5. Human-Ecosystem Co-evolution: Analysis of Bird Diversity and Structure with Human Land Transformation

> But when I consider that the nobler animals have been exterminated here - the cougar, panther, lynx, wolverine, wolf bear, moose, deer, the beaver, the turkey, etc., etc. - I cannot but feel as if I lived in a tamed, and as it were emasculated country ... I listen to a concert in which so many parts are wanting ... for instance, thinking that I have here the entire poem, and then to my chagrin, I hear that it is but an imperfect copy that I possess and have read, that my ancestors have torn out many of the first leaves and grandest passages ...
>
> -HENRY DAVID THOREAU, *Journal*, 1861

Biodiversity is suffering losses at an accelerated rate due to human action and biologists are increasing their efforts to understand this decline and develop appropriate conservation responses (Wilson, 1988; Lubchenco et al., 1991; Soulé, 1991; Dale et al., 1994; Pimm et al., 1995; Margules and Pressey, 2000). Although there is little consensus about the most appropriate response strategy (Mace et al., 2000), systematic approaches such as complementary networks, species richness "hotspots" and gap analysis (Pressey et al., 1993; Scott et al., 1993; Williams et al., 1996; Mittermeier et al., 1998; Reid, 1998; Schwartz, 1999; Myers et al., 2000) all employ species or community assemblage patterns derived from biological surveys. These data are systematically interpreted in a spatially explicit manner to identify "ideal" or "real world" conservation land-use plans.

An understanding of the structure of human modification dynamics across a landscape and its co-relation with species presence and abundance is required. In contrast to the degree of human influence on ecosystems, ecologists have concentrated their research on relatively pristine areas (Cairns, 1988; Lubchenco et al., 1991; O'Neill and Kahn, 2000) and have failed to incorporate human beings and their institutions as explicit agents in the functioning of ecosystems (McDonnell and Pickett, 1990; McDonnell et al, 1993; McDonnell et al., 1995, Breitburg et al., 1998; O'Neill and Kahn, 2000). This focus of research has led to a lack of information on how land-use affects biological diversity in general and in particular within developing regions of the world. Landscape ecology, however, and its methods have advanced the farthest in attempting to understand landscape pattern shaped by humans as explanatory variables to biological pattern and processes (Turner, 1989; Nevah and Lieberman, 1993; Forman, 1995; Brooker et al., 1999). Several studies have looked at the results of human induced changes through pattern development (i.e., fragmentation) and linked the pattern to biodiversity dynamics (e.g., Lynch et al., 1984; Quinn and Harrison, 1988; Burkey, 1989; Opdam, 1991; Farina, 1997; White et al., 1997).

5.1 Factors Associated with Regional Variation in Species Composition

Identifying the factors controlling the distribution, abundance, and diversity of species in ecological communities continues to be a central problem in ecology, with increasing emphasis on human dimensions of change to explain the patterns, at least partially (Forman, 1995; Lubchenco et al., 1991; Turner, 1989; McDonnell and Pickett, 1993). Community structure is considered not only a product of local physical condition and interactions among species, but also of regional constraints such as climate, and of historical processes such as dispersal and speciation, migration, and extinction (Menge and Olson, 1990; Latham and Ricklefs, 1993; Ricklefs and Schulter, 1993). Plant community ecologists have long devoted considerable effort to quantifying local to landscape-scale variation in vegetation with recent efforts to quantify broad scale determinants (Denton and Barnes, 1987; Ohmann and Spies, 1998; Fairbanks and McGwire, 2000). In contrast, animal community ecologists have spent much effort in understanding local and increasingly more landscape-scale variation in species and communities (Wiens and Rottenberry, 1981; Opdam et al., 1984; Cody, 1985; Maurer and Heywood, 1993; McGarigal and McComb, 1995; Villard and Maurer, 1996; Flather, 1996). Still there are few systematic, quantitative, regional-scale descriptions to provide contexts for interpreting landscape differences (but see Wiens, 1973; Wiens, 1974; Rotenberry 1978; Rotenberry and Wiens, 1980; McGarigal and McComb, 1995; Flather, 1996). Yet, the collation, examination, and synthesis of species-community data in regional analysis has been cited as a major research need for conservation (Soulé and Simberloff, 1986; Balmford and Gaston, 1999).

In an effort to understand avian community temporal dynamics, pattern and scale, this chapter undertakes a quantitative, systematic analysis of avian species data at the South African extent followed by a more detailed analysis for the KwaZulu-Natal province. It is instructive to consider these in a hierarchical fashion, from the broadest to the most localized. Broad and landscape-scale factors are examined as contributions to regional variation in community composition, and the influences of physical environment, biotic factors, and human disturbance processes are explored. The study objectives were to identify and quantify environmental and landscape pattern factors associated with regional gradients in avian species diversity between the two survey periods outlined in Chapter 1. This chapter addresses questions about factors controlling avian species assemblages by considering a broader region and a large data set from two periods, and uses contemporary multivariate statistical and spatial analytical tools to accomplish its task.

5.2 Influence of Geographical Extent and Location

Within a local area, the range of climatic conditions is usually small, and most sites fall within an animal species' physiological tolerances. Thus, shifts in species' relative abundances are thought to be associated with local variation in topography, microclimate, vegetation, biotic interactions, and human impact, as well as with stochastic disturbances that are highly variable over time and space. Therefore, one can hypothesize that species variation explained by regional climate decreases, and variation explained by local factors increases, with decreasing geographic extent.

Different environmental factors probably assume varying degrees of importance among localities within a region, and landscape pattern or land cover proportion are likely to dominant in importance in a similar manner. In KwaZulu-Natal, the hypothesis that topographic, temperature and moisture factors assume the greatest importance for explaining variation in bird diversity at coarser scales, and landscape pattern and land cover proportion explains the remaining variation in diversity in a hierarchically scaled manner is explored. In Chapter 4 this concept was explored on a reduced data set of species targeted for conservation (Table 1.3), with results showing that the climatic factors and the landscape-vegetation complex are interacting to define communities by limiting species ranges. This chapter continues the examination in more detail to study community changes and how they might affect the use of systematic conservation procedures conducted in chapter four.

5.3 Biological Indicators and Monitoring

Biological atlases routinely strive to incorporate appropriate sampling designs, data collation and interpolation procedures (Prendergast et al., 1993) to minimize sampling errors caused by differences in sampling effort, sampling duration, the degree of ecological specialization and patchy habitat occupancies flowing from metapopulation characteristics of species (Brown, 1984; McArdle, 1990; Hanski et al., 1993). Therefore, in practice, species richness and community assemblage data derived from contemporary biological atlases are considered adequate (Donald and Fuller, 1998), or at least, the best available basis from which to conduct conservation planning.

The relationship between distribution and abundance has important implications for species richness and conservation planning. The term distribution here is referred to as a species' geographical range, though recognizing that, given a set of observations with geographical coordinates, a range boundary may be drawn in different ways (Gaston, 1990). Abundance refers to the size of a "local" population found in an arbitrarily defined study area. Species richness is a problematic indicator (Stoms, 1994). Sampling effort, sampling period, size of sampling area, and human influence can hugely effect the final species distribution and abundance for a taxon (e.g., birds) found in a particular area. Where effort is recorded for species, however, for inventorying exercises over a short time frame, richness correction techniques have been suggested (e.g., Soberon and Llorente, 1993; Fagan and Karivera, 1997).

Since distribution and abundance may change over time, they should both be estimated within a sufficiently short period. This is a potentially serious problem for faunal atlasing studies and national biological surveys, on which estimates of distribution are often based, because such studies typically accumulate observations over a long period. The results from these larger longer-term studies of distribution are used to develop simple indices of species richness or diversity that gets used in reserve selection analyses to derive strategic decisions. The unique characteristics of atlas studies, however, may allow for the study of species assemblage responses to degrees of human disturbance (disturbance hypothesis; sensu Connell, 1978; Burel, 1998). This could allow for a more informed approach to conservation planning.

In addition to viewing human land transformation as a threat to conservation, this chapter explores the phenomena as a shaping force of species richness or community assemblage patterns, which can be derived from biological atlases. This chapter examines the interactions between bird species richness, assemblage characteristics, and the degree of land transformation at the South African (including Lesotho) spatial extent and then a more detailed analysis is conducted for KwaZulu-Natal.

5.4 Methods

5.4.1 Diversity-evenness and Human Transformation Patterns

Three ecological measures were used to characterize bird species assemblages (e.g., Burel, 1998) per quarter-degree grid cell: Species richness, Shannon diversity, and an adjusted evenness measure to reduce sampling effort bias. Species richness (*S*) is simply the total number of bird species recorded in a grid cell. Evenness (*E*) is a relative measure to quantify unequal species representation against a hypothetical assemblage in which all which species are equally common (Krebs, 1989). Evenness was calculated using:

$$E = \frac{H' - H'_{\min}}{H'_{\max} - H'_{\min}}$$

where H' is the observed Shannon index of species diversity as given by the following formula:

$$H' = -\sum_{i=1}^{S} p_i \log p_i$$

where S is the total number of birds species with proportional abundances $p_1, p_2, \ldots, p_S$ (Ludwig and Reynolds, 1988). In addition to providing information on presence/absence, the ADU data also provided a simple measure of abundance based on reporting rates. A reporting rate is the percentage of checklists on which a species was recorded relative to the total number of checklists for a grid cell. This form of relative abundance from the atlas data has been quantitatively evaluated previously to correspond well to other field data and deemed fit for use in general population studies (Robertson et al., 1995). As a result, the relative abundance of a species was estimated by the ratio of number of observations reported for species i over the total number of observations for all species in a grid square (Harrison and Martinez, 1995). The variables $H'_{\min}$ and $H'_{\max}$ are the minimum and maximum values of the index respectively. The maximum value of the index is simply $H'_{\max} = \log(S)$ and the minimum is given by the following formula (Krebs, 1989):

$$H'_{\min} = \log(N) - \left(\frac{N - S + 1}{N}\right) \log(N - S + 1)$$

where N is the total number of species presences observed in a grid square (Harrison et al., 1997). The evenness index (E) varies from 0, when a few species are dominant, to 1, when all species are equally abundant. In general, the total number of species in the sample and sampling effort (Magurran, 1988) can largely influence the Shannon diversity index and the evenness index. However, since evenness is measured as a ratio with the number of species in both the numerator and the denominator, it may effectively cancel the impact of the number of species in the sample, which is a product of effort (Magurran, 1988; Ludwig and Reynolds, 1988; Krebs, 1989). In this study, species richness is significantly positively correlated with the Shannon index ($r = 0.91$, $N = 1844$, $p < 0.001$) and the pre-correction relationship to evenness was significantly negatively correlated ($r = -0.62$, $N = 1844$, $p < 0.001$), but after correcting for sampling effort, the correlation was negligible ($r = 0.09$, $N = 1844$, $p < 0.1$).

Two levels of analysis, South Africa and KwaZulu-Natal, are reported to examine the influence of geographic extent on the analysis. Two datasets are reported for the South African study extent: original species richness (Figure 5.1a) and evenness (Figure 5.1b), and smoothed measures (e.g., Prendergast and Eversham, 1997; Williams and Gaston, 1998) generated by performing neighborhood averaging (Figure 5.1c, d). Smoothing of the richness and evenness maps was carried out to further remove the vagaries of sampling and to make larger scale variation more apparent. For each grid cell, species richness and evenness measure are calculated as the median for the group including the core cell and the surrounding neighborhood of eight cells (i.e., equivalent to an area approximately 75 x 75 km). Simple median filtering has the effect of reducing local differences in species richness and evenness. Given a relationship between two variables, smoothing will tend to reduce the local variance about that relationship, reducing the impact of outliers. This operation also changes the scale of analysis to provide a regional estimate of biodiversity. The original local scale human disturbance patterns of low and high intensity transformation were retained (Figure 5.2). The two data sets provide local scale and regional scale estimates of measured biodiversity co-variation with human disturbance for South Africa.

The assessment of human disturbance on species richness and evenness was conducted at the South African extent and then by biome (Figure 5.3) to control for expected variation in species richness and evenness. This is particularly the case since high intensity land-use is concentrated in only a few of the biomes (Figure 5.2b and 5.3). Not controlling for this effect assumes that all biomes have the same mean species richness and evenness, which is certainly not true. This was confirmed using analysis of covariance (ANCOVA). Spatially corrected Pearson correlation coefficients (r_s) are calculated between the data sets using the procedure developed by Dutilleul (1993), which corrects for spatial autocorrelation (using Morans *I*; Cliff and Ord, 1981) when calculating the significance (*p*) of the correlation coefficients. The procedure does not change the value of the coefficient but reduces the degrees of freedom and hence alters the *p* significance. This exploratory analysis accounts for the spatial dependence of the data and their covariance patterns. For KwaZulu-Natal, the assessment was conducted on species richness, Shannon diversity, and evenness measures for the province by life history bird assemblage (Chapter 1; Table 1.3) from the ADU database.

5.4.2 Geostatisical Analysis of Spatial Variation and Extent in Ecological Pattern

It is clear that ecologists have a great need to incorporate spatial information into their analyses. Spatial pattern reflects the underlying structure in the variation of a variable of interest, and it often provides clues as to possible cause. The development of geostatistics by Matheron (1963) provides a theoretical and methodological framework for addressing problems unique to spatial data. Variables that characterize a spatial property or process generally exhibit a localized spatial dependence (i.e., autocorrelation) within a measurement field, which satisfies some reasonable level of stationarity at a more global scale. Geostatistical techniques are based on the general regionalized variable model (Cressie, 1993). The model is a linear model of spatial process that includes both an explanatory component and a random component. Geostatistics embody a set of methods applicable throughout the Earth sciences for investigating spatial variation and extent in a continuous random variable (Cressie, 1993; Burroughs, 1986).

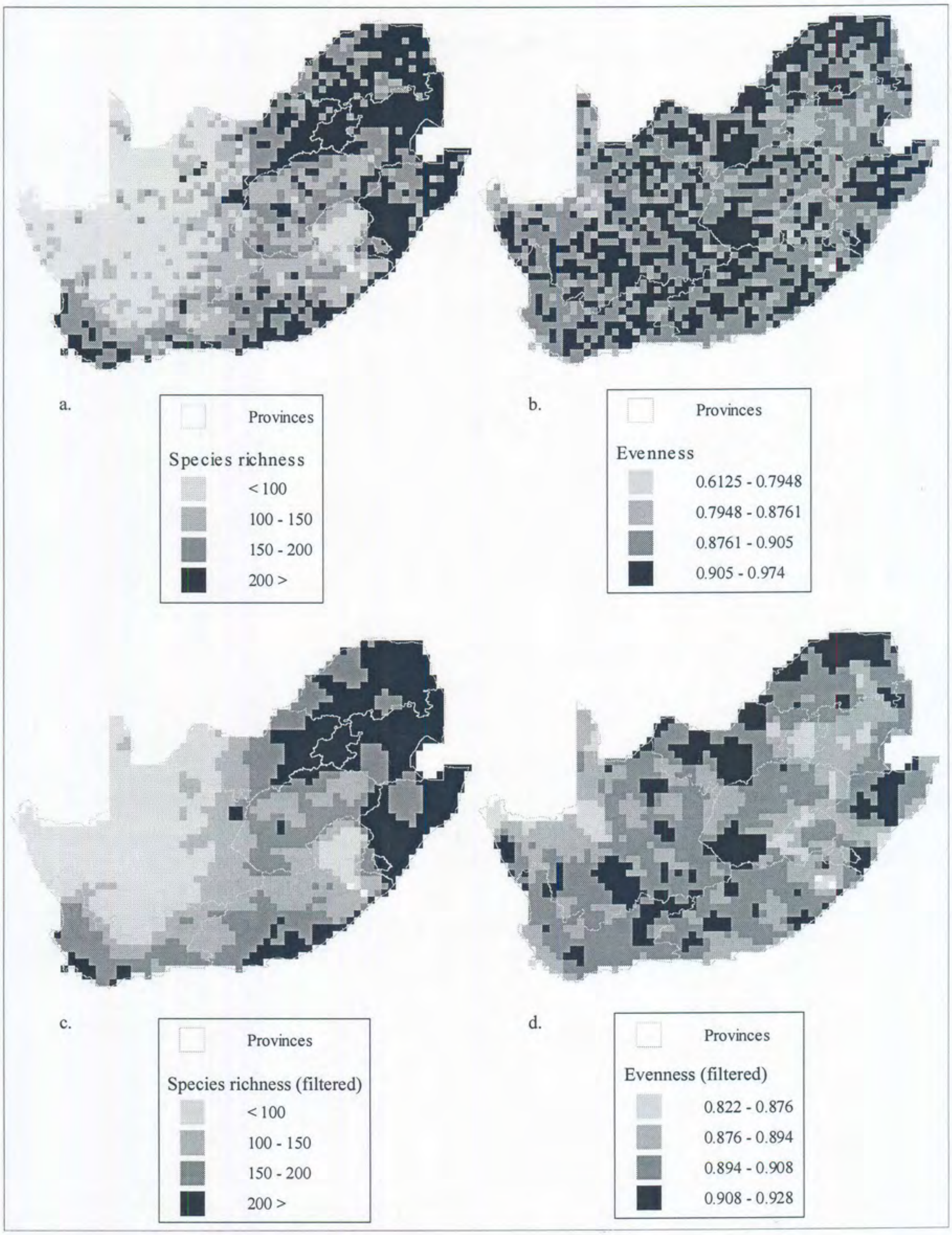

Figure 5.1: (a) Bird species richness across South Africa; (b) evenness structure of birds across South Africa; (c) Bird species richness using smoothed data; and (d) evenness structure using smoothed data.

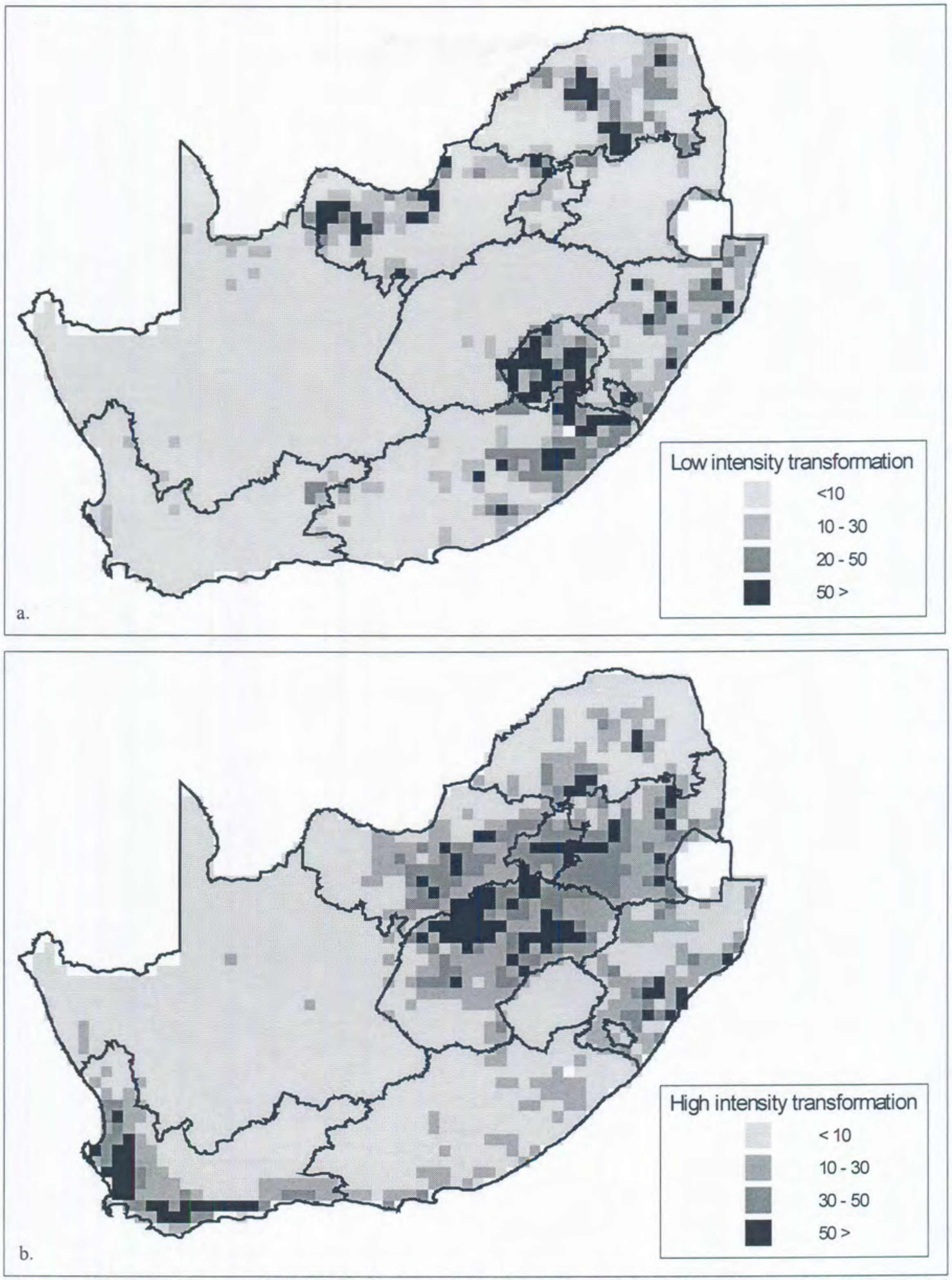

Figure 5.2: The separation between the transformation categories illustrates the spatial heterogeneity found within South Africa, particularly highlighting the development differences between: (a) low intensity transformation representing African ex-homeland areas; and (b) high intensity transformation representing "White" developed South Africa.

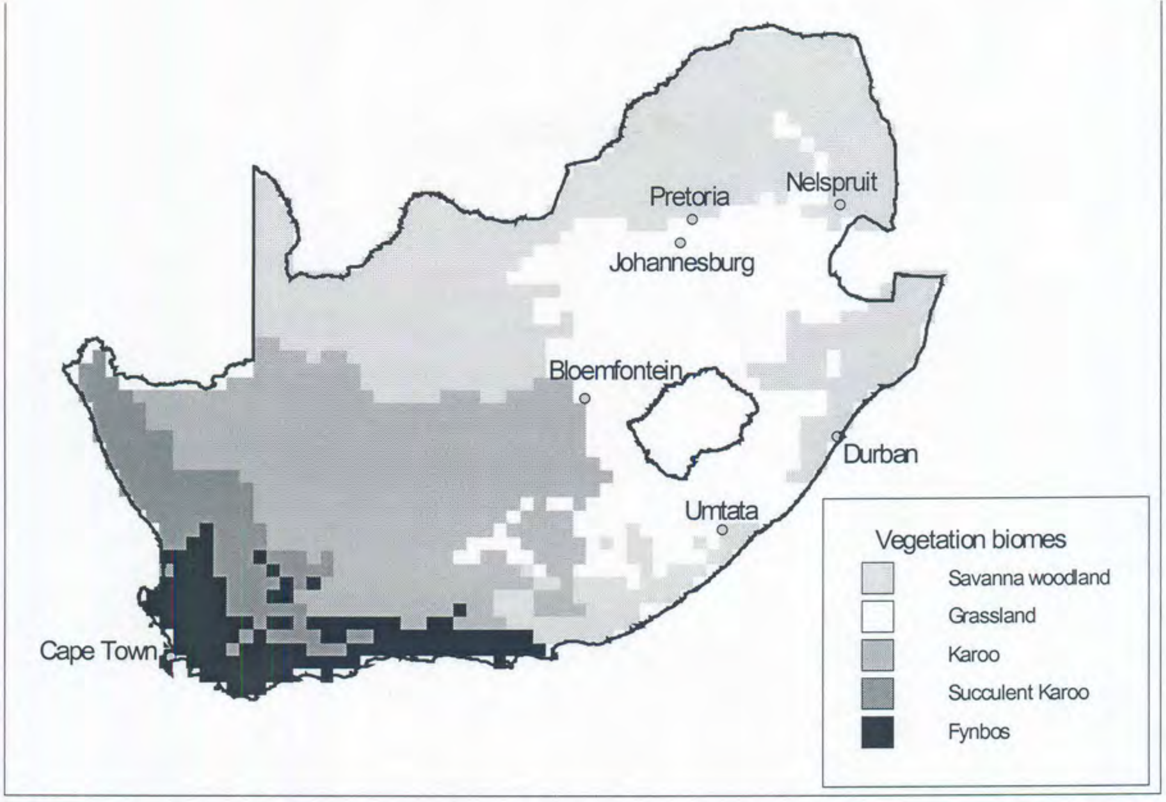

Figure 5.3: The vegetation biomes of South Africa based on the map by Low and Rebelo (1996) and from the original classification work by Rutherford and Westfall (1986).

