at the junction of two phytogeographic zones. *Journal of Biogeography*, **25**, 1115-1131.

Krebs, C. J. (1999) *Ecological methodology*, 2nd edition. Addison-Wesley Educational Publisher, Inc..

Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, **76**, 5-13.

Lawes, M. J. (1990) The distribution of the Samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffroy, 1843) and forest history in southern Africa. *Journal of Biogeography*, **17**, 669-680.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*. 2nd English edition. Elsevier Science BV, Amsterdam.

Lennon, J. J. (2000) Red-shifts and red herrings in geographical ecology. *Ecography*, **23**, 101-113.

Lennon, J. J., Koleff, P., Greenwood, J. J. D. & Gaston, K. J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966-979.

Low, A. B. & Rebelo, A. G. (1996) *Vegetation of South Africa, Lesotho, and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria, South Africa.

Macdonald, I. A. W. (1989) Man's role in changing the face of southern Africa. *Biotic diversity in southern Africa. Concepts and conservation* (ed. by B. J. Huntley), pp. 51-77. Oxford University Press, Cape Town.

MacNally, R. (1997) Monitoring forest bird communities for impact assessment: the influence of sampling intensity and spatial scale. *Biological Conservation*, **82**, 355-367.

MacPhee, R. D. E. (ed.) (1999) *Extinctions in near time: causes, contexts, and consequences.* Kluwer Academic/Plenum.

Magurran, A. E. (1988) *Ecological diversity and its measurement.* Princeton Univ. Press, Princeton, NJ.

McInnes, S. J. & Pugh, P. J. A. (1998) Biogeography of limo-terrestrial Tardigrada, with particular reference to the Antarctic fauna. *Journal of Biogeography,* **25**, 31-36.

McKinney, M. & Drake, J. A. (1994) *Dynamics of biodiversity: origination and extinction of populations, species, communities, and higher taxa.* Chicago.

Morrone, J. J. (1994) On the identification of areas of endemism. *Systematic Biology,* **43**, 438-441.

Morrone, J. J. (1998) On Udvardy's Insulantarctica province: a test from the weevils (Coleoptera: Curculionoidea). *Journal of Biogeography,* **25**, 947-955.

Morrone, J. J. (2002) Biogeographical regions under track and cladistic scrutiny. *Journal of Biogeography,* **29**, 149-152.

Morrone, J. J. & Crisci, J. V. (1995) Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics,* **26**, 373-401.

Muller, C. F. J. (1969) *Five hundred years, a history of South Africa.* Academica, Pretoria.

Myers, A. A. & Giller, P. S. (1988) *Analytical biogeography. An integrated approach to the study of animal and plant distributions.* Chapman and Hall, London.

Nekola, J. C. & White, P. S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography,* **26**, 867-878.

Newbegin, M. I. (1936) *Plant and animal geography.* Methuen, London.

O'Brien, E. M. (1993) Climate gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography,* **20**,181-198.

O'Brien, E. M. (1998) Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography,* **25**, 379-398.

O'Brien, E. M., Whittaker, R. J. & Field, R. (1998) Climate and woody plant diversity in southern Africa: relationships at species, genus and family levels. *Ecography,* **21**, 495-509.

O'Brien, E. M., Field, R. & Whittaker, R. J. (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. *Oikos,* **89**, 588-600.

Osborne, P. E., & Tigar, B. J. (1992) Interpreting bird atlas data using logistic models: an example from Lesotho, southern Africa. *Journal of Applied Ecology,* **29**, 55-62.

Pitelka, F. A. (1941) Distribution of birds in relation to major biotic communities. *American Naturalist,* **25**, 113-137.

Polo, V. & Carrascal, L. M. (1999) Shaping the body mass distribution of Passeriformes: habitat use and body mass are evolutionarily and ecologically related. *Journal of Animal Ecology,* **68**, 324-337.

Poynton, J. C. (1961) Biogeography of south-east Africa. *Nature,* **189**, 801-803.

Poynton, J. C. & Boycott, R. C. (1996) Species turnover between Afromontane and eastern African lowland faunas: patterns shown by amphibians. *Journal of Biogeography,* **23**, 669-680.

Rahbek, C. & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academic of Science, USA*, **98**, 4534-4539.

Recher, H. F. (1969) Bird species diversity and habitat diversity in Australia and North America. *American Naturalist*, **103**, 75-80.

Redford, K. H. & Dinerstein, E. (1994) Biological diversity and agriculture. *Science*, **265**, 457-458.