The central tool of geostatistics is the empirical semivariance illustrated by the variogram. Variograms can be computed to determine the strength and spatial scale of any pattern, and to summarize the variation. Biodiversity measures (e.g., species richness, Shannon diversity and evenness) and human impact vary spatially and the same qualities apply. Semi-variograms may be used to examine the spatial variation in species distribution data as a function of ecological and sampling parameters. Research has indicated direct ties between measured map components and variogram form (Burroughs, 1986). The information content of a multi-species diversity map is a function of both the complexity of the terrestrial area and the spatial and temporal resolution of the sampling routine. Multi-species diversity map variance can be directly related to the frequency of observation of a species relative to the spatial resolution of the sampling unit and that this relationship is manifested in both the local and the overall variance of the diversity map (see Woodcock and Strahler, 1987 for remote sensing parallels). Recently Pearson and Carroll (1999) conducted a study of the congruency of species richness scale and extent for comparison between taxa using a semi-variogram methodology. In bird atlasing, analysis scale may vary from that of individual birds, to communities of birds, to large-scale gradients in bird turnover over tens or hundreds of kilometers. The purpose in this chapter is to use semi-variograms to describe and analyse biodiversity measures and human transformation data, and to suggest how they could be used in a complementary way to predict biodiversity changes in the future.

Variograms compare the similarity between pairs of points a given distance and direction apart (the lag), and expresses mathematically the average rate of change of a property with separating distance, which provides a measure of the form and scale of variation in a variable. Empirically derived semi-variograms may be fitted with a model, which quantifies observed patterns in spatial autocorrelation. Characteristically, the semivariance tends to increase with increasing distance. Figure 5.4 provides some examples of idealized semi-variograms fitted by the common spherical model, where a minimum nugget variance (c) is found between adjacent samples and sample variance increases throughout a region of influence (a) beyond which an asymptote, or sill ($\omega + c$), is reached.

The following is summarized from Webster and Oliver (1990). Interpreting the variogram can provide insight into the structure of the variation. In most instances, the variance increases with increasing separating distances. This corresponds with more or less strong correlation or spatial dependence at the shortest distances, which weakens as the separation increases. Variograms often flatten when they reach a variance known as the sill variance; they are bounded (Figure 5.4). Such flattened variograms are second order stationary and suggest that there are patches or zones with different levels of species richness for instance, whereas unbounded ones suggest continuous change over a region. The distance at which the 'sill' is reached, the 'range', marks the limit of spatial dependence. The variogram often has a positive intercept on the ordinate, the 'nugget variance'. This part of the variation cannot be predicted. Much of it derives from spatially dependent variation within the smallest sampling interval, somewhat less from measurement error and purely random variation. A completely flat variogram, 'pure nugget', means that there is no spatial dependence in the data.

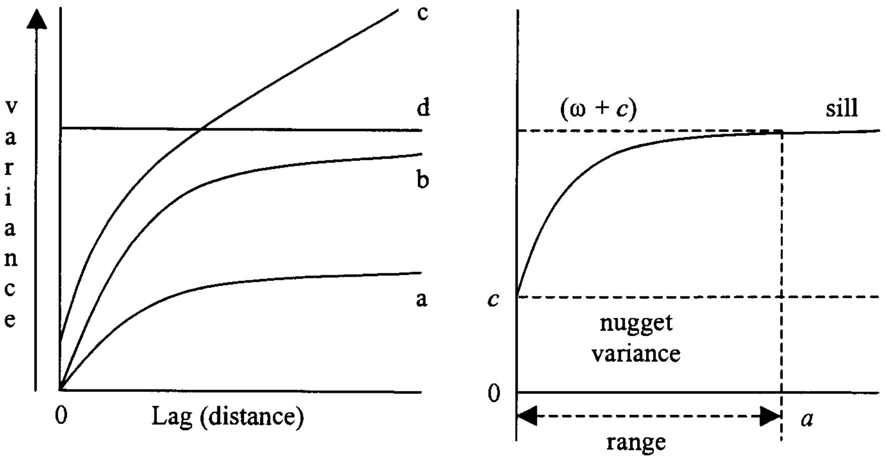

Figure 5.4: Some examples of forms of variograms: (a) and (b) bounded variograms; (c) unbounded variogram; and (d) pure nugget variogram.

Empirical semi-variograms were generated for transformation class, species richness, and evenness for the extent of each biome in South Africa. In KwaZulu-Natal, semi-variograms were generated for species richness, Shannon diversity, evenness, transformation class, road disturbance and 1996 population density estimates using the extents of each bird community class identified from ordination and clustering for each ADU life history bird assemblage. The center coordinate of each grid cell was used as the spatial component for all analyses. Semi-variograms were fitted with a spherical model in order to allow quantitative comparisons. The spherical model was chosen based on visual inspection of plots and because this model's region of influence parameter (a) provides a quantitative measure of autocorrelation distance. Other models were tried, but found to be inadequate. Visual assessments of the fit of the model to the data were made and displayed for the national analysis, but due to the large number of estimates that were required (~344) for the KwaZulu-Natal analysis, only a table of the range value based on the sill is provided.

5.4.3 Pattern and Process Measurement from Ordination Analysis

Gradient analysis may provide a promising analytical approach to understanding the effects of multiple stressors on ecosystem function (Whittaker, 1967; McDonnell and Pickett, 1993; Breitburg et al., 1998) by integrating multiple stress effects across the landscape. The gradient approach relies on the assumption that graduated spatial environmental patterns govern the structure and function of ecological systems. Changes in population, community, or ecosystem variables along the gradient can then be related to the corresponding spatial variation in the environmental and socio-economic variables, with specific statistical techniques dependent upon whether or not environmental variation is ordered sequentially in time or space, and whether single or multiple variables are being considered. In the case of system responses to multiple stressors, complex, nonlinear gradients are apt to be present and ordination techniques may provide insight into the biotic responses to these gradients (ter Braak and Prentice, 1988; Jongman et al., 1995).

Canonical correspondence analysis (CCA; ter Braak and Prentice, 1988), a direct gradient analysis method used widely in community ecology (Palmer, 1993), and detrended correspondence analysis (DCA), an indirect gradient analysis method (Gauch, 1982) was used as the analytical tools. CCA was chosen because the goal was to better understand environmental factors associated with avian diversity patterns. In CCA, sites and species are arranged in a multidimensional space, with the restriction that the ordination axes must be linear combinations of the specified environmental variables. DCA (using 2nd order polynomial detrending) was used before CCA to determine the dominant unconstrained avian diversity trends for the first two axes of variation based only on the species-site matrix. The two axes of variation were then hierarchically classified by Euclidean distance using Ward's linkage (Legendre and Legendre, 1998) to identify bird communities within each life history bird assemblage. The program CANOCO, version 4.0 (ter Braak and Smilauer, 1998), was used to conduct all gradient analyses. Environmental data (e.g., the 11 environmental parameters found under topography and climate in chapter one, Table 1.1) were entered with the species data using stepwise CCA, with detrending by 2nd order polynomials to avoid the arch effect. All other CANOCO defaults were used. All CCA plot scores in this chapter are linear combinations. In CCA and in this chapter, the fraction of species variation explained by a set of explanatory variables (total variation explained, TVE) is the sum of all constrained eigenvalues divided by the total variation (TV) in the species data (or "total inertia," sensu ter Braak and Smilauer, 1998), which is the sum of all unconstrained eigenvalues. The TV is the ratio of the dispersion of the species scores to the dispersion of the plot scores (ter Braak and Smilauer, 1998), a property of the species-by-plot data matrix. Data matrices with greater TV contain many species and little overlap of species occurrence among plots, and thus higher beta diversities (similar to Whittakers, 1960 beta diversity measure, $\beta_w = (S/\alpha) - 1$).

Explanatory variables are added to the model in the order of greatest additional contribution to total variation explained, but only if they were significant ($p < 0.01$), where significance was determined by a Monte Carlo permutation test using 499 permutations (H_0: additional influence of variable on avian diversity is not significantly different from random), and if adding the variable did not cause any variance inflation factors to exceed 20. Variables with large inflation factors are strongly multi-collinear with other variables and contribute little unique information to the model (ter Braak and Smilauer, 1998). These were excluded to improve the interpretability and parsimony of the model. Although several of the explanatory variables included in the stepwise models were still intercorrelated, CCA is robust to this multi-collinearity (Palmer, 1993).

CCA was also performed with variance partitioning (ter Braak, 1988; Borcard et al., 1992; Økland and Eilertsen, 1994; Ohmann and Spies, 1998), using partial CCA, to quantify the relative contributions of variable subsets to explained variation. In partial CCA, species variations associated with explanatory variables that are not of direct interest (i.e., covariables) are partialled out, in order to examine a selected set of explanatory variables of interest. The usual explanatory variables are replaced by the residuals obtained by regressing each of the variables of interest on the covariables. Those regional-scale factors (climate and topography) found to be of importance for each bird assemblage became covariables and then landscape pattern and land cover proportion factors (chapter one, Table 1.5 and 1.6) were analyzed as local scale operators to explain the residual variation. In this way the CCA with variance partitioning quantified the relative contributions to explained variation of regional-scale environmental factors vs. landscape scale spatial land pattern factors.

The CCA results are graphed as a biplot, in which arrow length and position of the arrowhead indicate the correlation between the explanatory variable and the CCA axes, arrow direction indicates how the variable is correlated with the CCA axes, and smaller angles between arrows indicate stronger correlations between variables (ter Braak and Smilauer, 1998). A comparison between CCA and DCA eigenvalue scores showed how well environmental variables accounted for variation in the avian data and suggested whether important environmental variables were overlooked. Intraset correlations and the change in eigenvalues for the first and second axes were evaluated.

5.4.4 Assessing Multi-species Temporal Distributional Changes

Community dynamics are an important area of analysis in ecology and for conservation efforts. The two survey periods provided by the bird atlases (Cyrus and Robson, 1980; Harrison et al., 1997) used in this study allow the opportunity to assess the similarity between the two sampling periods. The case provided here for the detection of species association over time has important ecological implications. Some human land transformation processes may result in continued similar species distribution patterns or impart dissimilar patterns of change. However, the detection of pattern does not provide a causal understanding of why such a pattern might exist. Rather, pattern detection should ideally lead to the generation of hypotheses of possible underlying causal factors. The study of two data sets involves two distinct components. The first is a statistical test (denoted by the χ^2 distribution) of the hypothesis that the two sampling areas are similar between times or not at a predetermined probability level ($\alpha = 0.005$). The second is a measure of the degree or strength of the association. These are regarded as separate characteristics of an association. The analysis used here relies on the properties of a contingency matrix (Table 5.1), where two survey dates are compared for each of their sampling units. The value *d*, which is joint absences, is usually disregarded in ecology when determining association by species, but in this study, *d* is important. Therefore, instead of using one of the common binary indexes of association commonly used in ecology, Jaccard or Sorenson, the Kappa index (κ) has been shown to be more sensitive in assessing agreement using the entire matrix (Foody, 1992; Fielding and Bell, 1997).

The Kappa index (κ) is typically used to adjust for expected chance occurrences on the diagonal (Congalton, 1991; Foody, 1992):

$$\kappa = \frac{P_o - P_e}{1 - P_e}$$

Table 5.1: Setup of a 2 x 2 contingency table used to compare species sampling surveys per sampling unit. [†]

	Survey 1		
Survey 2	Species Present	Species Absent	P_r
Species Present	a	b	$a + b / N$
Species Absent	c	d	$c + d / N$
P_c	$a + c / N$	$b + d / N$	

[†] $N = a + b + c + d$; P_o = observed agreement = $a + d / N$
a = Species present in sampling unit during both survey periods.
b = New species are present. Species may possess unique behavioral or physiological adaptations that have allowed it to colonize locations outside previously recorded range, or sampling unit may have been poorly surveyed originally.
c = May reflect species loss due to human impacts (i.e., fragmentation) or recent survey of sampling unit may have been poorly sampled.
d = Species absent from sampling unit during both survey periods.

Where P_o is the observed proportion of agreement, and P_e is the proportion of agreement that may be expected to occur by chance. Kappa can be calculated from the row and column marginals as:

$$P_e = \sum P_r(\mathrm{i})\, P_c(\mathrm{i})$$

where P_r is the row marginal error, and P_c is the column marginal error. The result is $0 < \kappa < 1$, where zero represents agreement no better than chance, and 1.0 is perfectly agreeing survey data with all elements on the diagonal. This implies that a high kappa (> 0.8) is better than the agreement that would result from a random survey assignment, or a high association between the two surveys was acquired. For most purposes values larger than 0.8 represent almost perfect agreement, those below 0.4 signify poor agreement, and values between 0.4 and 0.8 represent moderate to substantial agreement.

5.5 Results

5.5.1 South African level

5.5.1.1 Correlation Results

The analysis of covariance (ANCOVA) determined that there is significant covariation between species richness and transformation classes while controlling by biome (low intensity, $p < 0.014$; high intensity, $p < 0.0001$; total, $p < 0.0001$). While, the significance with evenness and transformation was not as great across all transformation classes, except for high intensity transformation (low intensity, $p = 0.185$; high intensity, $p < 0.001$; total, $p = 0.57$). These results confirm that overall correlations between land-use intensity and species richness/evenness should be controlled for expected variation in species richness and evenness with biome. Tables 5.2 and 5.3 present the spatially corrected Pearson correlation results considering all of South Africa and broken down by biome, with values for $p < 0.30$ highlighted in bold. As evidenced by the ANCOVA the national result is largely driven by the differing levels of species richness/evenness in different biomes, while the high intensity land-use is concentrated in only a few of the biomes.

At the national extent, species richness patterns are positively correlated with high intensity human disturbance (Table 5.2). This correlation is weaker for total disturbance, which also incorporates non-significant low intensity disturbance patterns, illustrating the effects when not considering spatial heterogeneity in the analysis transformation processes (no spatial co-variance between the two levels of disturbance; $r_s = -0.001$, $N = 889$, $p = 0.98$). The increased artificial landscaping and an increased number of artificial water impoundments contained in several of the biomes across the country can explain this positive relationship between species richness and human dominated areas, as artificial habitat is created for many species. Or, alternatively, the increase in species richness is a product of attracting weedy generalist taxa to developed landscapes. In contrast with richness, the evenness of the bird assemblages is negatively correlated with high intensity transformations suggesting that bird assemblage evenness could be adversely affected by high intensity human disturbance.

Table 5.2: Spatially corrected Pearson correlation coefficients (r_s) for comparisons of species richness and evenness against transformation classes among South African grid cells (only cells with records for all data sets are included). Richness and human disturbance data were square root and log-transformed before analysis to improve normality.

Analysis level	Low intensity transformation		High intensity transformation		Total disturbance	
	r_s	p	r_s	p	r_s	p
South Africa (N = 1046, 1405, 1562)						
Richness	0.004	0.98	**0.49**	0.002	**0.38**	0.07
Evenness	0.006	0.90	**-0.16**	0.009	**-0.10**	0.11
Woodland (N = 521, 499, 582)						
Richness	0.06	0.67	**0.43**	0.003	**0.29**	0.16
Evenness	**0.13**	0.03	**-0.15**	0.03	0.04	0.58
Grassland (N = 275, 464, 486)						
Richness	**-0.41**	0.02	**0.39**	0.03	0.04	0.77
Evenness	-0.03	0.66	-0.05	0.55	**-0.07**	0.26
Shrub Steppe (N = 139, 235, 280)						
Richness	**0.28**	0.03	**0.41**	0.009	**0.36**	0.002
Evenness	-0.003	0.97	-0.05	0.63	-0.05	0.57
Succulent Desert (N = 43, 92, 98)						
Richness	-0.17	0.32	**0.44**	0.000	**0.40**	0.002
Evenness	-0.12	0.50	**0.11**	0.27	**0.13**	0.20
Fynbos (N = 73, 115, 116)						
Richness	-0.06	0.66	**0.39**	0.004	**0.37**	0.006
Evenness	-0.02	0.85	**-0.18**	0.13	**-0.17**	0.12

Table 5.3: Spatially corrected Pearson correlation coefficients (r_s) for comparisons of smoothed species richness and evenness against transformation classes among South African grid cells (only cells with records for all data sets are included). Richness and human disturbance data were square root and log-transformed before analysis to improve normality.

	Low intensity transformation		High intensity transformation		Total disturbance	
Analysis level	r_s	p	r_s	p	r_s	p
South Africa (N = 1046, 1405, 1562)						
Richness	0.07	0.69	**0.51**	0.005	**0.43**	0.08
Evenness	-0.04	0.60	**-0.23**	0.02	**-0.18**	0.08
Woodland (N = 516, 495, 578)						
Richness	0.13	0.42	**0.47**	0.009	**0.35**	0.14
Evenness	0.09	0.33	**-0.17**	0.09	0.008	0.94
Grassland (N = 275, 464, 486)						
Richness	**-0.40**	0.05	**0.42**	0.05	0.03	0.82
Evenness	-0.11	0.33	-0.08	0.56	**-0.14**	0.17
Shrub Steppe (N = 139, 235, 280)						
Richness	**0.35**	0.04	**0.39**	0.06	**0.35**	0.02
Evenness	0.03	0.75	-0.12	0.37	-0.07	0.55
Succulent Desert (N = 43, 93, 99)						
Richness	-0.04	0.79	**0.37**	0.003	**0.39**	0.005
Evenness	0.15	0.43	**0.21**	0.16	**0.27**	0.07
Fynbos (N = 73, 118, 119)						
Richness	-0.12	0.48	**0.47**	0.003	**0.46**	0.003
Evenness	-0.12	0.48	**-0.22**	0.27	**-0.20**	0.27

Vegetation biome analyses highlight bird-vegetation sensitivities (Table 5.2). Low intensity disturbance tends to be correlated with bird richness in grassland and shrub steppe biomes. Low intensity disturbance in grasslands has an inversely negative effect on bird species richness, but a positive effect in shrub steppe. This could assert that heavily grazed or near to barren grassland ranges promote reduced richness in grassland related birds, while heavy grazing in shrub steppe regions opens up the shrub cover, which seems to increase bird richness. Only woodland bird assemblages are affected by low intensity disturbance, however, in a positive trend (Table 5.2). This possibly reflects the opening up of woodland areas through heavy grazing and fuelwood removal, which in turn creates grass patch mosaics favoring grassland birds, lowering the dominance of woodland species (Harrison et al., 1997). High intensity disturbance tends to promote increased species richness across all biomes, with a slight emphasis on drier biomes of woodland, shrub steppe, and succulent desert (Cowling et al., 1997). The woodland and fynbos biomes have bird assemblage evennesses that reflect an inverse relationship to high intensity transformation. While for the succulent desert biome the bird assemblage evenness has a positive effect from high intensity transformation. The tendency towards single species dominance reflected in the woodland and fynbos biomes seems to reflect the total removal of vegetation structure from these areas for replacement by low stature annual and permanent agricultural landscapes. The birds of these biomes are sensitive to land transformations, with generalist species tending to dominate (Harrison et al., 1997). The succulent desert biome has low species richness (Figure 5.1a), and typically, only a few of the species tend to dominate within these resource strained environments (e.g., Rottenberry and Wiens, 1980; Wiens and Rottenbery, 1981; Harrison et al., 1997). The slight positive influence in bird assemblage evenness may reflect the increase number of species brought about by water impoundments, wells, and tree cover around human habitation. Total disturbance in all biomes, with the exception of the grassland biome, shows increased species richness. Transformation relationship with woodland biome bird assemblage evenness is not significant, and significance is reduced for grassland, succulent desert and fynbos biome birds (Table 5.2).

The application of the data smoothing procedure improves the correlations across all analytical extents (Table 5.3). One exception includes the loss of statistically significant correlation between woodland bird evenness and low intensity transformation. The other relationships have mostly reduced significance in *p* against low intensity disturbance, while *p* is increased for high intensity transformation and richness but reduced for evenness. These exceptions may reflect instances where the smoothing of biological richness and evenness data reduced their spatial overlap with transformed areas.

5.5.1.2 Semi-variogram results

Empirical semi-variograms were generated for each measurement by biome at a distance resolution of 22.5km (distance from grid cell midpoint to neighboring grid cell midpoint). Range values representing the autocorrelation pattern for each variable by biome are provided in Table 5.4 with the modeled semi-variogram shapes shown in Figure 5.5 (Shannon diversity plots are not provided). The richness and Shannon diversity spatial extents tended to provide the same results as would be expected for the variables because of their high correlation. In grassland and fynbos this relationship does not hold with the Shannon diversity measure reaching a sill, where the variance measurements remains stable at a range of less than 112.5 km. This may show that in the case of these two biomes the Shannon diversity measure is more sensitive to the overall erosion in bird diversity than species richness especially when compared to the semi-variogram results for high intensity transformation (HI) and total transformation (TT). The spatial extent of Shannon diversity for grassland is nested within the influence extent for HI and similar in spatial extent to TT.

The spatial extents of each measurement with respect to the degree of nestedness of the spatial phenomena are important indicators. Savanna, grassland, shrub steppe, and succulent desert bird assemblages have extents greater than the human transformation processes. The fynbos bird spatial variation (richness and evenness) is completely dominated by the human transformation extent. Grassland evenness structure is also nested within the human

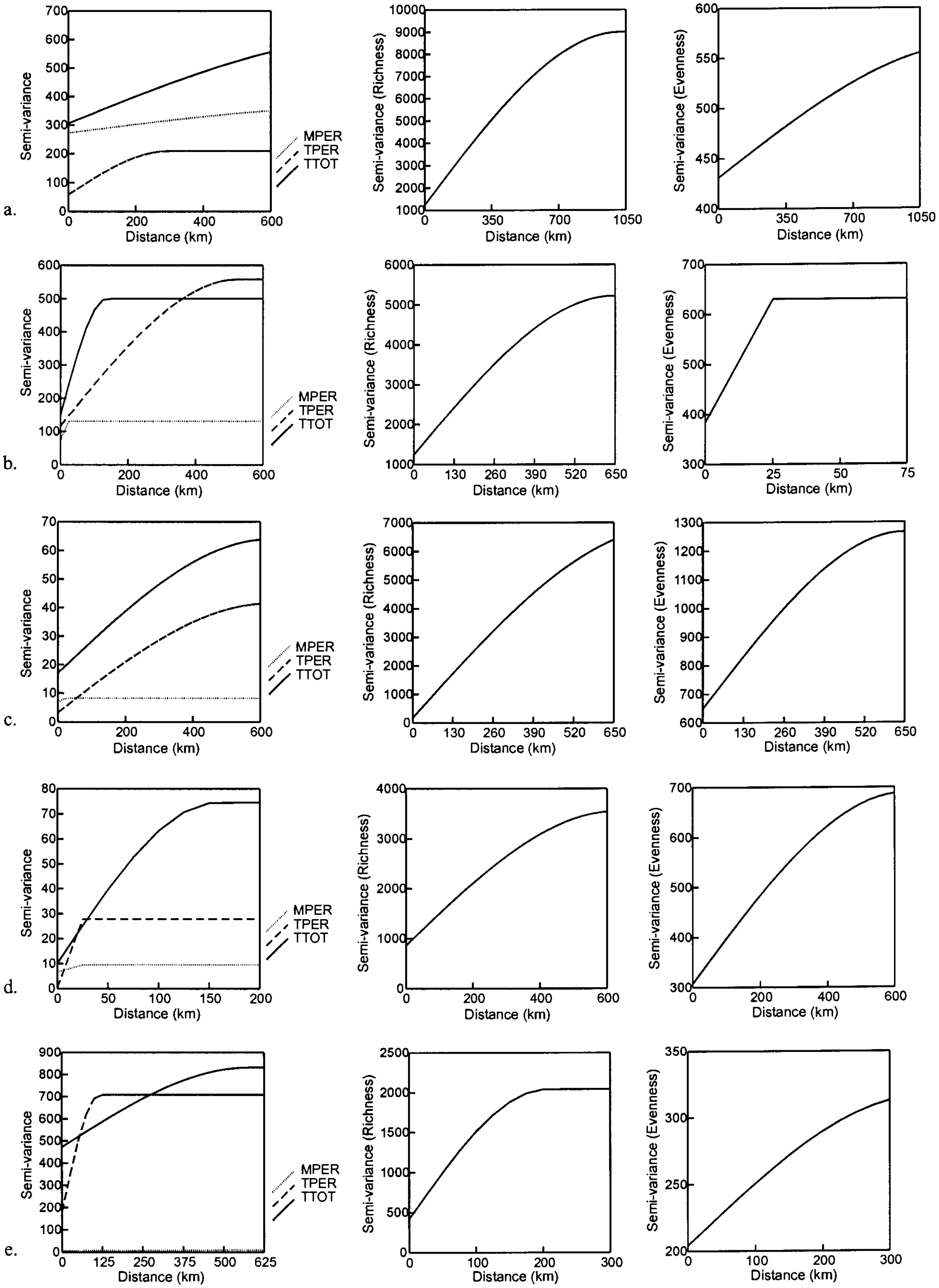

Figure 5.5: Model semi-variograms of transformation level, bird richness and community evenness in South African biomes: (a) savanna woodland; (b) grassland; (c) shrub steppe; (d) succulent desert; and (e) fynbos. (MPER - Low intensity transformation; TPER - high intensity transformation; and TTOT - total transformation).

Table 5.4: Spherical model estimates of range (km) lag value derived from the sill when a stable variance is reached for South African biomes: species richness (*S*), Shannon diversity (*H'*), evenness (*E*), low intensity transformation (LI), high intensity transformation (HI), and total transformation (TT).

Biome	*S*	*H'*	*E*	LI	HI	TT
Woodland	1260.0	1260.0	1057.5	45.0	247.5	832.5
Grassland	517.5	112.5	22.5	22.5	472.5	112.5
Shrub Steppe	832.5	832.5	652.5	22.5	562.5	540.0
Succulent Desert	630.0	630.0	630.0	45.0	22.5	22.5
Fynbos	202.5	112.5	337.5	652.5	652.5	652.5

transformation extent, but the spatial extent of richness is still just greater than the transformation indices. These geographic-scale results may provide evidence for non-randomly distributed areas of decline throughout the ranges of birds species as measured by the evenness index, with or without range contractions.

5.5.2 KwaZulu-Natal level

5.5.2.1 Ordination Results

Dataset results are denoted by the following: CR (Cyrus and Robson, 1980) and ADU (Harrison et al., 1997). Two sets of results comparing the CR and ADU bird census datasets using presence/absence data are provided, each detailing the life history bird assemblages (chapter one, Table 1.3). Analyses of the ecological habitat bird assemblages are only conducted from the ADU survey as they use the relative abundance values of the bird species to drive the ordination analyses.

For the CR bird assemblages representing all birds, summer, winter, passerine, breeding, and human, eigenvalues and gradient lengths were higher for detrended correspondence analysis (DCA) than for detrended canonical correspondence analysis (DCCA) for the first two axes (Table 5.5), indicating that a portion of the species variation was not accounted for by the environmental variables identified in DCCA. Moderate to weaker eigenvalues and gradient lengths were derived for the non-passerine, non-breeding, and non-human bird assemblages. Gradient lengths derived from DCA for the first axis showed some large species turnover pattern for all birds, non-passerine, non-breeding, and non-human bird assemblages. The human bird assemblage had the lowest species gradients. Strong correlations between the DCA for axis 1 and the explanatory variables suggested that much of the variation in avian diversity is related to the measured explanatory variables. Geographic patterns of DCA scores also were quite similar to

DCCA for the first two axes. The first two axes of significance for DCA were hierarchically clustered to identify avian community groups for each bird assemblage (Figure 5.6), except in the case of non-breeding and non-human bird assemblages that had three significant axes.

ADU bird assemblage eigenvalues were also near similar between DCA and DCCA for the first two axes (Table 5.6) with each bird assemblage showing only a small portion of its species variation not being accounted for by the explanatory variables identified in DCCA. The weakest fit was obtained for the non-breeding bird assemblage. Gradient lengths derived from DCA for the first axis showed some large species turnover pattern for non-breeding and non-human influenced bird assemblages. The human influenced assemblage had the lowest species gradients. In comparison with the CR data all the ADU data sets had lower eigenvalues, TV and gradient lengths. Strong correlations between the DCA for axis 1 and the explanatory variables suggested, however, that much of the variation in avian diversity is related to the measured explanatory variables. Geographic patterns of DCA scores were also quite similar to the DCCAs for the first two axes. The first two axes of significance for DCA were hierarchically clustered to develop avian communities for each bird assemblage (Figure 5.7).

Results from stepwise CCAs varied across CR bird assemblages and numbers of species (Table 5.5). Total variation (TV) increased and total variation explained (TVE) decreased, with increasing gradient length (Table 5.5). TV, representing beta diversity, was highest for non-breeding, non-human influenced, winter, and non-passerines. TVE was highest for non-human influenced (76%), non-breeding (64%), and winter (56%) bird assemblages. ADU bird assemblage details are in Table 5.6. TV for ADU bird assemblages was highest for non-breeding and non-human influenced; however, all bird assemblages from this census period had lower TVs than for the CR data sets. TVE was highest for non-human influenced (74%) and non-breeding (51%) bird assemblages. Unfortunately, the statistical significance of TVE differences among CCA models cannot be tested (ter Braak and Smilauer, 1998), and thus interpretations of differences are somewhat subjective.

Results of stepwise CCAs for each bird assemblage and census period are presented below. The analyses of the bird assemblages revealed considerable variation in associations between environment and compositional gradients. These within-region bird assemblage differences underscored the importance of ecological modelling approaches that consider a locations' particular biota, physical environment, and history. For each bird group, species with highest and lowest scores on stepwise CCA axes are show in Appendix B.

Table 5.5: Eigenvalues and gradient lengths (1 Standard Deviation) for the first two axes from DCA and CCA of all bird species groups in KwaZulu-Natal from the Cyrus and Robson (1970-1979) survey.

					Eigenvalue		Gradient length
Bird assemblage	Species (no.)	TV	TVE[†]	Axis	DCA	DCCA	DCA
All	614	1.974	0.398	1	0.28	0.23	2.514
				2	0.12	0.10	1.742
Summer	576	1.864	0.491	1	0.27	0.25	2.147
				2	0.12	0.10	1.704
Winter	591	2.642	0.558	1	0.31	0.28	2.384
				2	0.15	0.12	2.129
Passerine	260	1.469	0.422	1	0.26	0.24	2.150
				2	0.10	0.09	1.481
Non-passerine	354	2.295	0.426	1	0.35	0.24	2.632
				2	0.15	0.13	1.987
Breeding	506	1.538	0.444	1	0.25	0.23	2.111
				2	0.10	0.09	1.567
Non-breeding	108	4.146	0.640	1	0.69	0.33	3.039
				2	0.32	0.24	2.821
				3	0.14	0.06	2.423
Human	334	1.154	0.285	1	0.17	0.15	1.727
				2	0.07	0.05	1.426
Non-Human	280	3.625	0.763	1	0.49	0.42	3.780
				2	0.25	0.22	2.296
				3	0.13	0.04	1.835

[†] Decimal fraction of TV

Table 5.6: Eigenvalues and gradient lengths (1 Standard Deviation) for the first two axes from DCA and CCA of all bird species groups in KwaZulu-Natal from ADU Bird Atlas (1987-1992) survey.

					Eigenvalue		Gradient length
Bird assemblage	Species (no.)	TV	TVE[†]	Axis	DCA	DCCA	DCA
All	600	1.326	0.391	1	0.21	0.20	1.958
				2	0.10	0.08	1.587
Summer	595	1.501	0.420	1	0.22	0.21	2.022
				2	0.10	0.08	1.736
Winter	558	1.777	0.464	1	0.25	0.23	2.302
				2	0.11	0.09	1.861
Passerine	256	1.142	0.358	1	0.23	0.21	2.204
				2	0.09	0.07	1.268
Non-passerine	344	1.451	0.380	1	0.20	0.18	1.752
				2	0.09	0.08	1.582
Breeding	501	1.155	0.366	1	0.21	0.19	1.954
				2	0.08	0.07	1.359
Non-breeding	99	2.567	0.511	1	0.34	0.27	2.691
				2	0.12	0.08	2.028
Human	335	0.847	0.227	1	0.12	0.11	1.357
				2	0.06	0.04	1.332
Non-human	265	2.467	0.737	1	0.40	0.38	3.587
				2	0.19	0.	2.242
Woodland[‡]	135	0.821	0.391	1	0.22	0.20	1.981
				2	0.10	0.07	1.859
Forest[‡]	91	0.888	0.412	1	0.31	0.29	2.531
				2	0.08	0.07	1.792
Thicket[‡]	38	0.951	0.422	1	0.28	0.25	2.020
				2	0.16	0.13	2.195
Grassland[‡]	137	0.898	0.362	1	0.21	0.19	2.091
				2	0.10	0.09	1.571

[†] Decimal fraction of TV.

[‡] The following number of samples were used: woodland, 71; forest, 114; thicket, 162; and grassland, 162. Results are derived from relative abundance values of the birds instead of presence/absence.

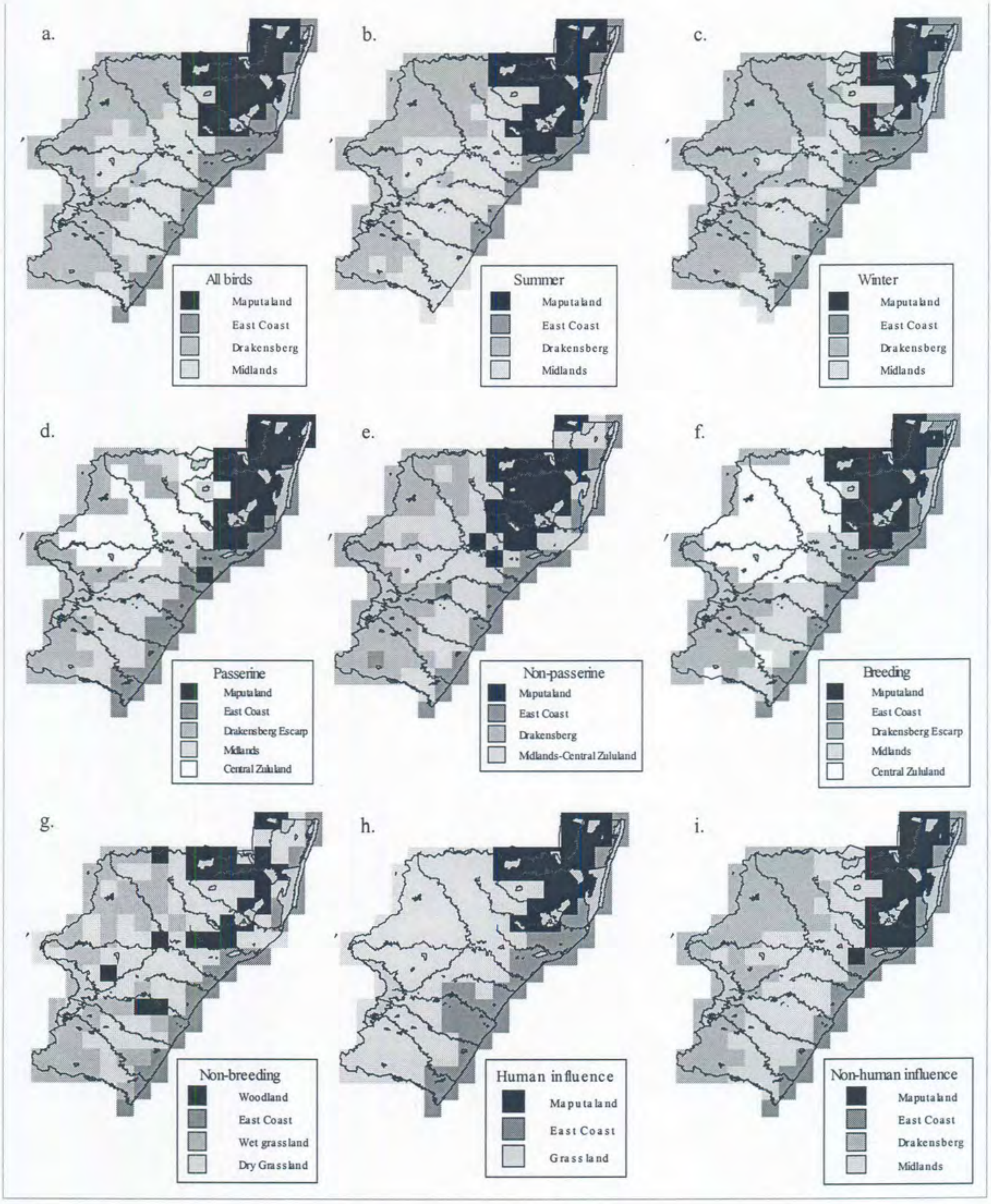

Figure 5.6: Assemblage classifications derived from ordination analysis of the CR life history bird datasets.

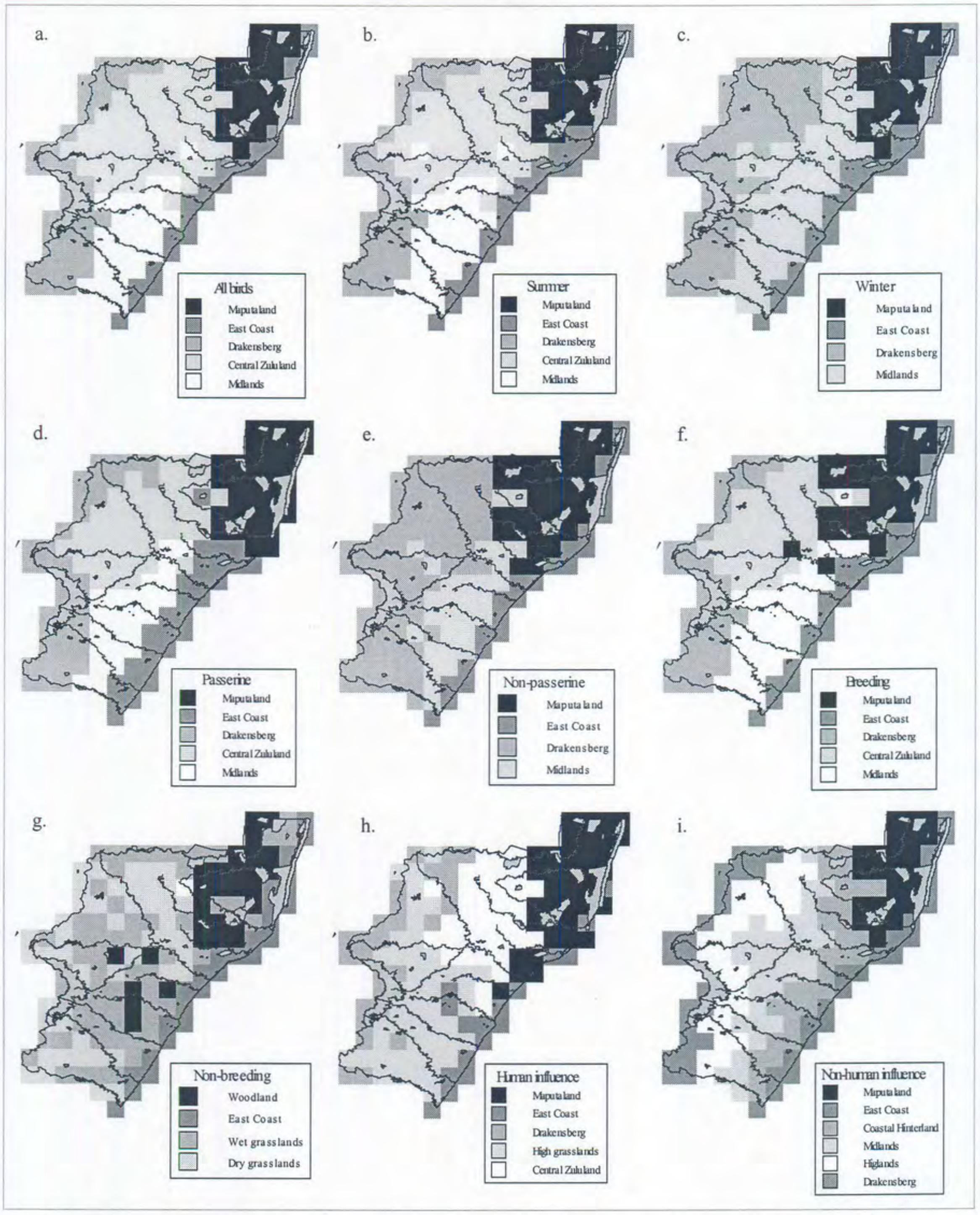

Figure 5.7: Assemblage classifications derived from ordination analysis of the ADU life history bird datasets.

All birds.—The dominant compositional gradient (CCA axis 1) reflected a gradient in elevation and topographic heterogeneity from the humid Maputaland plain and northern coast to the temperate montane climate of the Drakensberg (Figures 5.8a and 5.9a) with a TVE of 29% (Table 5.7). Grid cells with the lowest scores on axis 1 were at higher elevations and experienced higher seasonal variability in temperature, colder maximum and minimum temperatures, and higher rainfall. These plots were concentrated along the length of the Drakensberg Escarpment (Figure 5.8a) within the high grassland zone. Grid cells with high score on axis 1 were at lower elevations and experienced lower seasonal variability in temperature, warmer maximum and minimum temperatures, and higher evapotranspiration. The highest grid cell scores were concentrated along the coast from Durban north and encompassing the Maputaland plain, with the highest score situated over Ndumo nature reserve (Figure 5.8a). High-scoring grid cells fell largely within the moist and arid woodland zones (Chapter 1, Figure 1.3). With minor exceptions, the axis 1 gradient was longitudinal from the coast to the Drakensberg escarpment, reflecting the strong climatic influence of the Indian Ocean, the pronounced sharp rise in elevation from the coast, and the generally north-south orientation of the Drakensberg escarpment. The second CCA axis was a gradient in growing season moisture stress, from areas of warm, dry growing seasons to areas of humid, wet growing seasons along the coast (Figures 5.8a and 5.9a) with a TVE of 12%. Areas of low summer precipitation, high evapotranspiration and high summer temperature included the interior valleys on the western side of the Lebomo Mountains, especially the Pongola and Mfolozi River valleys, and the Tugela River valley. Lowest grid cell scores were concentrated in these areas, and tended to be in arid and mixed woodland and thicket (Chapter 1, Figure 1.3). Highest grid cell scores on axis 2 were situated at coastal river mouths, wetlands and bays. These areas included Durban Bay, Richards Bay, Kosi Bay, St. Lucia wetland, Mfolozi River mouth, Tugela River mouth and Mvoti River mouth (Chapter 1, Figure 1.2). The species at these points reflect the coastal wetland environment (Appendix B).

The ADU data set had a similar pattern and gradient on axis 1 (Figure 5.10a and 5.11a) with the addition of temperature variables and the seasonality in precipitation (TVE of 27.5%; Table 5.8). The spatial pattern of the low scores along the Drakensberg Escarpment were not as wide, but rather shrunk along the escarpment edge compared to the CR data set. High values covered the Maputaland plain and coast as far down as Durban Bay. The second axis was also similar to the CR result and identified variables, however, with the addition of seasonal variability in evapotranspiration (TVE of 10.5%). High values however were calculated down the coast to cover the region from Richards Bay to the southern border of the province.

Table 5.7: Increases in total variation explained (TVE) by explanatory variables in stepwise canonical correspondence analysis of CR bird species, by group type; the three greatest contributors to TVE in each group type are show in boldface.[†]

	Additional variation explained (proportion of TVE)								
Variable	All	Summer	Winter	Passerine	Non-passerine	Breeding	Non-breeding	Human	Non-human
Topography									
DEMMEAN	**0.23**	**0.23**	**0.26**	**0.22**	**0.22**	**0.22**	**0.27**	**0.14**	**0.42**
DEMSTD	**0.05**	**0.04**	**0.05**	**0.03**	**0.05**	**0.04**	**0.13**	**0.03**	**0.08**
Climate									
GDMEAN	**0.10**	**0.09**	**0.11**	**0.08**	**0.11**	**0.08**	‡	§	**0.21**
MAP	‡	§	§	§	‡	§	‡	0.02	§
GTMEAN	‡	‡	‡	§	‡	0.03	**0.23**	§	‡
NGTMEAN	‡	‡	‡	‡	‡	§	‡	§	‡
MAT	‡	‡	‡	‡	‡	§	‡	‡	‡
HOTMNTHMN	‡	‡	‡	‡	‡	§	§	‡	‡
MINMNTHMN	‡	§	‡	§	‡	§	‡	‡	‡
EVANNMN	0.03	0.02	0.03	0.02	0.04	0.02	‡	**0.05**	0.06
PSEAS_MN	‡	0.01	‡	0.01	‡	§	‡	0.01	‡
TSEAS_MN	‡	0.04	0.03	0.04	‡	0.02	‡	0.01	‡
MXSEAS_MN	‡	0.03	0.04	0.02	‡	0.02	‡	0.01	‡
EVSEAS_MN	‡	0.01	0.02	‡	‡	0.01	‡	0.01	‡

[†] Increase in TVE is additional species variation explained by adding the variable after previously selected variables already are included, expressed as a proportion of TVE, and thus reflects selection order. Values are for variables included by forward selection ($P < 0.01$, where significance was determined by a 499 iteration Monte Carlo permutation test, H_0: additional influence of variable on vegetation is not significantly different from random), and where adding the variable did not result in inflation factors > 20.

[‡] Variable was not significant in the stepwise procedure.

[§] Variable was significant in the stepwise procedure but excluded because of multi-collinearity.