Reyers, B, Fairbanks, D. H. K., Wessels, K. J. & van Jaarsveld, A. S. in press. A multicriteria approach to reserve selection: addressing long-term biodiversity maintenance. *Biodiversity and Conservation*.

Rice, W. R. (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223-225.

Richardson, D. M., van Wilgen, B. W., Higgins, S. I., Trinder-Smith, T. H., Cowling, R. M. & McKell, D. H. (1996) Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity and Conservation*, **5**, 607-647.

Ricklefs, R. E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167-171.

Risser, P. G. (1995) The status of the science examining ecotones. A dynamic espect of landscape is the area of steep gradients between more homogeneous vegetation associations. *BioScience*, **45**, 318-325.

Rodrigues, A. S. L. & Gaston, K. J. (2002) Rarity and conservation planning across geopolitical units. *Conservation Biology*, **16**, 674-682.

Rosenzweig, M. L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, United Kingdom.

Rotenberry, J. T. & Wiens, J. A. (1980) Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. *Ecology*, **61**, 1228-1250.

Rutherford, M. C. & Westfall, R. H. (1994) Biomes of southern Africa: an objective categorization. *Memoirs of the Botanical Survey of South Africa*, **63**, 1-94.

Ryti, R. T., & Gilpin, M. E. (1987) The comparative analysis of species occurrence patterns on archipelagos. *Oecologia*, **73**, 282-287.

Scholtz, C. H. & Chown, S. L. (1993) Insect conservation and extensive agriculture: The savanna of southern Africa. *Perspectives on insect conservation* (ed. by K. J. Gaston, T. R. New and M. J. Samways), pp. 75-95. Intercept, Andover.

Schulze, R. E. (1998) *South African atlas of agrohydrology and climatology* (Report TT82/96). Water Research Commission, Pretoria, South Africa.

Smith, A. B. (1994) *Systematics and the fossil record. documenting evolutionary patterns*. Blackwell Science, Oxford.

Srivastava, D. (1999) Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**, 1-16.

Stotz, D. F. (1998) Endemism and species turnover with elevation in montane avifaunas in the neotropics: implications for conservation. *Conservation in a changing world*. (ed. by G. M. Mace, A. Balmford and J.

R. Ginsberg), pp. 161-180. Cambridge University Press, Cambridge.

Theal, G. M. (1964) *History of South Africa before 1795: the Portuguese in South Africa from 1505 to 1795.* Struik, Cape Town.

Thompson, M. (1996) The standard land-cover classification scheme for remote-sensing application in South Africa. *South African Journal of Science*, **92**, 34-42.

Udvardy, M. D. F. (1987) The biogeographical realm Antarctica: A proposal. *Journal of the Royal Society of New Zealand*, **17**, 187-194.

Van Rensburg, B. J., Chown, S. L., & Gaston, K. J. (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *American Naturalist*, **159**, 566-577.

Van Rensburg, B. J., Chown, S. L., McGeoch, M. A., & van Jaarsveld, A. S. (2000) Spatial variation and biogeography of sand forest avian assemblages in South Africa. *Journal of Biogeography*, **27**, 1385-1401.

Verner, J. & Larson, T. A. (1989) Richness of breeding bird species in mixed-conifer forests of the Sierra Nevada, California. *The Auk*, **106**, 447-463.

Wallace, A. R. (1876) *The geographical distribution of animals*, vols. 1 and 2. London, Macmillan.

Wiebe, K. L. & Martin, K. (1998) Seasonal use by birds of stream-side riparian habitat in coniferous forest of northcentral British Columbia. *Ecography*, **21**, 124-134.

Wiens, J. A. (1991) Ecological similarity of shrub-desert avifaunas of Australia and North America. *Ecology*, **72**, 479-495.

Williams, P. H. (1996) Mapping variations in the strength and breath of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London B* **263**, 579-588.

Williams, P. H., de Klerk, H. M. & Crowe, T. M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography*, **26**, 459-474.

Williamson, M. (1996) *Biological invasions*. Chapman and Hall, London, United Kingdom.

Williamson, M. (1999) Invasions. *Ecography*, **22**, 5-12.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661-1665.

Wilson, M. V. & Shmida, A. (1984) Measuring beta-diversity with presence-absence data. *Journal of Ecology*, **72**, 1055-1064.

Winterbottom, J. M. (1978) Birds. *Biogeography and ecology of southern Africa* (ed. by M. J. A. Werger), pp. 949-979. W. Junk, The Hague.

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

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

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

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