Table 5.8: Increases in total variation explained (TVE) by explanatory variables in stepwise canonical correspondence analysis of ADU bird species, by functional type; the three greatest contributors to TVE in each group type are show in boldface.[†]

	Additional variation explained (proportion of TVE)								
Variable	All	Summer	Winter	Passerine	Non-passerine	Breeding	Non-breeding	Human	Non-human
Topography									
DEMMEAN	**0.19**	**0.20**	**0.22**	§	**0.17**	§	**0.19**	**0.11**	**0.37**
DEMSTD	0.02	0.03	0.03	0.02	0.02	0.02	0.03	**0.02**	0.03
Climate									
GDMEAN	**0.07**	**0.07**	**0.08**	**0.03**	**0.07**	**0.03**	**0.13**	0.01	**0.15**
MAP	‡	§	§	§	§	§	‡	§	§
GTMEAN	§	‡	§	§	§	§	‡	§	§
NGTMEAN	‡	‡	§	§	‡	§	‡	§	‡
MAT	‡	§	§	§	‡	§	‡	§	§
HOTMNTHMN	‡	§	§	§	‡	§	‡	§	‡
MINMNTHMN	§	§	§	**0.20**	§	**0.18**	§	§	§
EVANNMN	**0.03**	**0.03**	0.02	**0.07**	0.03	**0.06**	0.04	**0.04**	**0.06**
PSEAS_MN	0.01	0.01	0.02	0.02	0.01	‡	‡	0.01	0.03
TSEAS_MN	0.03	0.03	0.04	§	0.02	0.02	0.02	0.01	0.05
MXSEAS_MN	0.02	0.02	**0.04**	0.02	**0.03**	0.02	**0.05**	0.01	0.05
EVSEAS_MN	0.01	0.01	‡	‡	0.01	0.01	0.04	0.01	‡

[†] Increase in TVE is additional species variation explained by adding the variable after previously selected variables already are included, expressed as a proportion of TVE, and thus reflects selection order. Values are for variables included by forward selection ($P < 0.01$, where significance was determined by a 499 iteration Monte Carlo permutation test, H_0: additional influence of variable on vegetation is not significantly different from random), and where adding the variable did not result in inflation factors > 20.

[‡] Variable was not significant in the stepwise procedure.

[§] Variable was significant in the stepwise procedure but excluded because of multi-collinearity.

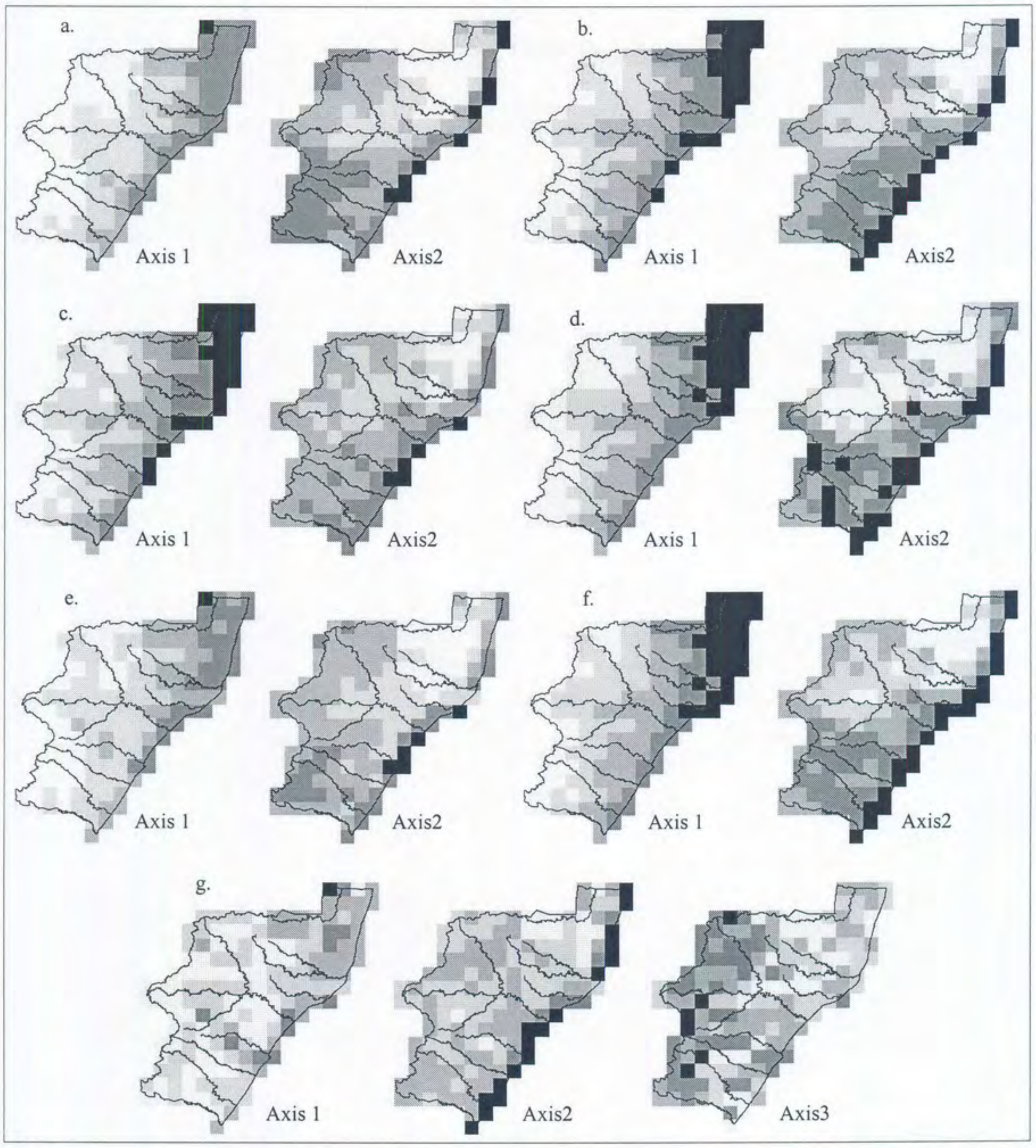

Figure 5.8: Patterns of variation in the first two axes of variation derived from detrended correspondence analysis (DCA) for each CR life history bird group, KwaZulu-Natal: (a) all birds; (b) summer; (c) winter; (d) passerine; (e) non-passerine; (f) breeding; (g) non-breeding; (h) human; and (i) non-human. (Figure continued on next page).

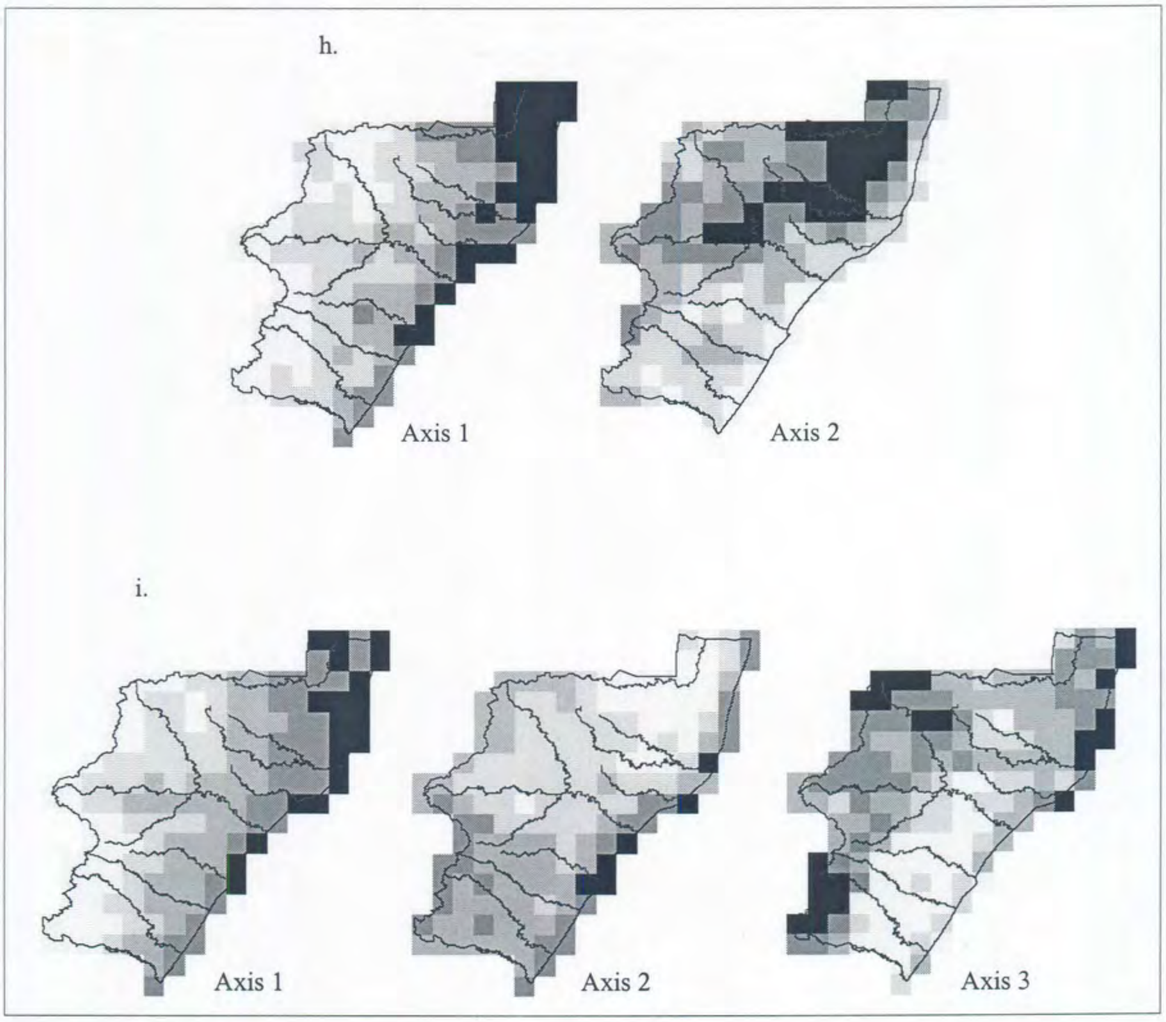

Figure 5.8: Continued.

Summer.—The first axis on the CR data set was strongly correlated with elevation and seasonality in precipitation and moderately correlated with topographic heterogeneity and seasonality in temperature and evapotranspiration (Figure 5.9b) with a TVE of 32% (Table 5.7). Low grid cell scores were on cooler, high-elevation sites along the Drakensberg Escarpment, and high scores were on warmer, low-elevation sites along the coast from Durban in the south to the Maputaland plain in the north (Figure 5.8b). The second axis was a gradient in growing season moisture stress and low variability in temperatures, from areas of warm, dry growing seasons to areas of humid, wet growing seasons along the coast (Figures 5.8b and 5.9b) with TVE of 13%. Low scores were in areas with arid and mixed woodland representing hot, moist summers along the Lebombo Mountains and the Tugela, Buffalo and White Umfolozi River valleys, and high scores were situated at coastal river mouths, wetlands, bays and south coast. These areas included Durban Bay, Richards Bay, Kosi Bay, St. Lucia wetland, Mfolozi River, Tugela River, Mkomazi River, and Mzimkhulu River mouths.

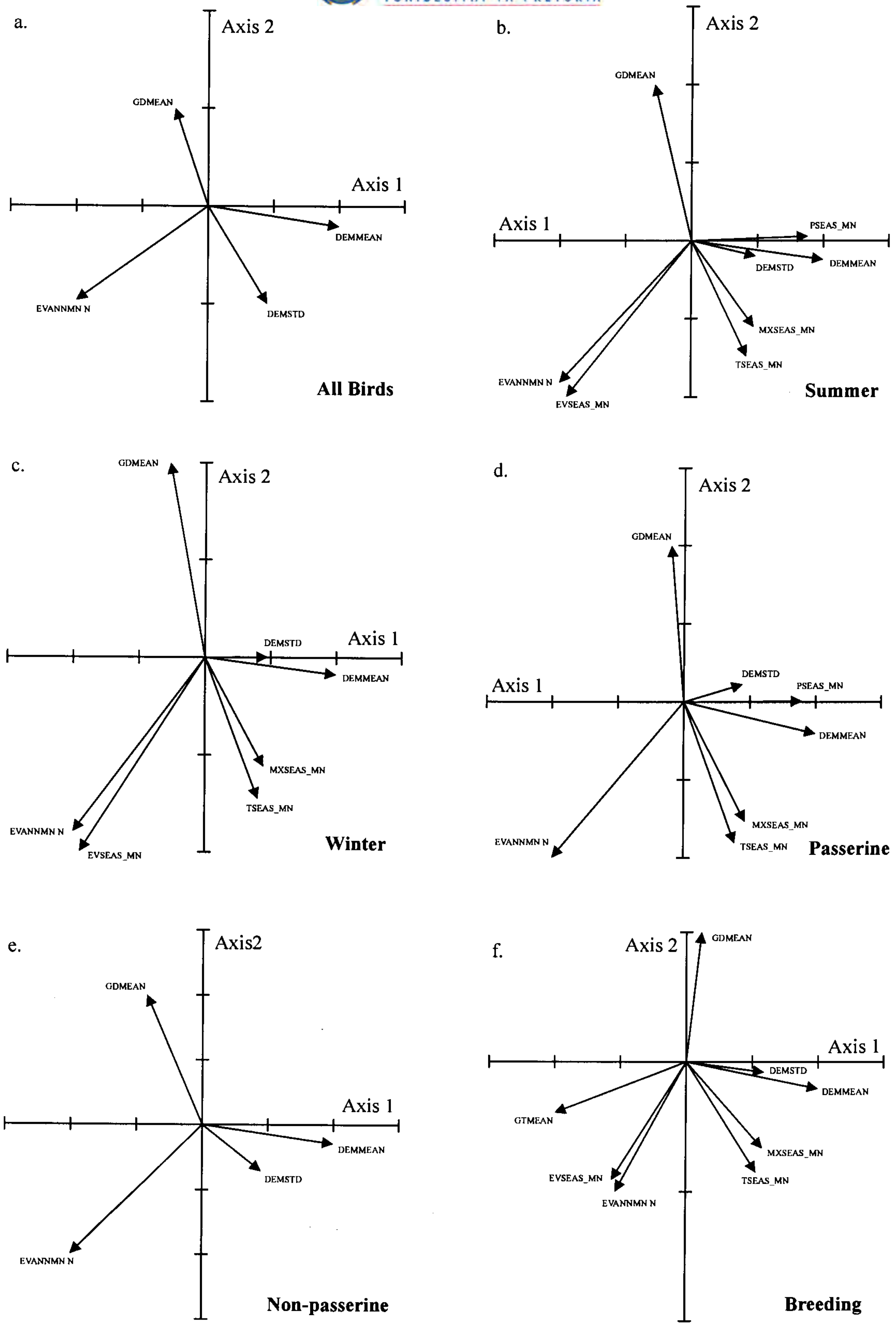

Figure 5.9: Biplots from canonical correspondence analysis of life history bird assemblages. All axes have been rescaled to range from –1.0 to 1.0. Axes for explanatory environmental variables that were not significant or that had very low correlations with the canonical axes are not shown.

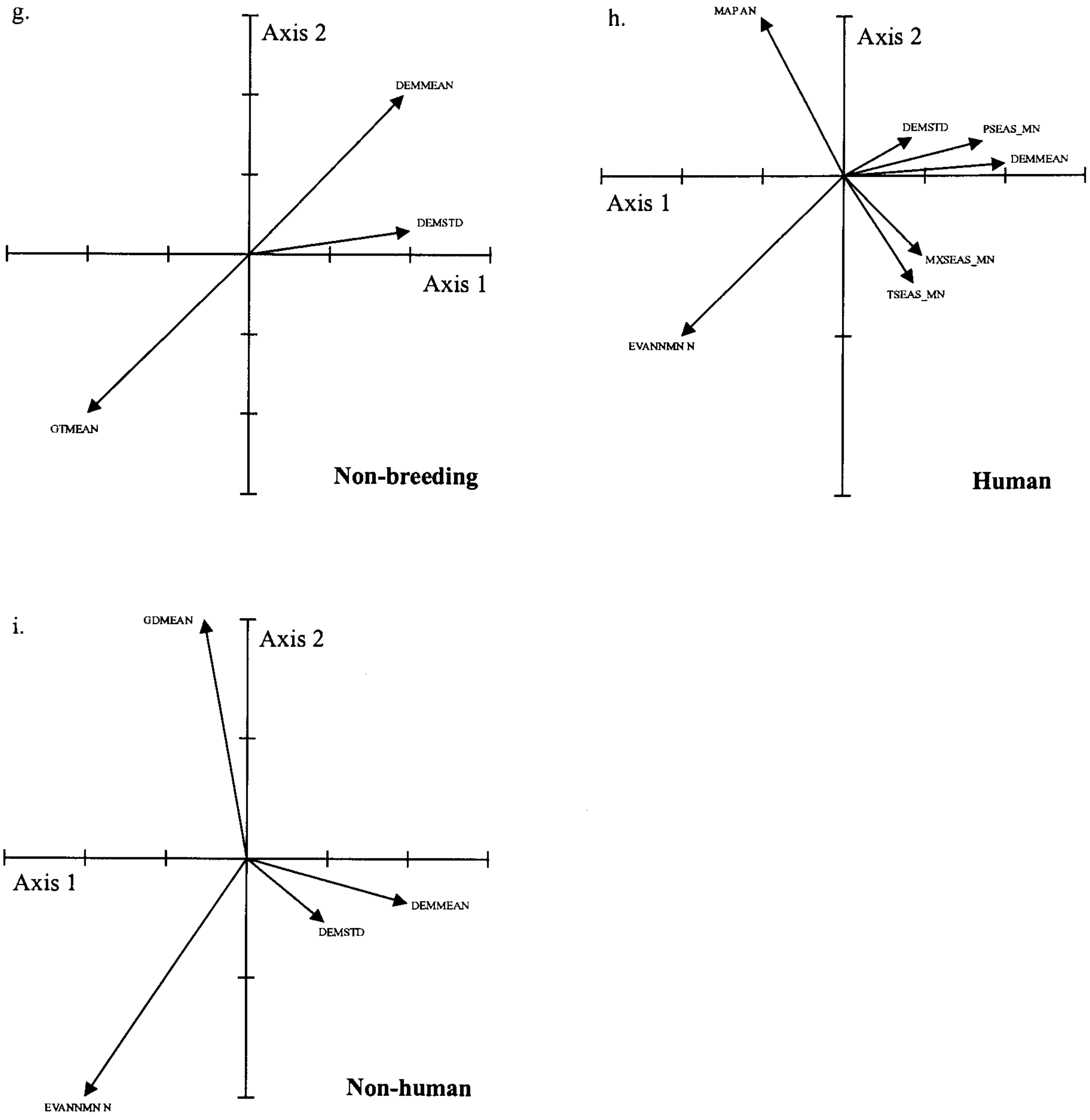

Figure 5.9: Continued.

The first axis results on the ADU data set correlate to similar variables (Figures 5.10b and 5.11b) with slight improvements in the relationships, but a lower TVE of 27.5% (Table 5.8). An arbitrary flip in scores by CANOCO derived low scores in the Maputaland plain and northern coast and high scoring grid cells in the Drakensberg Escarpment. The score calculations (between negative and positive values) are known to be calculated arbitrarily in CANOCO and have no influence on the results or for comparisons between data sets (ter Braak and Smilauer, 1998). Axis 2 was also related to water balance and seasonal variability in evapotranspiration with a similar TVE of 12.5%. Low and high scoring grid cells were in similar areas, but with reduced emphasis on high scoring cells along the north coast.

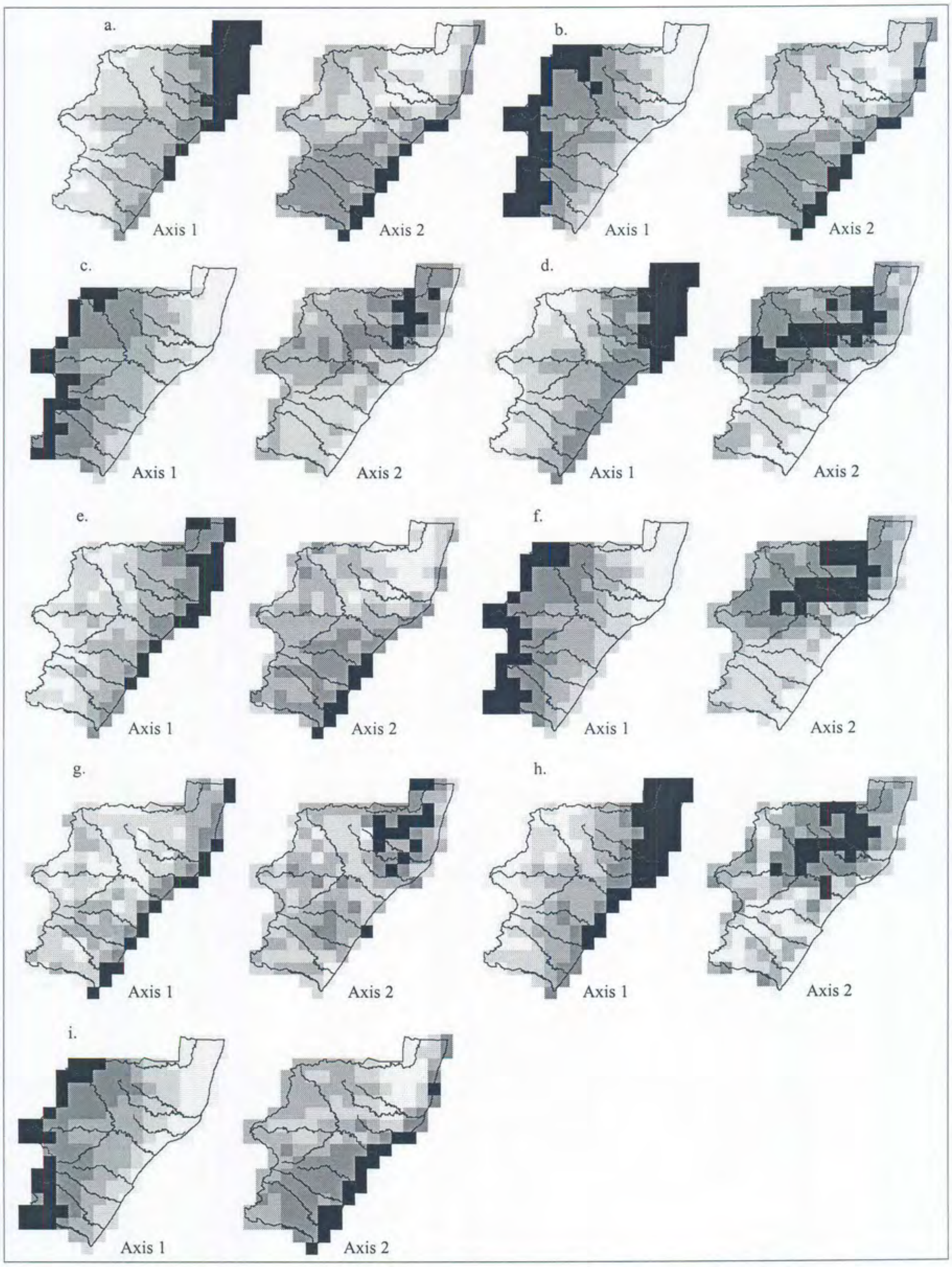

Figure 5.10: Patterns of variation in the first two axes of variation derived from detrended correspondence analysis (DCA) for each ADU life history bird group.

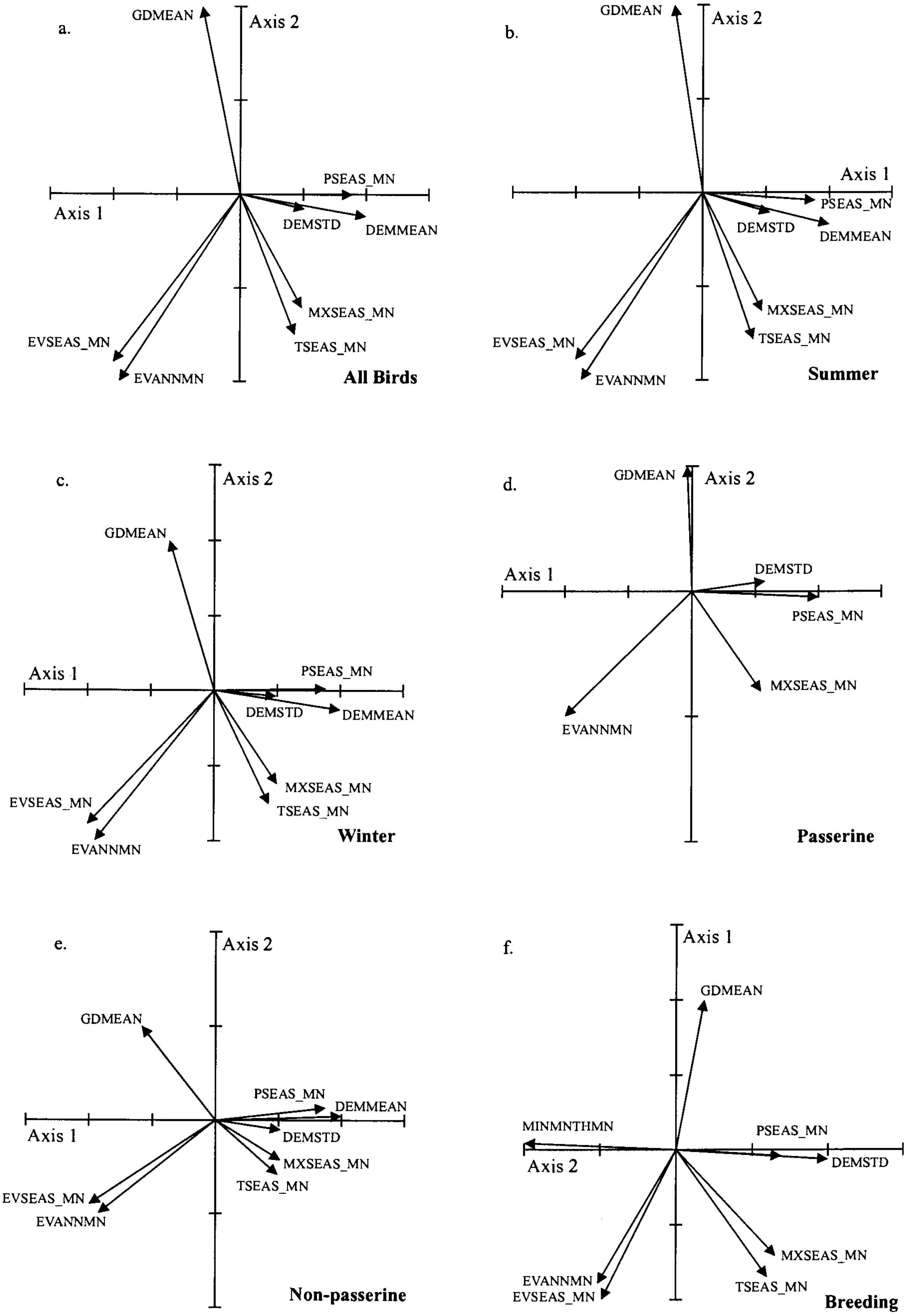

Figure 5.11: Biplots from canonical correspondence analysis of life history bird assemblages. All axes have been rescaled to range from –1.0 to 1.0. Axes for explanatory environmental variables that were not significant or that had very low correlations with the canonical axes are not shown.

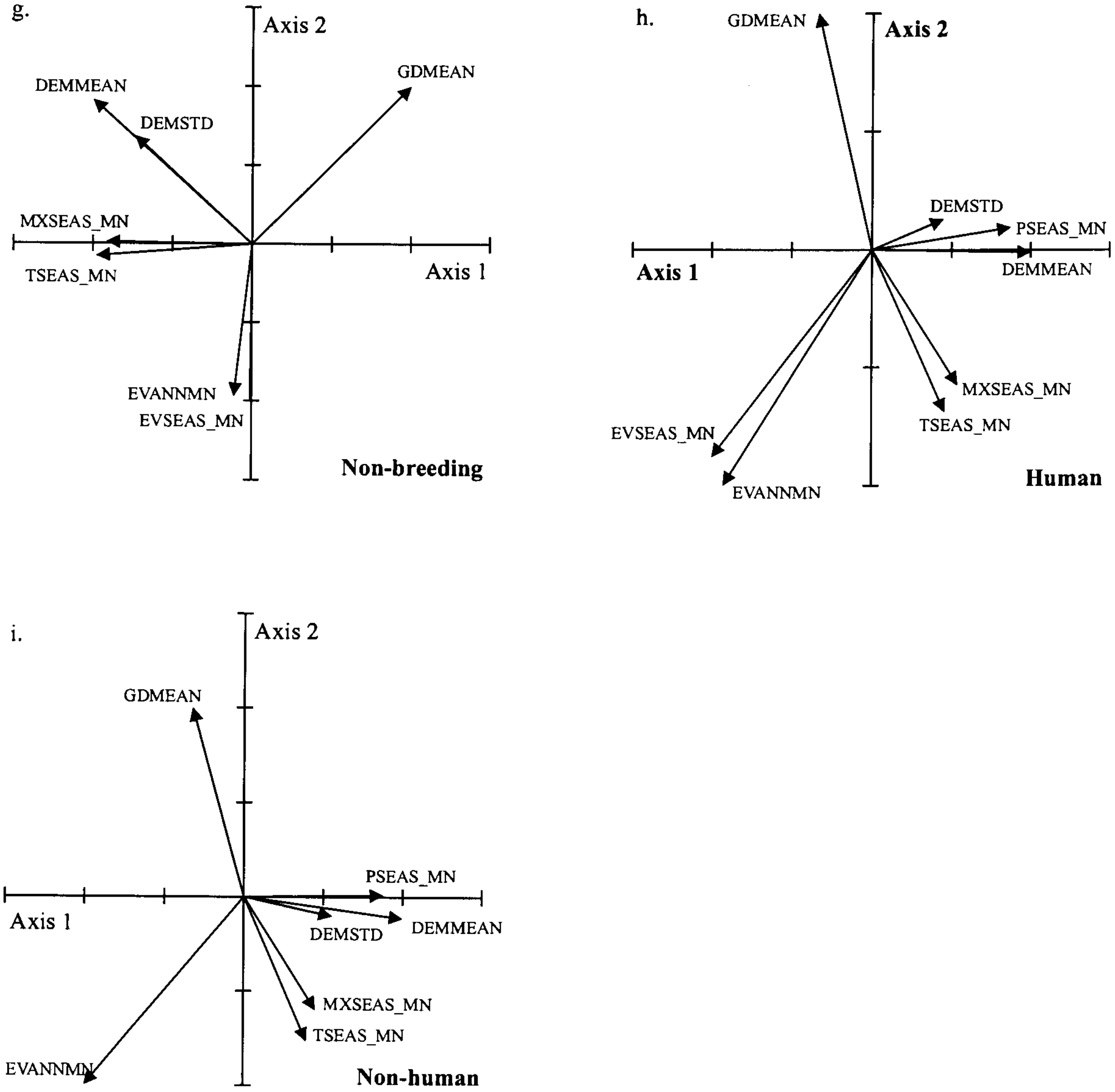

Figure 5.11: Continued.

Winter.—The first axis for the winter bird assemblage followed a similar gradient as for summer birds, an elevation gradient but with emphasis on seasonality in temperature (Figure 5.8c and 5.9c) with TVE of 29.5% (Table 5.7). The second axis was also similar to summer birds, where water balance and evapotranspiration represented the gradient, but with the addition of topographic heterogeneity and a TVE of 25%. The low scoring grid cells were in similar areas, however the high scoring grid cells were largely on the south coast and confined to Durban and Richards Bays and the Tugela River mouth.

The winter ADU data set of birds had arbitrary scoring flips on both axes of compositional variation (Figure 5.10c). Axis 1 was similar in pattern and variable selection (Figure 5.11c) with the added variable of seasonal variability in precipitation and a higher TVE of

33% (Table 5.8). Axis two had a much lower TVE of 12% with similar water balance and temperature variables selected to explain the variation.

Passerine.—The first axis gradient for the CR passerine bird assemblage was strongly correlated with elevation and seasonality in precipitation, and moderately correlated with topographic heterogeneity and maximum temperature (Figure 5.8d and 5.9d) with TVE of 25% (Table 5.7). Low scores were located in the high-elevation zone of the Drakensberg Escarpment, and high scores were located tightly covering the Maputaland plain and far north coast. Axis 2 was strongly associated with water balance, evapotranspiration and seasonality in temperature (TVE of 11%), with low scoring grid cells in the arid and mixed woodlands along the Pongola, Black and White Umfolozi, Buffalo and Tugela River valleys. High scoring plots were located either along the coast as far north as the St. Lucia wetland complex extending to the southern coast. Several of the grid cells were located in the southern interior comprising afromontane forest areas and high Drakensberg Escarpment grassland.

ADU axis 1 compositional variation was similar (Figure 5.10d and 5.11d), but with minimum temperature and seasonality in precipitation explaining the axis, however TVE was slightly lower at 25% (Table 5.8). The low and high scores were similar in location but low scores were tighter against the Drakensberg Escarpment. The second axis of variation had a flip in scores, but had similar variables explain the variation with a TVE of 11%. Low scoring grid cells were more clustered on the south coast than for the CR data set.

Non-passerine.—The dominant compositional gradient within the CR non-passerine bird assemblage was strongly associated with elevation and topographic heterogeneity (Figure 5.8e and 5.9e) with a TVE of 27% (Table 5.7). The pattern for axis 1 and environmental variables were similar to that derived using all birds. Axis 2 also related to similar variables, water balance and evapotranspiration, and elucidated similar pattern with a TVE of 15%. Exceptions to this pattern, are the confinement of high scores to only Durban and Richards Bays and the Tugela River mouth.

The non-passerine ADU data set required several more variables to explain the first axis of variation (Figure 5.11e). These were mostly variables describing seasonality in temperature and precipitation and TVE was mostly similar at 25% (Table 5.8). The low scoring grid cells were in similar areas along the Drakensberg Escarpment and high grasslands, but the high scoring areas were located along the coast from Kosi Bay to Durban Bay with clustering around the St. Lucia wetland (Figure 5.10e). Axis 2 contained similar variables with a slightly smaller TVE of 11%. Low scores were more northerly in the arid woodland and reduced in the mixed woodland

and Tugela River valley. High scoring grid cells were confined to the coast from Durban Bay southwards.

Breeding.—For breeding birds, axis 1 followed a gradient similar to that of the summer bird groups but with emphasis on temperature (Figure 5.8f and 5.9f): elevation, summer temperature, maximum temperature, and seasonal temperature variability contributed 34% of TVE (Table 5.7). Distribution of low and high grid cell scores was similar to that of the summer bird group. Axis 2 represented a water balance and evapotranspiration gradient related to the seasonality in temperature variability with a TVE of 10%. Grid cell scores and pattern were similar to axis 2 of the summer bird assemblage, but with greater emphasis on the differences between bird compositions of the interior arid and mixed woodlands and the coast.

The ADU data set of birds had arbitrary scoring flips on both axes of compositional variation (Figure 5.10f and 5.11f). Axis 1 was similar in pattern, but temperature variables largely explained this axis, but with a much lower TVE of 22% (Table 5.8). Axis two had a slightly higher TVE of 12% with similar water balance and seasonal temperature variability to explain the variation.

Non-breeding.—The non-breeding bird assemblage was much more variable than the other groups (Table 5.5). The gradients were not as well defined (Figures 5.8g and 5.9g), with axis 1 only moderately associated to elevation and summer temperature (TVE of 36%; Table 5.7). The low scoring cells were located along the Drakensberg Escarpment and in un-developed grassland areas within the Midlands and Central Zululand areas, and high scores were located in the Maputaland plain, Pongola River valley and the central coastal and Pietermaritzburg-Durban economic corridor. This pattern alignment with human dominated areas appears to relate to the summer visiting behaviour of Eurasian birds. The second axis associated moderately with elevation and topographic heterogeneity and a TVE of 14%. Low scores were undifferentiated, and high scores located along the coast. Axis 3 was less interpretable than the first two axes. Topographic heterogeneity and temperature were the correlates. Low scoring grid cells were on the river valleys and high scoring grid cells were in the Drakensberg Escarpment and foothills.

The non-breeding birds in the ADU data set were much less variable, yielding only two significant axes of variation (Figure 5.10g). Axis 1 required many more variables to explain the compositional variation (Figure 5.11g) with inclusions of topographic heterogeneity, and seasonal variabilities in temperature. The TVE was, however, higher at 36% (Table 5.8). Pattern was more interpretable with low scoring grid cells along the entire coast and high scores along the Tugela, Buffalo, Mzimkhulu, and Mooi River valleys. Axis 2 was associated with water balance and evapotranspiration variables, but with a much lower TVE of 14%. The low scores were undifferentiated, while the high scoring areas were in the arid woodland zone.

Human.—Axis 1 (Figures 5.8h and 5.9h) was correlated with elevation, seasonality in precipitation, topographic heterogeneity, and temperature (TVE of 19.5%; Table 5.7). Low scores were situated along the Drakensberg Escarpment and high scores were in Maputaland and along the coast. The second axis associated with evapotranspiration, mean annual precipitation, and seasonal temperature variability (TVE of 7.5%). Low scores were situated along the south coast and Midlands and high scores were in the arid and mixed woodland regions of the Zulu homeland.

The ADU data set for axis 1 was similar in pattern and explanatory variables (Figures 5.10h and 5.11h) but with a slightly lower TVE of 15.5% (Table 5.8). Axis 2 also required similar explanatory variables with a similar TVE of 6.5%, but the spatial pattern in allocated scores was different. Low scoring grid cells were located along the coast south of Sodwana Bay, the Midlands within the Pietermartizburg-Durban economic corridor, and along the main roads to Newcastle. The high scoring grid cells reflected these changes by becoming more constricted to the arid and mixed woodlands of Central Zululand, with a reduced presence in the Maputaland plain.

Non-human.—The non-human influenced bird assemblage was much more variable and elucidated three axes of variation (Figure 5.8i). The major compositional gradient on axis 1 was elevation and topographic heterogeneity (Figure 5.9i) with a large TVE of 50% (Table 5.7). Low scoring grid cells were located in the Drakensberg Escarpment and high scoring areas were situated along the coast from Durban north. These areas tended to be characterized by bays, river mouths, or large wetlands. Axis 2 was associated with water balance and evapotranspiration and a TVE of 27%. Low scores were in the arid and mixed woodland and thicket regions and high scores were on the coast at Durban and Richards Bays and the Tugela and Mfolozi River mouths. Axis 3 was moderately related to topographic heterogeneity and evapotranspiration with low scores throughout the Midlands and high scores in the southern Drakensberg Escarpment, northern Drakensberg Escarpment near Newcastle and Wakkerstroom, and along the coast from Richards Bay north.

The non-human influenced birds in the ADU data set were much less variable, yielding only two significant axes of variation (Figure 5.10i). Axis 1 required many more variables to explain the compositional variation with inclusions of seasonal variabilities in precipitation and temperature (Figure 5.11i). The TVE was, however, similar at 50.5% (Table 5.8). The spatial pattern was more interpretable with low scoring grid cells along the coast from Durban Bay to the Maputaland plain, and high scores were located along the Drakensberg Escarpment. Axis 2 was associated with water balance and evapotranspiration variables, with a slightly lower TVE of 23.5%. The low scores were in a much more confined area in the arid woodland and along the thickets in the river valleys. High scoring grid cells were situated along the coast from Richards Bay south, with one exception at Sodwana Bay.

5.5.2.1.1 Associations of Local and Regional Factors with Species Gradients

The relative contributions of explanatory variables to TVE in stepwise and partial CCA were influenced by location and illustrated the nested scales in processes, coarse to fine scale, that are required to explain variation within the life history species assemblages (Table 5.9). In partial CCA conducted on the ADU life history data sets, regional factors (climate and topography) accounted for more of the TVE (22-74%) than the landscape factors (8.6-32%) for all the bird assemblages (Table 5.9). Landscape factors contributed less to TVE for the human influenced (8.56%; Figure 5.12h), passerine (10.2%; Figure 5.12d) and breeding (11.1%; Figure 5.12f) bird assemblages. Contributions of landscape factors to TVE were greater for the non-breeding (32%; Figure 5.12g), non-human influenced (24.7%; Figure 5.12i), non-passerine (19.5%; Figure 5.12e), summer (18.4%; Figure 5.12b), all birds (15.4%; Figure 5.12a), and winter (14%; Figure 5.12c) bird assemblages. Passerine and breeding birds were the only assemblages not related to the richness and density of LCLU classes. The life history bird assemblages were mostly related to LCLU proportions than to the landscape mosaic pattern metrics. Passerine, breeding and non-human bird assemblages were related to the amount of woodland and forest coverage. While all, summer, winter, breeding and human bird assemblages were related to the amount of grassland coverage and extent of subsistence agriculture and degraded lands. Passerine, non-breeding, and human bird assemblage variations had the greatest relationships with human built landscapes, which included extent urbanized and road disturbance.

In order to resolve finer resolution in the power of landscape metrics to explain avian diversity patterns analysis was conducted on birds grouped by associated primary vegetation habitat (Table 1.3). These ecological habitat bird groups were ordinated using the relative abundance of each bird rather than presence/absence in order to understand the land-cover class patch characteristics relationship to bird population variation. This analysis was conducted to overcome any confusions associated with landscape mosaic measurements, which include all LCLU classes, and to come closer to an ecological explanation of bird reactions to landscape pattern that would be masked using life history assemblages. Figure 5.13 illustrates the dominant gradients derived from DCA analysis on the relative abundance of the birds group by primary associated habitat classes. Table 5.10 presents CCA results of the bird habitat groups in relation to the environmental variables chosen in the stepwise CCA to explain the ecological habitat birds.

Table 5.9: Proportion of total variation explained (TVE) by landscape variables while constrained by the topography and climate variables chosen for each group type in partial canonical correspondence analyses (CCAs) of ADU bird species; the three greatest landscape contributors to remaining TVE after constraining by the topography and climate variables in each group type are show in boldface. [†]

	Additional variation explained (proportion of TVE explained after constraining by covariables)								
	All	Summer	Winter	Passerine	Non-passerine	Breeding	Non-breeding	Human	Non-human
Partial CCA TV	0.934	1.081	1.313	0.784	1.071	0.790	2.056	0.619	1.730
Variable									
Landcover									
POPTOT96	§	‡	‡	‡	‡	‡	0.02	§	‡
POPDEN96	0.01	0.01	‡	‡	0.01	‡	‡	0.005	‡
FOR_PER	‡	0.01	‡	**0.02**	0.012	**0.02**	‡	‡	**0.03**
GRS_PER	**0.014**	**0.015**	**0.02**	‡	0.01	**0.011**	0.02	**0.01**	‡
WET_PER	0.01	0.014	0.012	‡	0.013	0.007	0.03	0.006	0.023
LOWI_PER	**0.015**	**0.02**	‡	‡	**0.02**	**0.012**	**0.02**	**0.013**	‡
PLNT_PER	0.013	‡	‡	0.012	‡	0.011	0.02	0.008	0.022
DRY_PER	0.01	0.011	0.013	‡	0.011	‡	0.02	‡	‡
IRR_PER	‡	‡	‡	‡	‡	‡	‡	‡	‡
URB_PER	0.01	0.012	‡	‡	**0.02**	‡	**0.05**	**0.015**	‡
M_PER	§	‡	**0.02**	‡	‡	‡	‡	‡	‡
T_PER	§	‡	‡	‡	‡	‡	‡	‡	0.02
T_TOTAL	§	‡	‡	0.01	‡	‡	‡	‡	‡
ROAD_INDEX	§	‡	‡	**0.014**	‡	‡	‡	‡	‡
Patchiness									
LPI	‡	‡	‡	‡	‡	‡	‡	‡	‡
NP	§	‡	‡	‡	‡	0.008	‡	‡	‡
PD	§	‡	‡	‡	‡	‡	‡	‡	‡
MPS	§	‡	‡	‡	‡	‡	‡	‡	0.02
PSSD	§	‡	‡	‡	‡	‡	‡	‡	‡
CI	‡	‡	‡	‡	0.01	‡	‡	‡	‡
Shape									
MSI	‡	§	‡	‡	‡	‡	‡	‡	‡
AWMSI	‡	‡	‡	‡	‡	‡	‡	‡	‡
FD	‡	§	‡	‡	‡	‡	‡	‡	‡
MPFD	§	0.01	‡	‡	0.01	0.007	‡	‡	‡
AWMPFD	0.01	‡	‡	0.011	‡	0.007	‡	‡	‡
Interior									
MCAPP	‡	‡	‡	‡	‡	‡	‡	‡	‡
PCASD	‡	‡	‡	‡	‡	‡	‡	‡	‡
MAPDC	‡	‡	‡	‡	‡	‡	‡	‡	0.022
DCASD	‡	‡	‡	‡	‡	‡	‡	‡	‡
DCACV	0.01	‡	‡	0.015	‡	‡	‡	‡	‡
Isolation									
MNND	‡	‡	‡	‡	‡	‡	‡	‡	‡
NNSD	‡	‡	‡	‡	‡	‡	‡	‡	‡
MPI	‡	‡	‡	‡	‡	‡	‡	‡	‡
II	‡	0.012	0.01	‡	0.012	0.008	‡	0.006	‡
Richness									
CR	0.012	0.015	0.014	0.01	0.014	0.01	0.03	0.01	0.02
CRD	**0.03**	**0.04**	**0.03**	‡	**0.04**	‡	**0.11**	0.007	**0.06**
Heterogeneity									
SHDI	§	‡	§	§	§	§	‡	‡	‡
SDI	§	‡	0.02	§	‡	§	‡	‡	§
MSDI	§	‡	‡	§	‡	§	‡	‡	‡
Evenness									
SHEI	§	‡	‡	§	0.013	§	‡	‡	‡
SEI	0.01	0.015	§	0.01	‡	0.01	‡	0.006	**0.03**
MSEI	§	‡	‡	§	‡	§	‡	‡	‡

[†] Same rules as for Table 5.8.

[‡] Variable was not significant in the stepwise procedure.

[§] Variable was significant in the stepwise procedure but excluded because of multi-collinearity.

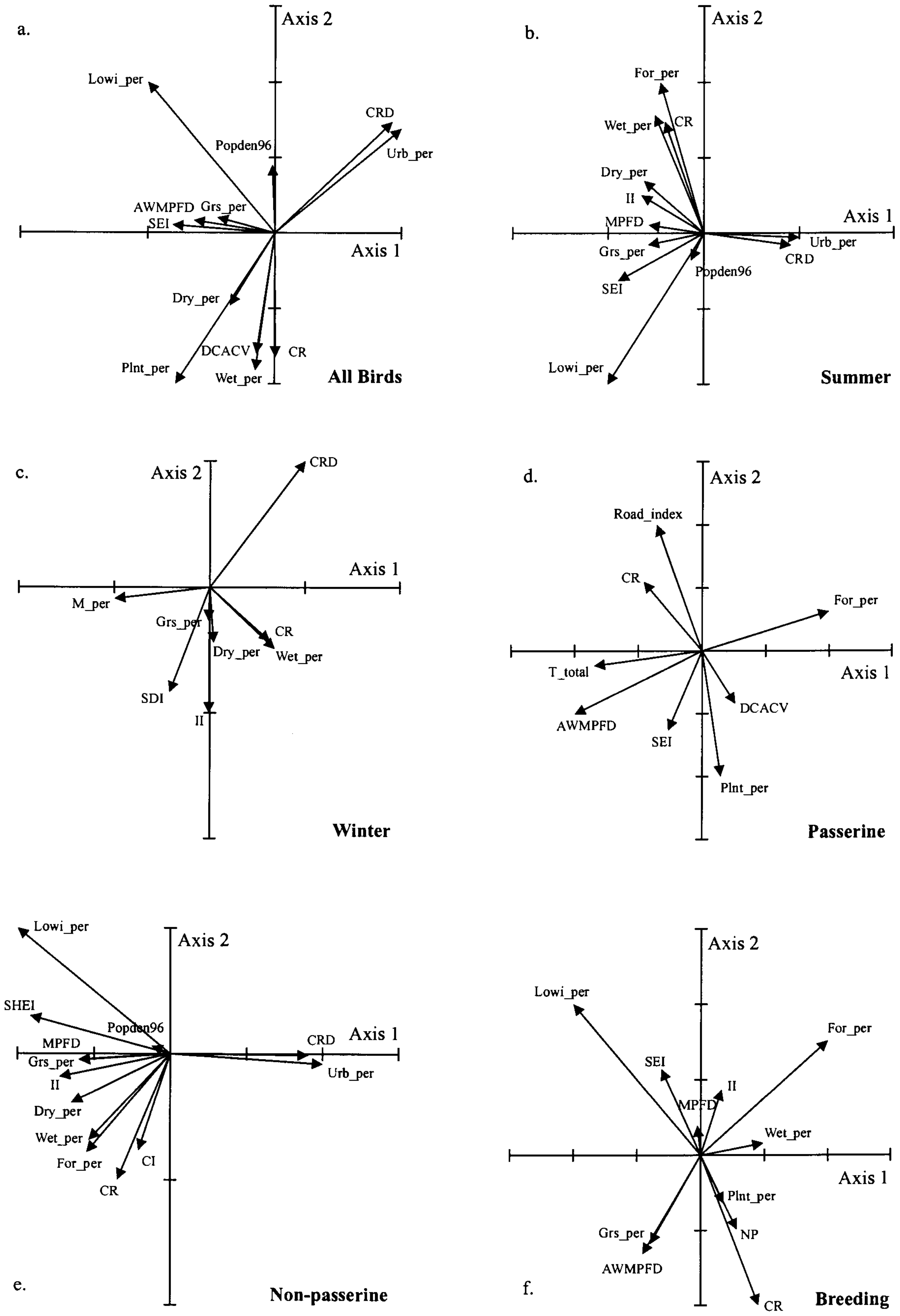

Figure 5.12: Biplots from canonical correspondence analysis of life history bird assemblages. All axes have been rescaled to range from –1.0 to 1.0. Axes for explanatory landscape variables that were not significant or that had very low correlations with the canonical axes are not shown.

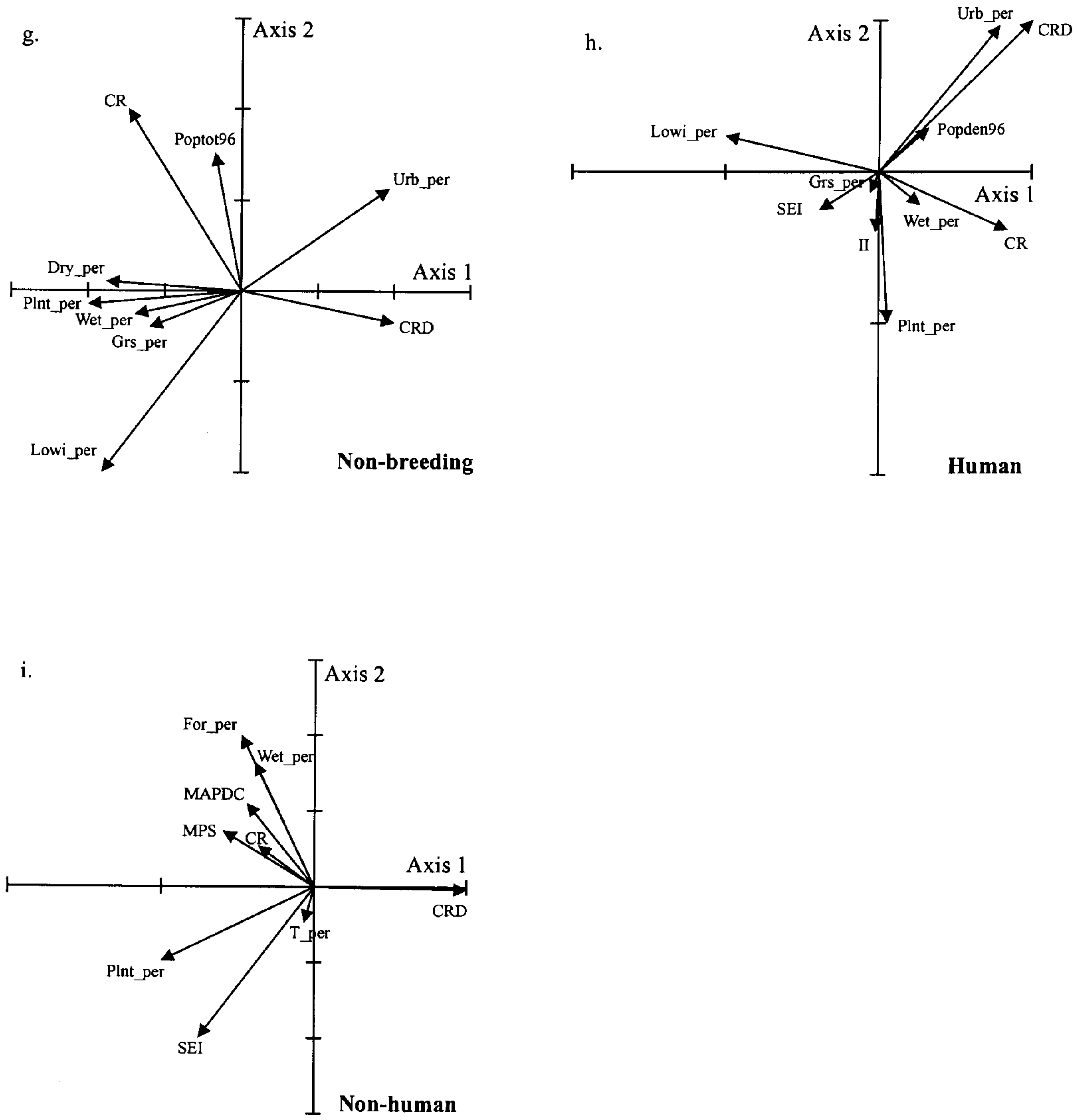

Figure 5.12: Continued.

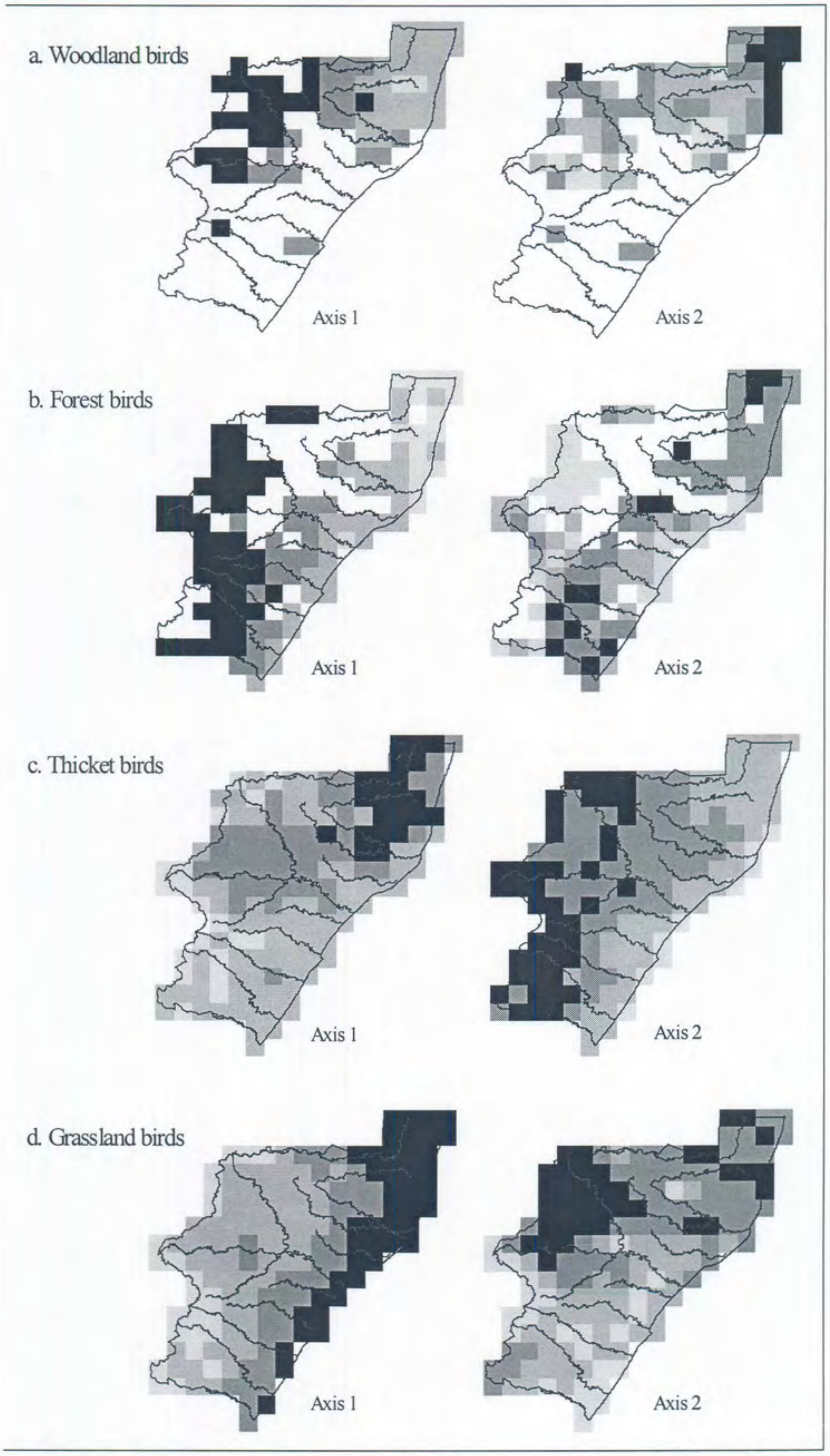

Figure 5.13: Patterns of variation in the first two axes of variation derived from detrended correspondence analysis (DCA) for each ADU ecological habitat bird group. Areas with no coverage of the respective vegetation class are depicted in white.

Table 5.10: Increases in total variation explained (TVE) by explanatory variables in stepwise canonical correspondence analysis of ADU bird species, by ecological type; the three greatest contributors to TVE in each group type are show in boldface. †

	Additional variation explained (proportion of TVE)			
Variable	Woodland	Forest	Thicket	Grassland
Topography				
DEMMEAN	§	§	**0.13**	**0.19**
DEMSTD	‡	0.02	0.02	**0.03**
Climate				
GDMEAN	0.03	**0.04**	**0.04**	0.02
MAP	‡	§	§	§
GTMEAN	**0.20**	§	§	§
NGTMEAN	§	§	§	§
MAT	‡	§	§	§
HOTMNTHMN	§	§	§	§
MINMNTHMN	§	**0.28**	§	§
EVANNMN	**0.10**	**0.07**	**0.21**	**0.08**
PSEAS_MN	0.02	‡	0.02	0.02
TSEAS_MN	§	‡	§	§
MXSEAS_MN	§	‡	0.01	0.02
EVSEAS_MN	**0.02**	‡	‡	0.01

† Increase in TVE is additional species variation explained by adding the variable after previously selected variables already are included, expressed as a proportion of TVE, and thus reflects selection order. Values are for variables included by forward selection ($P < 0.01$, where significance was determined by a 499 iteration Monte Carlo permutation test, H_0: additional influence of variable on vegetation is not significantly different from random), and where adding the variable did not result in inflation factors > 20.

‡ Variable was not significant in the stepwise procedure.

§ Variable was significant in the stepwise procedure but excluded because of multi-collinearity.

Woodland bird variation was related to temperature and precipitation seasonality on the first axis, with higher temperatures in Maputaland and stronger seasonality in precipitation in the Tugela and Buffalo River basins. The second axis gradient contrasted the northern coast versus the inland low-lying Tugela, Pongola, Mkuze and Mhalutze River valleys. The variables illustrated an aridity gradient represented by growth days and evapotranspiration. The forest bird's first axis gradient depicted a trend from the Drakensberg escarpment and southern midlands to the flat and warmer coastal plains of Maputaland, appropriately elevation heterogeneity and mean minimum temperature of the coldest month described the axis. The second axis of variation described the lower moisture regimes in the interior of the province and Maputaland from the wet southern coast and Drakensberg escarpment, with evapotranspiration and growth days explaining the pattern. The variation in thicket birds illustrated a trend from Maputaland and Zululand to the Drakensberg escarpment, which was explained by evapotranspiration and growth days. Axis two was related to elevation, elevation heterogeneity, seasonality in maximum temperature and a further contribution by growth days. The variation in grassland birds was the most complicated to explain with the available environmental variables, which lead to seven variables being chosen. Axis one depicted a gradient in elevation and seasonality in maximum temperature from the coast and Maputaland to the Drakensberg escarpment. Axis two was mostly represented by a moisture gradient between Tugela and Buffalo River basin and Maputaland grassland birds and birds in the Midlands, south coast and high central Drakensberg escarpment.

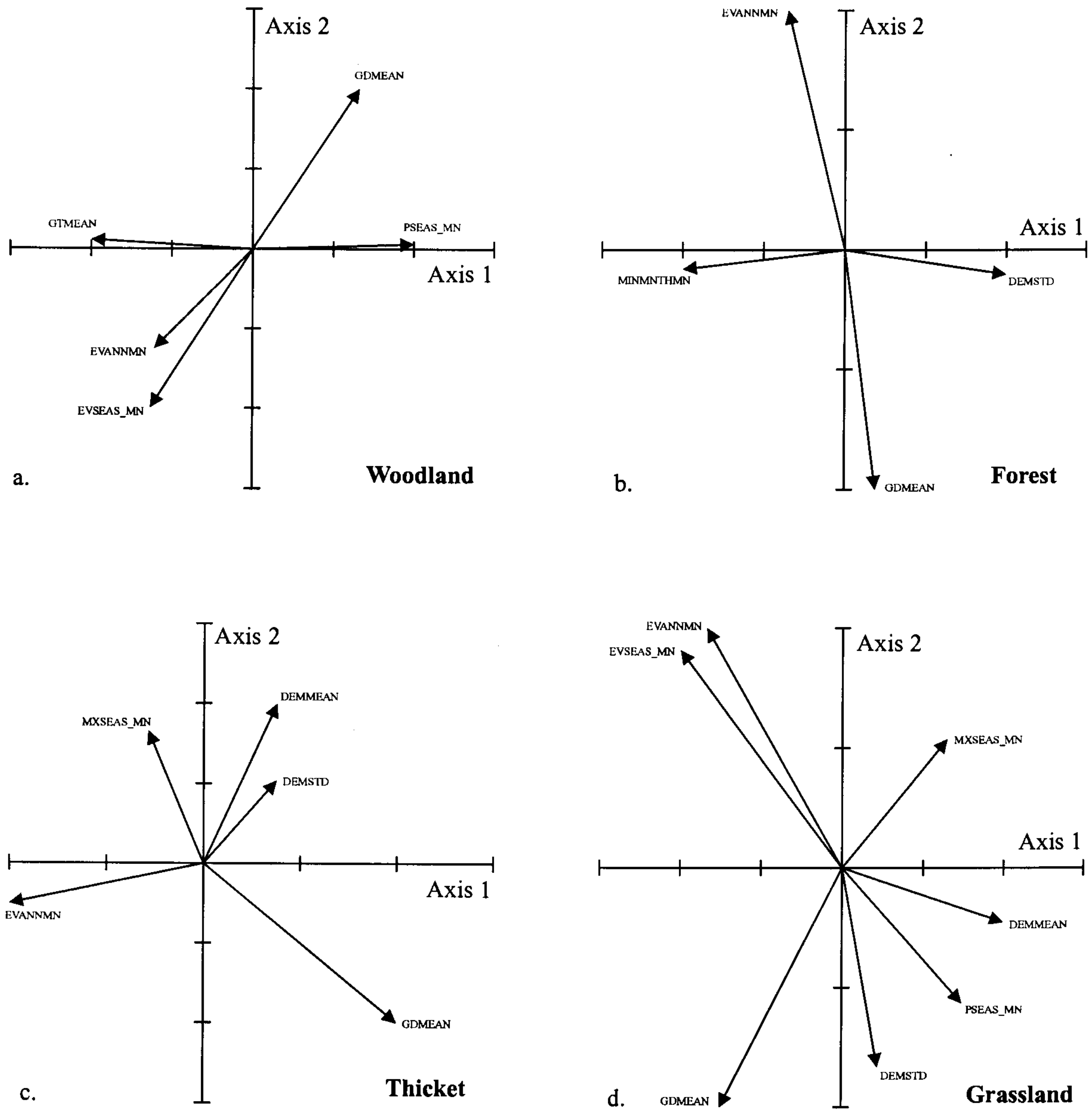

Figure 5.14: Biplots from canonical correspondence analysis of ecological habitat bird assemblages. All axes have been rescaled to range from –1.0 to 1.0. Axes for explanatory environmental variables that were not significant or that had very low correlations with the canonical axes are not shown.

In partial CCA conducted on the ecological habitat bird data sets, regional factors (climate and topography) accounted for the following in TVE: Woodland (47.6%); forest (46.4%); thicket (44.3%); and grassland (40.3%), with forest requiring the least amount of explanatory variables (Figure 5.14). The landscape class patch variables contributed to explaining a further 24.5% - 31.4% amongst the ecological habitat bird assemblages (Table 5.11), overall this is significantly higher than for the life history bird assemblages. The variable set included not only class patch pattern characteristics by vegetation type but also the proportion of human land-use and transformation impact indicators. Woodland and grassland bird variation responded more

Table 5.11: Proportion of total variation explained (TVE) by landscape variables while constrained by the topography and climate variables chosen for each group type in partial canonical correspondence analyses (CCAs) of ADU bird species; the three greatest landscape contributors to remaining TVE after constraining by the topography and climate variables in each group type are show in boldface. [†]

	Additional variation explained (proportion of TVE explained after constraining by covariables)			
	Woodland	Forest	Thicket	Grassland
Partial CCA TV	0.430	0.477	0.529	0.536
Variable				
Landcover				
POPTOT96	‡	§	‡	‡
POPDEN96	‡	§	‡	§
LOWI_PER	0.015	‡	0.01	‡
PLNT_PER	‡	**0.02**	‡	0.01
DRY_PER	‡	‡	‡	0.01
IRR_PER	‡	0.01	‡	‡
URB_PER	‡	**0.04**	**0.03**	**0.03**
M_PER	‡	‡	‡	‡
T_PER	**0.02**	‡	‡	‡
T_TOTAL	‡	‡	0.01	0.01
ROAD_INDEX	0.01	‡	**0.01**	0.01
Patchiness				
%LAND	‡	**0.02**	‡	‡
LPI	0.01	‡	‡	‡
NP	**0.02**	0.01	‡	‡
PD	**0.02**	‡	‡	‡
MPS	‡	‡	‡	0.01
PSSD	§	‡	‡	**0.02**
PSCV	§	‡	‡	‡
Shape				
MSI	‡	§	‡	‡
AWMSI	0.01	§	0.01	§
MPFD	‡	§	‡	‡
AWMPFD	§	0.01	‡	**0.01**
Interior				
CADI	‡	‡	‡	‡
TCA	‡	‡	‡	0.01
NCA	§	‡	‡	‡
CAD	0.02	‡	‡	0.01
MCAPP	‡	‡	‡	0.015
PCASD	‡	‡	‡	‡
PCACV	‡	0.01	‡	‡
MAPDC	‡	‡	‡	0.01
DCASD	‡	‡	‡	‡
DCACV	‡	‡	0.01	‡
TCA%	‡	‡	**0.04**	‡
MCA%	‡	0.01	0.01	‡
Isolation				
MNND	‡	‡	‡	‡
NNSD	‡	‡	‡	‡
NNCV	‡	‡	‡	‡
MPI	‡	0.01	0.01	‡
II	‡	‡	‡	0.01

[†] Same rules as for Table 5.8.

[‡] Variable was not significant in the stepwise procedure.

[§] Variable was significant in the stepwise procedure but excluded because of multi-collinearity.

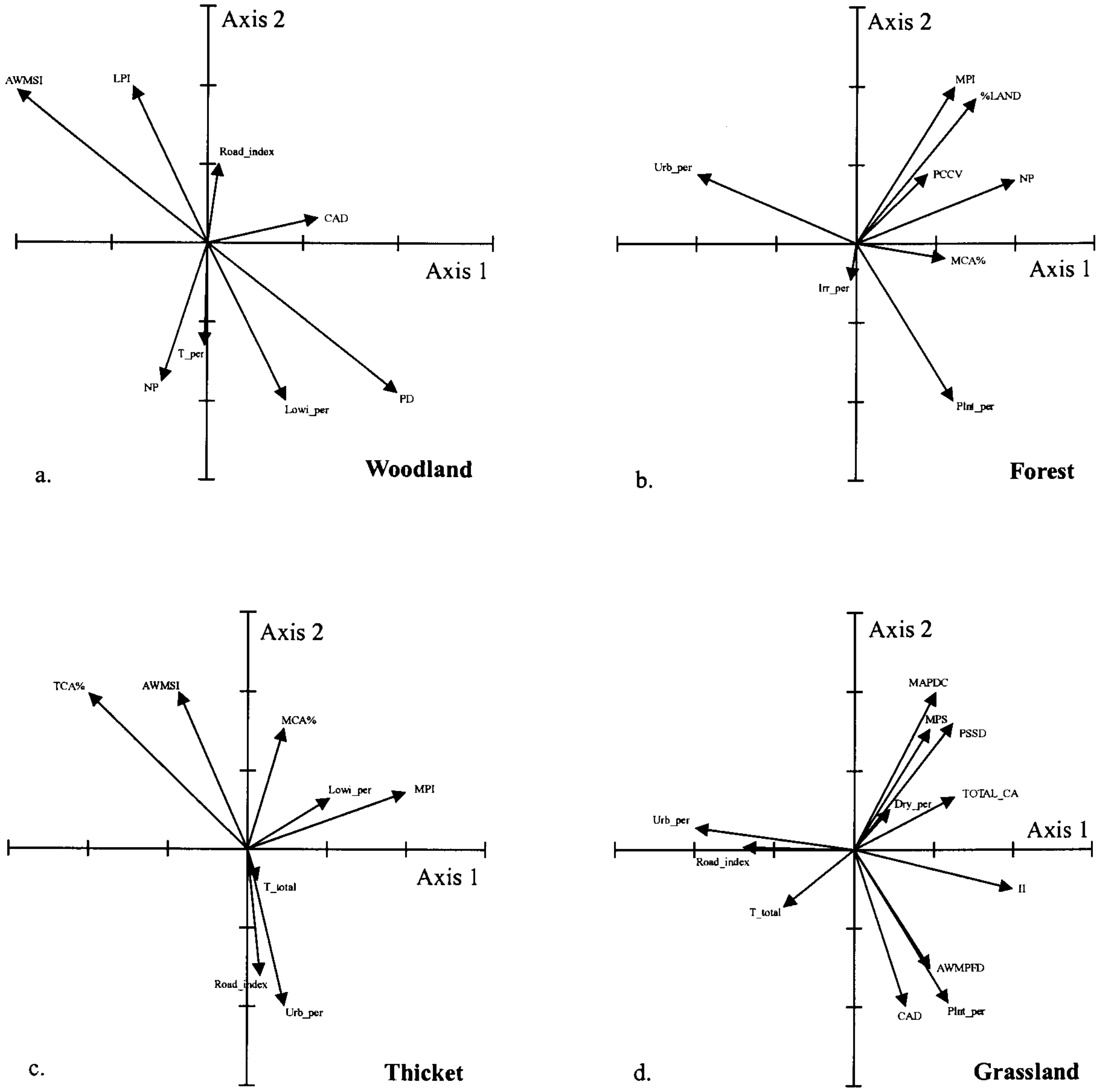

Figure 5.15: Biplots from canonical correspondence analysis of ecological habitat bird assemblages. All axes have been rescaled to range from –1.0 to 1.0. Axes for explanatory land-cover class type variables that were not significant or that had very low correlations with the canonical axes are not shown.

to the pattern metrics than to the human transformation indicators. The forest and thicket birds reacted mostly to variations in human transformation indicators. Overall the metrics explained 31.4% in woodland (Figure 5.15a), 28.3% in forest (Figure 5.15b), 24.5% in thicket (Figure 5.15c), and 27% in grassland (Figure 5.15d) bird variations. Grassland birds required the most variables to fit the remaining TV. The trend in the results suggests that as vegetation becomes more 2D in structure, i.e. trees to grass, the pattern metrics explain less of the local variations in birds. Forest, thicket, and grassland bird variation was related strongly to the extent of urbanization in the habitat class, and exotic tree plantations affected forest birds more strongly than grassland birds. Woodland birds were affected by total woodland removal, along with the number and density of the available woodland patches. Thicket bird variation was related to road disturbance and the total amount of thicket patch core area available. Grassland bird variation also related to the variability in patch size distribution of grassland patches and the shape complexity of the available patches which was related to the amount of exotic plantations in the area.

5.5.2.2 Correlation Results

These results only pertain to the ADU data sets for which biodiversity measures of assemblage structure could be calculated. Analysis by identify assemblage class within the life history bird assemblages, as derived from the ordination analysis, provides an ecological basis for the analysis from which landscape level descriptions can be made. Table 5.12 provides a breakdown of the biodiversity measure relationships to human impact for each assemblage class identified within a bird assemblage group. In almost all cases the identified East Coast and Midlands communities of each of the bird assemblages is tending towards single species dominance with a negative correlation with high intensity transformation. The correlations are even higher when compared to the road disturbance index. Exceptions include the negative correlation between high intensity transformation and evenness for the Central Zululand community of passerines, Maputaland community of non-human influenced birds, and high grasslands community of human influenced birds. The negative trends in evenness occur once grid cells in a community group record high intensity transformations of greater than 60%, which has been noted as a fragmentation transition point in other analyses (Andren, 1994; With and Crist, 1995; Bascompte and Sokal, 1996). High intensity transformation and road disturbance effects would appear to be the most important general indicators to monitor and assess the fate of bird assemblage structure. Again, the assessment of these relationships at the community extent has species richness positively correlated with high intensity transformation for many of the bird groups and assemblage groups. Exceptions to this relationship occur among the passerine and human influenced bird assemblages. Another notable exception is the Drakensberg Escarp community of non-human influenced birds, which is shown to be negatively associated with high intensity transformation and road disturbance. This alpine bird community type is not only sensitive environmentally but the majority of the birds are negatively influenced by human disturbance.

The relationship of low intensity transformation to species richness documents the negative effects of habitat degradation to overall species richness in all bird assemblages and the majority of assemblage classes were the phenomena is present. Reducing habitat quality is detrimental to interior species and because it adds no new novel land-use types through total transformation there is no immigration of edge dwelling and generalist species. This problem leads to a general reduction in sensitive species and a therefore a general evenness in bird assemblage for the areas were there was natural tendency towards single species dominance, i.e.,

Table 5.12: Pearson correlation coefficients for comparison of species richness (SR), Shannon diversity (H'), and evenness (E) against transformation and disturbance variables among classified groupings of ADU birds derived from ordination (DCA) and hierarchical classification. Human induced transformation data were square root-transformed before analysis to improve normality. [†]

	Low intensity transformation			High intensity transformation			Road disturbance index		
Community Group	SR	H'	E	SR	H'	E	SR	H'	E
All birds									
Maputaland	-0.44*	-0.47*	§	§	§	§	§	§	§
East Coast	§	§	§	0.36‡	§	-0.43*	0.48*	§	-0.68***
Drakensberg	§	§	0.31‡	§	0.29‡	§	§	§	§
Central Zululand	-0.41**	-0.28*	§	0.27‡	§	§	0.37**	§	-0.36**
Midlands	-0.74***	-0.34‡	0.42*	0.61*	§	-0.43‡	0.42*	§	§
Summer									
Maputaland	-0.56**	-0.56**	§	§	§	§	§	§	0.38‡
East Coast	§	§	§	0.40*	§	-0.44*	0.46*	§	-0.64***
Drakensberg Escarp	§	§	§	§	§	§	§	§	§
Central Zululand	-0.38**	-0.30*	§	§	§	§	0.42**	§	§
Midlands	-0.73***	-0.41*	0.38*	0.57**	§	-0.41*	0.38*	§	§
Winter									
Maputaland	-0.44*	-0.36‡	§	§	§	§	§	§	§
East Coast	§	§	§	0.36‡	§	-0.53**	0.41*	§	-0.74***
Drakensberg	-0.35**	-0.26*	§	§	§	§	§	§	§
Midlands-Zululand	-0.65***	-0.48***	§	0.61***	0.48***	§	0.50***	0.34*	§
Passerine									
Maputaland	§	§	§	§	§	§	0.38*	0.39*	§
Drakensberg	§	§	0.32‡	§	§	§	§	-0.33*	§
Central Zululand	-0.42**	§	§	§	§	-0.37*	0.38*	§	-0.28‡
East Coast	-0.32‡	§	§	§	§	§	§	-0.48**	-0.72***
Midlands	-0.74***	§	0.53**	0.61**	§	-0.42*	0.44*	§	§
Non-passerine									
Maputaland	-0.33*	-0.37*	§	§	§	§	§	§	§
East Coast	§	§	-0.43*	§	§	-0.54**	0.35‡	§	-0.73***
Drakensberg	-0.40***	§	§	0.37***	0.36***	§	0.36***	0.35**	§
Midlands	-0.62***	-0.52**	§	0.54**	0.33‡	§	0.56***	§	§
Breeding									
Maputaland	-0.39*	-0.39*	§	§	§	§	0.37*	0.44**	§
East Coast	§	§	§	0.35‡	§	§	0.43*	§	-0.49**
Drakensberg	§	§	0.34*	§	§	§	§	§	§
Central Zululand	-0.40*	§	§	§	§	§	0.36*	§	§
Midlands	-0.70***	-0.37*	0.32‡	0.61***	§	-0.37*	0.42*	§	§
Non-breeding									
Woodland	-0.41*	§	§	§	§	§	§	§	§
Wet Grasslands	-0.27*	§	§	0.33**	§	§	0.37**	§	§
East Coast	§	-0.44*	-0.35‡	§	§	§	0.42*	§	§
Dry Grasslands	-0.52***	-0.43**	§	0.39*	0.36*	§	0.25‡	0.29*	§
Human									
Maputaland	§	§	§	§	§	§	§	§	§
Drakensberg Escarp	-0.34‡	§	§	§	0.40*	§	§	§	§
High Grasslands	-0.31*	§	0.40**	§	§	-0.29*	§	§	§
Central Zululand	-0.35*	-0.34*	§	§	§	§	0.32‡	§	§
East Coast	§	§	§	0.71***	0.60*	§	0.57*	§	-0.68**
Non-human									
Maputaland	-0.45‡	-0.43*	§	§	§	-0.36‡	§	§	§
East Coast	§	§	§	§	§	§	§	§	§
Drakensberg Escarp	§	§	0.50*	-0.46*	-0.52*	§	§	-0.42‡	-0.48*
Highlands	§	§	§	§	§	§	§	§	§
Midlands	-0.47**	§	§	0.60***	§	§	0.43*	§	§
Coastal Hinterland	-0.53**	-0.38*	§	0.31‡	§	§	0.35‡	§	§

[†] Significance is denoted by the following: § not significant, ‡ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Drakensberg and Midlands. The East Coast bird assemblages for non-passerine and non-breeding birds have the only negative relationships of evenness to low intensity transformation.

5.5.2.3 Semi-variogram Results

Empirical semi-variograms were generated for each biodiversity measurement and human impact measurement, while also including a road disturbance index (Stoms, 2000; Reyers et al., in review) and the 1996 human population density. The analysis results are only for the ADU data sets, documenting the influence of extent on the variables from the identified assemblage class per bird life history group as derived from the ordination analysis. The same distance resolution of 22.5 km between grid cell centers was used to calculate the variograms. Range values where a flat sill is reached, which represents the autocorrelation pattern for each variable by assemblage class within a life history bird assemblage are provided in Table 5.13.

The semi-variogram estimates for most of the measures are bounded. As can be seen from the table, ranges with small local distances describe small autocorrelated patches in the distribution of low and high values of the measures. Large distances describe large uniform patches of uniform autocorrelated low or high values. Five situations had flat variograms (pure nugget) that depict those variables as random processes across the extents defined in the model. Focusing on all, summer and winter life history groups in Table 5.13 the winter groups measures and assemblage class extents tend to yield fine grained pattern, while the summer group generally has larger coarse grained pattern. Considering all the birds in the province further increases the coarse grained pattern in each of the assemblage classes. The trend in spatial pattern for the biodiversity measures in the other bird assemblages shows all but non-passerine bird assemblages as being generally coarse grained. A comparison between the spatial extents of evenness and high intensity transformation for the assemblage classes with negative relationships shows a trend in decreased correlation strength when the high intensity transformation pattern is larger grained than the evenness pattern. This pattern is also similar with comparisons against the road disturbance index. Any general trends in the relationship between species richness and high intensity transformation could not be discerned as changes were confounded by the changing extents among assemblage classes by bird assemblage group.

5.5.2.4 Association Analysis Results

Kappa index values and χ^2 tests were computed for each grid cell and bird assemblage between the two survey periods (1970-1979 and 1987-1992). Figure 5.16 provides a breakdown of the classified Kappa index values with indications of χ^2 tests that were not rejected (H_0: grid cells from two time period are dissimilar).

Table 5.13: Semi-variogram derived distances (kilometers) of spatial dependence for species richness (SR), Shannon diversity (H'), evenness (E), low intensity transformation (LI), high intensity transformation (HI), total transformation (TT), road disturbance index (RI), and 1996 population density (PD96) among classified groupings of ADU birds. [†]

Community Group	SR	H'	E	LI	HI	TT	RI	PD96
All birds								
Maputaland	45.0	112.5	157.5	157.5	90.0	157.5	67.5	157.5
East Coast	360.0	22.5	405.0	22.5	270.0	270.0	337.5	22.5
Drakensberg	337.5	337.5	292.5	337.5	45.0	337.5	22.5	90.0
Central Zululand	112.5	225.0	225.0	22.5	225.0	112.5	225.0	180.0
Midlands	135.0	22.5	235.0	112.5	180.0	180.0	22.5	112.5
Summer								
Maputaland	45.0	22.5	112.5	22.5	22.5	22.5	22.5	157.5
East Coast	405.0	22.5	405.0	22.5	202.5	270	405.0	22.5
Drakensberg Escarp	337.5	315.0	180.0	337.5	247.5	337.5	22.5	90.0
Central Zululand	135.0	180.0	225.0	22.5	225.0	112.5	225.0	180.0
Midlands	135.0	135.0	135.0	112.5	135.0	202.5	22.5	112.5
Winter								
Maputaland	45.0	45.0	22.5	22.5	90.0	112.5	22.5	157.5
East Coast	382.5	405.0	337.5	22.5	247.5	270.0	292.5	22.5
Drakensberg	157.5	337.5	337.5	337.5	247.5	45.0	22.5	22.5
Midlands-Zululand	67.5	45.0	22.5	67.5	22.5	337.5	337.5	22.5
Passerine								
Maputaland	22.5	112.5	180.0	22.5	180.0	180.0	180.0	157.5
Drakensberg	157.5	157.5	112.5	337.5	247.5	247.5	22.5	90.0
Central Zululand	112.5	225.0	225.0	67.5	225.0	112.5	225.0	112.5
East Coast	22.5	22.5	45.0	22.5	22.5	135.0	157.5	22.5
Midlands	112.5	22.5	135.0	112.5	22.5	225.0	225.0	225.0
Non-passerine								
Maputaland	67.5	22.5	202.5	22.5	202.5	‡	202.5	90.0
East Coast	22.5	22.5	405.0	22.5	247.5	270.0	292.5	22.5
Drakensberg	67.5	67.5	337.5	292.5	90.0	292.5	337.5	157.5
Midlands	135.0	112.5	112.5	22.5	45.0	157.5	202.5	22.5
Breeding								
Maputaland	225.0	225.0	225.0	22.5	180.0	180.0	180.0	225.5
East Coast	405.0	‡	22.5	22.5	247.5	270.0	292.5	22.5
Drakensberg	337.5	‡	22.5	337.5	22.5	337.5	22.5	90.0
Central Zululand	202.5	202.5	202.5	90.0	157.5	22.5	202.5	22.5
Midlands	22.5	135	135.0	22.5	157.5	22.5	202.5	22.5
Non-breeding								
Woodland	67.5	247.5	‡	202.5	315.0	315.0	292.5	270.0
Wet Grasslands	67.5	292.5	202.5	225.0	22.5	202.5	22.5	22.5
East Coast	22.5	22.5	22.5	22.5	247.5	270.0	292.5	270.0
Dry Grasslands	202.5	157.5	247.5	270.0	22.5	22.5	157.5	180.0
Human								
Maputaland	22.5	247.5	202.5	22.5	247.5	247.5	247.5	247.5
Drakensberg Escarp	157.5	‡	180.0	315.0	247.5	315.0	22.5	67.5
High Grasslands	135.0	202.5	22.5	315.0	22.5	112.5	180.0	135.0
Central Zululand	157.5	157.5	202.5	202.5	22.5	202.5	22.5	202.5
East Coast	292.5	292.5	67.5	22.5	135.0	180.0	202.5	22.5
Non-human								
Maputaland	45.0	22.5	45.0	157.5	90.0	157.5	67.5	157.5
East Coast	247.5	22.5	22.5	22.5	247.5	270.0	337.5	22.5
Drakensberg Escarp	337.5	180.0	337.5	337.5	157.5	337.5	135.0	247.5
Highlands	157.5	157.5	22.5	270.0	202.5	270.0	157.5	22.5
Midlands	157.5	202.5	22.5	22.5	157.5	202.5	270.0	22.5
Coastal Hinterland	22.5	337.5	337.5	22.5	180.0	180.0	247.5	202.5

[†] Semi-variogram models have been fit using a spherical function.

[‡] Variable represented a completely flat variogram (pure nugget), meaning no spatial dependence in the data, i.e. no discernible pattern, and that deriving a semi-variogram is inappropriate.

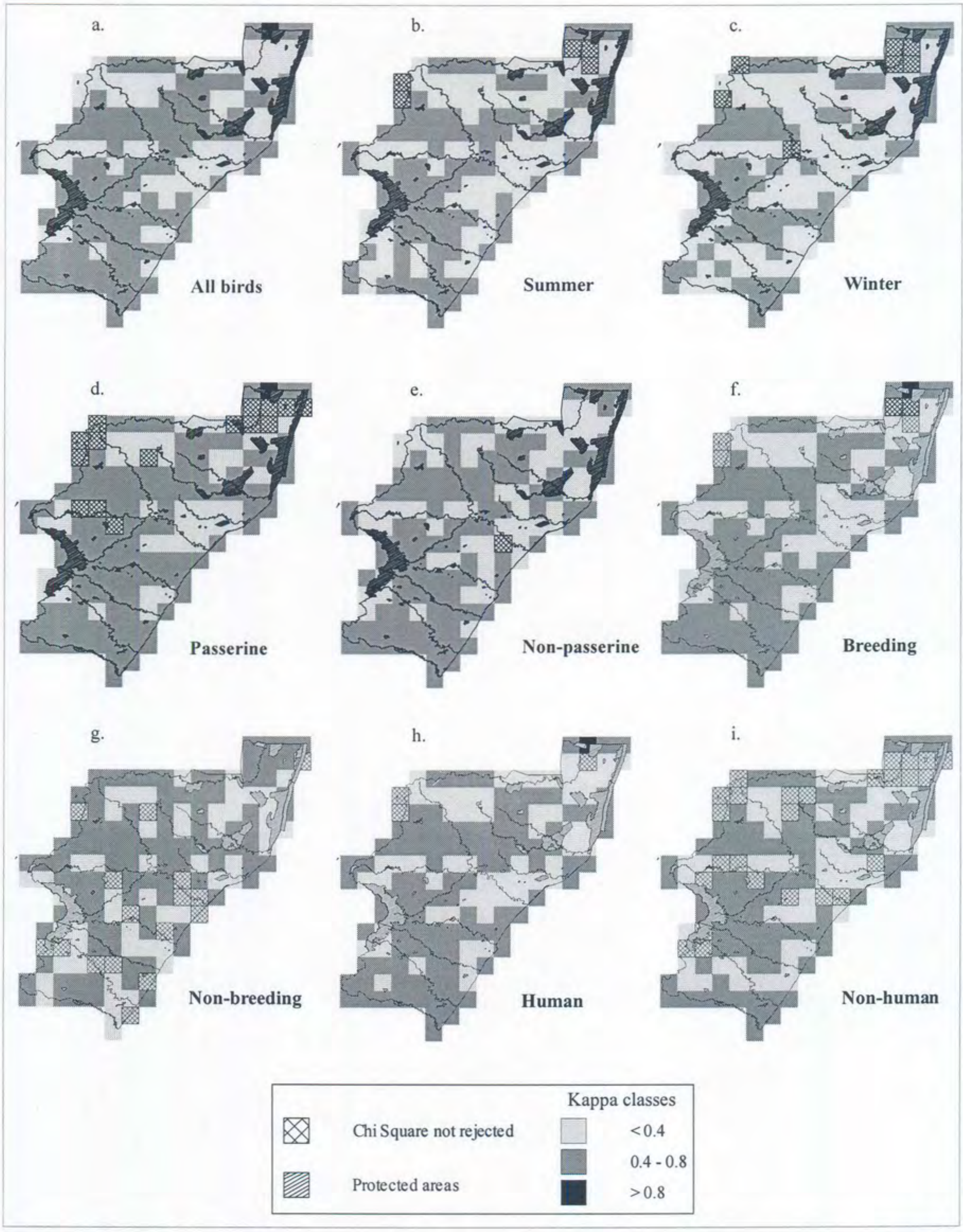

Figure 5.16: Kappa coefficient maps of each comparison between CR and ADU surveys and life history bird assemblages.

The summer, winter and non-human influenced bird assemblages have ≥ 50% of their grid cells with Kappa values < 0.4, which equates to agreements no better than chance. The only grid cell to have almost perfect agreement (> 0.8) with all, passerine, breeding and human influenced birds covered the Ndumo and Tembe nature reserves on the Mozambique border in Maputaland. This grid cell is remote, > 50% protected and the lands on the Mozambique side were in a near pristine condition with little to no human habitation during the bird census periods. Areas of moderate to substantial agreement for all bird assemblages tend to contain protected areas, are in remote regions, or have continued with substantial levels of either low intensity or high intensity development since prior to 1970. It is possible that bird inventories had either already changed prior to 1970 to a stable inventory in the previously developed areas (coastal areas in and around Durban and Pietermaritzburg since 1911) or no changes in "natural" areas up to 1992. Many of the high intensity developed areas were that way before at least 1970 (Midlands, Durban and coastal regions), while the low intensity developed areas could have expanded between census periods due to the demarcation of the KwaZulu homeland areas during the mid-1970s. Several areas are consistently represented with dissimilar bird inventories (< 0.4) for all the bird groups. These areas were also the ones targeted for development between the two governments (Republic of South Africa and KwaZulu government) between the census periods (Fair, 1975; South African Government, 1975; Thorington-Smith et al., 1978). These areas consist of the coastal and coastal hinterland regions south of Umfolozi game reserve, the areas south of Ndumo and Tembe nature reserves on the Maputaland plains, grid cells to the west of Pongola dam along the Pongola River, grid cells in the Newcastle, Vryheid and Utrecht areas, grid cells in the Bergville area and down along the Tugela River valley, and grid cells along the Pietermartizburg-Durban economic corridor fanning out north and south along the coastal hinterland. Appendix D provides a list of the birds found in the CR survey but not recorded in the ADU survey, and birds found in the ADU survey but not found during the CR survey.

5.6 Discussion

There is a growing recognition that biogeographic-scale studies are needed to gain a more comprehensive assessment of faunal response to anthropogenic disturbance. Because it is often impractical for individual investigators to collect the necessary biogeographic data (Kodric-Brown and Brown, 1993), one must rely on the independent efforts of others to develop relations. The use of comprehensive biological atlases, developed with consistent methodologies in surveying can help in this task. In this study, consistent methodologies were applied to examine two temporally distinct avian atlases, landscape structure and environmental variables. The two spatial extents of analysis provided useful insight into the avian assemblages relation to land-use intensity and pattern with spatial extent. While the two time periods provide the landscape dynamics for a selected region.

The ADU data supporting the spatial correlation and variogram analyses can be considered both comprehensive and reliable. While for South Africa the average number of bird checklists having been compiled for each grid was 30, KwaZulu-Natal Province was one of the most thoroughly surveyed regions during the atlassing effort, with an average of 105 bird check-lists having been compiled per grid cell in the province. The distributional data were also subjected to a rigorous vetting procedure by both experienced amateur and professional ornithologists. A quantitative testing against independent and more sensitive survey techniques (Allan, 1994; Robertson et al., 1995), also confirmed its reliability in reflecting relative abundance in terms of reporting rates. However, Harrison et al. (1997) do note that there were still problems in identification between species, consistency of species probability of being sighted in different habitats and the technique used in this chapter to dampen the effects of bias in recording effort cannot help in some areas of South Africa were reporting rate was less than 10 check-lists. Some may even argue that using cumulative data from a five year period is quite risky for vertebrate populations. Nevertheless, these challenges in using biological atlases should not deter from their importance for recording distributions and relative changes in bird assemblages, as their survey frameworks have the added advantages of representing less common species due to the longer survey period (Preston, 1948), which also has the added effect of not having to worry about high frequency spatial and temporal effects (Preston, 1960). In this case the averaging effects over any high frequency population changes due to the longer survey period should provide a clearer pattern of true compositional and structural changes due to large-scale land-use developments. However, the limitations noted will temper the results and discussion accordingly.

South Africa and KwaZulu-Natal correlation analyses.—Areas of high intensity human disturbance across South Africa and for each biome demonstrate the fragmentation process in developing new landscape mosaics and therefore changes in bird assemblages. Bird species richness increased, but the bird assemblage evenness across South Africa, and for the woodland and fynbos biomes showed a trend towards single species dominance. In contrast, the succulent desert biome showed increases in species richness and bird assemblage evenness. Each of these responding biomes has areas comprising urban residential, industrial, and commercial agriculture land-uses (Fairbanks et al., 2000), with fynbos, woodland, and then succulent desert ranked accordingly for the relative importance of these land-uses covering each biome. Urban, industrial and commercial agriculture forms of land-use lead to structural habitat changes (i.e., tree planting, water impoundments, infrastructure) that appear to positively influence the number of bird species found, but would also promote selected species dominance in those species adaptable to the new environments. This trend towards single species dominance may not require reduced sightings of rare species, but may simply reflect increasing populations of species that thrive in modified human landscapes due to their specific life-history requirements. These patterns, however, appear to be intimately tied to the evolving natural-urbanizing landscape. In contrast low intensity disturbance has a negative effect on the species richness of birds in the grassland biome, but a positive effect on birds in the shrub steppe. As opposed to degraded woody biomes where some level of tree or shrub structure remains, degraded grassland is highly detrimental to bird richness. In the shrub steppe biome the opening up of shrub patches from heavy grazing, which would allow for an increase in mosaic diversity (i.e., shrub, grass, and bare) appears to have a positive effect on bird richness. The woodland biome is typically over grazed and coppiced for fuelwood in South Africa (Fairbanks, 2000), which appears to cause a trend towards dominance in the assemblage structure.

The South African and biome extent analysis shows that species distributions and assemblage patterns change between natural and highly transformed areas. First, species richness increases and peaks in areas with optimal environmental resource levels containing a high proportion of highly transformed land. Secondly, the relative evenness of bird assemblages' decrease from natural to more highly transformed areas. This suggests that high intensity transformation may bring in novel resources for birds not normally found in areas, but that this does not directly translate into evenly structured communities. It appears that some species (high intensity transformation exploiters) are adept at exploiting these changes and reach their highest densities with a tendency for assemblage structure to drift towards single species dominance.

The correlation analysis amongst biodiversity measures and land transformation values by identified assemblage class in KwaZulu-Natal provided further support for the preponderance of species assemblages with negative relationships to human disturbance patterns. Also, since assemblage structure and total bird species richness summarizes a composite response of the habitat needs of individual species (Hansen and Urban, 1992), the performance of separate spatial correlation analysis for the main life history groups of birds allows to increase the predictive power of the model. Two community assemblages identified in several of the bird assemblages show this relationship: The East Coast assemblage is tending towards single species dominance in all, summer, winter and non-passerine bird assemblages, and the Midlands assemblage in all, summer, passerine, breeding, and human bird assemblages (Table 5.11). Two other communities were identified once for two bird groups: Central Zululand for passerines and Maputaland for non-human influenced birds. The non-human influenced bird assemblage structure in Maputaland could be a serious problem. These birds are neutral or negatively influenced by human activities. The Maputaland region represents South Africa's only link to the Afrotropical avifauna (Harrison et al., 1997) and therefore a greater share of the sensitive species in the region. The results in Table 5.11 show a tendency towards reduced species richness for low intensity disturbance and towards single species dominance under high intensity transformation for areas < 30% transformed. Another important aspect is the affect road disturbance has on the biodiversity measures by bird assemblage. Generally there is a similar positive relationship of roads to species richness as there is for high intensity transformation, and a negative relationship to evenness. However, these results should be interpreted cautiously as the species inventorying may be partly affected by road bias (e.g., Freitag et al., 1998), even though surveying procedures were developed to avoid this bias during the development of both atlases. Therefore, there is no reason to expect potential errors or biases to be systematically or non-randomly distributed throughout the country.

Changing the spatial extent and scale of the correlation analysis in a meaningful manner between national, vegetation biome, and ecologically identified sub-regional assemblages brought to bear important relationships regarding pattern and process. The importance of space has become a paradigm in many fields of ecology. Studies in community ecology, biodiversity, landscape ecology, and biogeography all rely on the analysis of spatial patterns. It is well known that the spatial pattern that we observe depends on the scale of the study (Wiens, 1981; Wiens, 1989b), which is conveniently summarized by its grain or resolution and by its spatial extent. While the effect of grain size has been formally explored in many studies (Turner et al., 1989), the effect of spatial extent has not always been thoroughly considered. However, this study illustrates the crucial role spatial extent can play for prominent operational definitions of richness, diversity, and community structure. The biome level results for birds incorporate a lot of variation in the biodiversity measures in association with the spatially structured response of the human transformation activity. Therefore, the results at this level of analysis are not as strong as the community level results for KwaZulu-Natal. This is probably because the bird communities, as shown in the ordination analysis, are being shaped more by the human developed land-covers at this scale rather than general vegetation characteristics (i.e., grassland or woodland). The identified communities would seem to provide a more appropriate measure of each bird groups relationship with the degree of human disturbance in a particular area. However, as identified for the national level analysis, the patterns of the birds in each group do not seem to be consistent with the intermediate disturbance hypothesis for human land-use as proposed by McDonnell et al. (1993). Therefore the results at the community extent of analysis provides little support for this suggested pattern, except for possibly the Drakensberg Escarp community of the non-human influenced birds. The smaller extent of analysis did provide some empirical support for the theoretical results found from percolation theory, which has been used to describe multi-species persistence in simulated fragmented landscapes (Gardner et al., 1987; Gardner et al., 1989;

Pearson, 1993; Bascompte and Sole, 1996). In all of the negative associations for evenness versus high intensity transformation the regression line was pulled down once sampling sites within the population were > 60% transformed. The positive relationship between species richness and high intensity transformation occurred when grid cells were > 40% transformed.

This pattern for South African birds is not consistent with the intermediate (natural) disturbance hypothesis (Connell, 1978) or with its extension (McDonnell and Pickett, 1990; McDonnell et al., 1993) to include human land-use. It has been suggested that species richness should peak at intermediate levels of human landscape development because biotic limitations are high in natural landscapes and physical limitations high in highly transformed landscapes (McDonnell et al., 1993). These results, at the coarse grid cell scale of analysis, provide little support for this suggested pattern in South African birds, and may instead provide some support for declining assemblage evenness regimes among cumulative local scale bird communities within a grid cell in response to high intensity transformation. The correlation slope increase in species richness appears to be significant once greater than 40% of the land-cover within a grid cell is transformed to high intensity land-uses. This situation would allow for both new human adaptable exploiters and the remnant natural vegetation related birds to co-exist, but with increasing high intensity land transformation the transformation exploiters appear to become dominant in the landscape. However, in the absence of land-use time series, interpretation is difficult since the rate of land-use change may be high in the woodland, grassland, and fynbos biomes (e.g., Fairbanks et al., 2000).

The use of the index of relative abundance tells us something of the changes of numerical relationship between two or more species, but nothing on the true abundance of each of them. If species #2 becomes much more numerous, it does not imply that species #1 is less abundant than before but only that species #2 has become more abundant. Therefore, an uneven assemblage in a high transformation area is not necessarily an impoverished community, but rather one that has a few species that are overly abundant in comparison to the total assemblage within an area. The potential causes for the correlations between species richness and high land-use intensity could be a function of time since transformation (i.e., recently transformed areas being richer than previously transformed areas), apparent increase due to better sampling, or to compositional or habitat differences in highly transformed versus un-transformed local scale communities that alter conspicuousness between land-use types. The apparent increase in species richness and decrease in assemblage evenness for some of the biomes may be due to maintenance of species richness in untransformed fragments in highly transformed grid cells combined with species that exploit transformed habitats well in the transformed areas (Quinn and Harrison, 1988). The pattern explored could be highly dependent on the scale and homogenizing character of grid cells on local scale bird community attributes (Wiens, 1981; Wiens, 1989a).

South Africa and KwaZulu-Natal geostatistical analyses.--Variograms also provide valuable information on the ability to sample and characterize bird assemblages at the defined grid cell resolution. The semi-variograms provide information on the spatial autocorrelation of the bird assemblage measures within each biome. Distances less than the sill derived range values are spatially autocorrelated and thus provide information about the processes and structures of the bird assemblages. The evenness assemblage measure derived for the grassland biome shows that to correctly characterize the bird assemblage structure in grassland the sampling resolution would need to be smaller than the current grid cells used for biological atlasing in South Africa. This result for grassland bird fauna may mean that characterizing birds using fine scale survey data may be required to completely understand their distributions and abundance, especially in response to land-use impact. This is important as the grassland bird species are tending towards the same problems as the fynbos species (Table 5.2), thus the current analysis may be limited because of scale. Nevertheless, the measures for all the other biomes confirm that the grid cells used for sampling are a small enough grain size to characterize the bird groups.

The variogram results for the KwaZulu-Natal provide more power in explaining the grain pattern of the life history bird assemblages within ecologically defined zones. An important aspect of the analysis points out the ecological extent of these bird assemblages against the land-use development within the assemblage classes. Most of the bird assemblages generally have a coarse autocorrelated measurement similarity across the zones, but this is not the case for species richness in non-passerine and non-breeding birds which tends to show fine scale detail. The non-passerines include the raptors, kingfishers, cranes, rollers, etc. These birds tend to have very specialized habitat requirements (i.e., river frontage, wetlands, cliffs) and are not as abundant or gregarious as the passerines. The non-breeding birds are Afrotropical and Eurasian visitors that also have special habitat requirements (e.g., blue swallow in mist belt grassland; European swallow in areas providing cliffs). Therefore, both assemblage types will tend to congregate at very specific locations producing fine scale species richness patterns. The results of the geostatistical analysis confirm the special landscape management nature that these birds would require for population persistence. The evenness index generally illustrated coarse grain pattern, except for several assemblage classes within the non-human influenced bird assemblage. The fine grained pattern in evenness structure occurs in assemblage classes that are dominated by high intensity transformation, which could reflect the fine scale abruptness in assemblage structure these birds reflect owing to their mainly negative relationship to human activity.

KwaZulu-Natal bird ordination and survey association analysis.—Ordination analysis of KwaZulu-Natal Province birds provided insight into the unique bird assemblage structures that have evolved within the region. Comparisons between the two survey periods highlighted several important changes in bird community structure over the 10-year period between surveys. Many of the shifts, contractions and splits in the assemblages are primarily associated with broad scale climate regimes and secondly to finer scale habitat patchiness and human land-use impacts. In particular the creation of woody patches of alien trees in the grasslands, the addition of water impoundment's, dryland agriculture, and urbanization have all played a part in changing the geography of bird distributions. This was reflected in the general decrease of the gradient lengths for each species assemblage, with the more recent ADU survey reflecting the homogenising affects land-cover changes are having on bird diversity. Comparisons between Figures 5.6 and 5.7 show several general trends: thinning of the East Coast bird zone around Richards Bay, compaction and stretching of the Maputaland zone southwards, shrinking of the Drakensberg zone, and a general split in the Midlands zone from the CR period into a Midlands and Central Zululand zones during the ADU survey. Several hypotheses could be driving these changes. First, rainfall varies above or below the mean in approximately 10-year cycles (Dyer and Tyson, 1977) in the region, with the CR survey coinciding in with a pluvial cycle and the ADU survey coincided with a dry and in some areas drought cycle. Therefore, species responding to this wet cycle could have moved into KwaZulu-Natal down along the Mozambique coast, or some species from the dry interior of South Africa could have moved in during the ADU period. Second, an increase in land transformation within the economically active areas along the coast and Midlands could have added more artificial habitats for transformation exploiters to distribute against (Figures 5.6h and 5.7h), or alternatively sensitive species could have withdrawn from those areas into the underdeveloped Zululand region (e.g., Winterbottom, 1962). Finally, there is still the possibility that despite the thorough surveys conducted in both periods, a majority of the species could still reflect biased distribution estimates.

Elevation contributed more to total variation explained (TVE) than any other variable (Tables 5.7 and 5.8). However, elevation is a complex-gradient (sensu Whittaker, 1960; 1965) that co-varies with a host of historical and environmental factors such as vegetation and climate. Therefore, in many of the datasets the elevation gradient was collinear with climate variables, such as minimum temperature. Nevertheless, the strong association between elevation and species composition observed in both sampling periods is consistent with other studies (e.g., Liversidge, 1962; Brown and Barnes, 1984).

One could debate excluding elevation from the analyses because it measures spatial position and only indirectly reflects physical environment. Excluding DEMMEAN from stepwise

CCAs, however, did not appreciably affect TVE, probably because of multicolinearity with other climate measures, nor the relations among species, grid cells, and explanatory variables. This robustness to multicolinearity among explanatory variables is a strength of CCA (Palmer, 1993). Therefore, DEMMEAN was retained in the analyses because of its value in interpreting results.

Results for the gradient analysis supported the hypothesis of primary importance of macroclimate and the secondary role of land-cover proportion and pattern in controlling regional compositional gradients in the bird diversity of KwaZulu-Natal. These findings can only be compared indirectly with previous studies because of differences in methods. Similar type studies in North America used plot sampling or linear sampling along predefined road transects, and examined relative contributions of regional climatic measures and plot based vegetation pattern statistics or coarse-scale land-cover (Flather, 1996; Wiens and Rotenberry, 1980; Rotenberry, 1978; Wiens, 1973; McGarigal and McComb, 1995; Flather, 1996; O' Connor et al., 1996).

Evapotranspiration, seasonal variability and extremes in climate were more important in explaining species gradients than were mean annual climatic conditions. The two dominant species gradients were associated with elevation, which integrates temperature extremes, seasonal variability in moisture and temperature related to the Indian Ocean and escarpment (continentality), and climatic gradients that integrate elements of both temperature and moisture. The importance of continentality in this study was consistent with Rotenberry's (1978) study that spanned a west-east gradient from Oregon to Colorado, although this present study spanned a much narrower latitudinal range (see also Cody, 1981; Cody, 1985; Cody, 1993). Species gradients for all groups and survey periods were much more strongly associated with minimum temperature during winter and moisture stress during summer. This association was consistent with observed correspondence between growing season precipitation and temperature gradients and latitudinal vegetation gradients in the grassland (Ellery et al., 1995) and woodland (Fairbanks, 2000) biomes of South Africa.

Topographic heterogeneity contributed slightly more to TVE for the non-breeding and non-human influenced bird groups in the CR datasets, but had a smaller contribution across all the ADU datasets (Tables 5.7 and 5.8). The CR datasets all responded more significantly to topographic heterogeneity than to evapotranspiration and seasonal variability's in temperature and precipitation. In the ADU datasets, only the gradients in human influenced birds showed significant relationships with topographic heterogeneity. In western KwaZulu-Natal, moisture is substantial and temperatures are colder and more variable, topography is deeply dissected from the rivers flowing off the Drakensberg Escarpment, and topographic effects would be more pronounced (Fairbanks and Benn, 2000).

Analysis of the birds grouped by ecological habitat associations and using their relative abundance values to examine relationships illustrated that the effects of elevation were only substantial for the thicket and grassland bird assemblages, and elevation heterogeneity was only significant for the grassland bird assemblage. These two vegetation types were found to extend across the entire province and thus reflect the strong gradient between coastal and Drakensberg Escarpment grassland and thicket type bird variation. Climate variables of temperature and evapotranspiration explained most of the variation in bird variation. Structural changes in woodland types between the arid woodlands of Maputaland and the mixed woodland of the Tugela and Buffalo River basins are largely determined by growing season temperature (Fairbanks, 2000). Growing season moisture stress accounted for the variation in forest and thicket associated birds, with minimum monthly temperature explaining the differences in bird community type in forest. This reflects the differences in forest structure and composition between the coast and afromontane forests of the Midlands and canyons along the Drakensberg Escarpment (Everard et al., 1995).

The findings on the influence of landscape structure variables on regional species gradients were not very conclusive with the life history bird assemblages and varied widely in importance with regard to remaining TVE (Table 5.9). Under partial CCA the landscape variables explained between 8.6-32% of TVE for the life history bird assemblages, with the most sensitive bird assemblages more significantly influenced. Non-breeding, non-human influenced and non-passerine bird assemblage gradients were associated the strongest with landscape variables. For all the bird assemblages, however, the proportion of land-cover was more important to TVE under the stepwise CCA than landscape mosaic pattern variables. There were several exceptions with class richness density having significance for all, summer, winter, non-passerine, non-breeding, and non-human influenced bird assemblages. LCLU evenness was important for the non-human influenced birds and the variability in patch size with distance was important for explaining the passerine assemblage. Contrary to the idea that landscape structure (i.e., configuration) plays a dominant role in the regulation of wildlife populations (e.g., Turner, 1989), these results suggest that LCLU proportion (i.e., habitat and land-use area) in southern African landscapes explain most of the TVE. Of the 9 life history bird assemblages studied, landscape variables typically explained less than half of the variation in presence/absence distributions among grid cells. Grassland, forest, subsistence agriculture, low intensity transformation, urban, and road disturbance percentages contributed significantly to the partial CCAs. In contrast, passerine, breeding and human influenced bird assemblage gradients were conspicuous by their "insensitivity" to variation in landscape structure with only 8.6-11.1% of TVE from the partial CCAs. The remaining data sets of all, summer and winter bird assemblages had moderate explanation and really only represent more homogeneous combinations of the other stratified bird assemblages. The moderate performance of the landscape structural variables may be explained by the CCA partialling procedure. Though partialling out covariables allows one to test other data without the confounding effects of other unwanted pattern. Those co-variables may have a confounding relationship with the new variables of interest and therefore reduce the explanatory power of the new variables, once they are removed. Table 5.14 presents the relationship of the primary environmental variables to the landscape structure variables. There are an abundance of collinear effects between DEMMEAN, MINMNTHMN and MXSEAS_MN and the landscape variables of interest. However, what is more striking in this table, is the strong presence of collinearity in bird species gradients (identified by environmental variables) and historical human development (identified by land-cover variables) within the province. The two biotic processes are competing and evolving together along the same environmental gradients. These results would suggest that policy makers and managers should consider emphasizing the landscape-avian diversity-human development relationship for defining and implementing conservation policy. Avian community structure seems to react well to changes in the landscape brought about by human development and therefore could be good monitoring agents (sensu Furness and Greenwood, 1993; Dufrene and Legendre, 1997).

These results also suggest that temperate migrants, non-passerines and species deemed neutral or negatively affected by humans are related to landscape structure in a way that is unique when compared to species from other functional groups. Past studies from North America have noted differences among migratory habitat categories with respect to population trends (Robbins et al., 1989b). Explanations for these differences include: differential susceptibility of Neotropical migrants to forest fragmentation (Robbins et al., 1989a); differential susceptibility of permanent residents, and to a lesser degree, tropical migrants, to severe weather (Robbins et al., 1989b); and the broader environmental tolerances expected in permanent residents (O'Connor, 1992). The patterns of association between the compositional gradients in bird assemblages and landscape structure (Table 5.9) seem to be consistent with these explanations. Flather and Sauer (1996) uncovered similar associations to landscape structure for Neotropical migrants in North America.

Analysis of the birds assembled by their association with ecological habitat, using relative abundance and patch level statistics of their habitat sharpened the relationships, with landscape structure explaining roughly half of the variation in abundance among landscapes. Examination by habitat association brought forth clearer results that tied in well with biome level results and past studies (e.g., Armstrong et al., 1998; Allan et al., 1997). The variation in woodland bird species related closely to gradients in high intensity land transformation, which related to fragmentation represented by the number of patches and the patch density. In relation to the other

Table 5.14: Spearman's rank correlations of landscape variables with the five important climate and topography variables from the ADU CCAs, by bird group. Values > 0.5 are in boldface.

Variable	Spearman's rank correlation				
	DEMMEAN	GDMEAN	MINMNTHMN	EVANNMN	MXSEAS_MN
POPTOT96	-0.27	0.04	0.25	-0.03	-0.42
POPDEN96	-0.26	0.05	0.25	-0.04	-0.43
FOR_PER	-0.49	-0.39	0.49	0.38	-0.24
GRS_PER	**0.81**	0.03	**-0.80**	-0.18	**0.71**
WET_PER	0.16	0.27	0.14	-0.02	0.02
LOWI_PER	-0.35	-0.25	0.34	0.10	-0.31
PLNT_PER	0.14	0.46	-0.11	-0.34	-0.18
DRY_PER	0.06	0.37	-0.07	-0.26	-0.22
IRR_PER	0.37	0.07	-0.39	-0.23	0.20
URB_PER	0.18	0.30	-0.21	-0.23	-0.01
M_PER	-0.32	-0.26	0.31	0.09	-0.29
T_PER	0.06	**0.51**	-0.06	-0.38	-0.27
T_TOTAL	-0.24	0.17	0.24	-0.18	-0.48
ROAD_INDEX	-0.17	0.21	0.15	-0.12	-0.35
LPI	**0.56**	0.06	**-0.53**	-0.14	0.47
NP	0.42	0.09	-0.40	-0.14	0.22
PD	0.14	0.37	-0.15	-0.23	-0.01
MPS	-0.14	-0.37	0.14	0.23	0.01
PSSD	**0.53**	-0.19	-0.51	-0.02	**0.50**
CI	**0.68**	-0.01	**-0.67**	-0.17	**0.54**
MSI	**-0.77**	-0.19	**0.76**	0.36	**-0.53**
AWMSI	**0.51**	-0.10	-0.49	0.02	0.42
FD	-0.35	-0.15	0.36	0.41	-0.12
MPFD	**-0.72**	-0.14	**0.71**	0.29	**-0.53**
AWMPFD	0.45	-0.12	-0.43	0.06	0.38
MCAPP	-0.09	-0.36	0.09	0.20	0.05
PCASD	**0.52**	-0.18	-0.49	-0.02	0.48
MAPDC	0.20	-0.30	-0.20	0.04	0.23
DCASD	**0.59**	-0.14	**-0.56**	-0.09	**0.51**
DCACV	**0.71**	0.12	**-0.68**	-0.24	**0.51**
MNND	0.03	-0.04	-0.06	-0.06	0.00
NNSD	-0.07	-0.11	0.05	0.04	-0.06
NNCV	-0.21	-0.18	0.23	0.22	-0.14
MPI	0.06	-0.19	-0.04	0.17	0.06
II	**-0.58**	0.14	**0.57**	0.03	**-0.51**
SHDI	**-0.68**	0.03	**0.66**	0.17	**-0.54**
SDI	**-0.67**	-0.03	**0.66**	0.19	**-0.53**
MSDI	**-0.67**	-0.03	**0.66**	0.19	**-0.53**
CR	-0.04	0.04	0.01	0.05	-0.02
CRD	-0.30	0.35	0.26	-0.08	-0.25
SHEI	**-0.69**	-0.02	**0.68**	0.18	**-0.54**
SEI	**-0.68**	-0.04	**0.67**	0.19	**-0.54**
MSEI	**-0.67**	-0.06	**0.66**	0.19	**-0.53**

habitat assemblages studied it would appear that woodland bird variations at the landscape level are highly related to structural relations brought forth at the landscape level from human impact.

This was noted as a factor in changing species richness and structure at the woodland biome level of examination. These results are similar to other bird-forestry studies conducted in North America (e.g., Askins et al., 1987; Derleth et al., 1989; McGarigal and McComb, 1995). Though always small in extent to begin with (e.g., Midgley et al., 1997), birds of indigenous forest habitat are being strongly affected by the amount of surrounding exotic tree plantations and urbanization. The size and number of patches of forest play an important part in the variation in bird species, but the surrounding human land-use matrix is overshadowing them. Thicket birds are also responding to increased levels of urbanization, which is being caused by actual urban extent and the dissection of habitat caused by roads, this leads the thicket birds to be sensitive to the amount of core area in thicket. Grassland bird variation is being influenced by urbanization, planations, and dryland agriculture, which creates gradients in patch size variability and increased flexibility in grassland patch shape. Grassland birds are the most sensitive functional bird group in South Africa, and respond strongly to changes in the continuous cover in grasslands required for their maintenance (Allan et al., 1997).

No single landscape descriptor is likely to consistently explain variation in assemblage composition across sets of landscapes. A descriptors explanatory power is probably a function of its range of variation, which typically increases with the area encompassed (Wiens, 1989b), as well as the biota's sensitivity to change in the descriptors. For example, elevation and elevation heterogeneity were dominant explanatory variables for bird variation recorded in the 1970s, but for the ADU birds they had a reduction in significance or were replaced with temperature related variables. Changing landscape structure (i.e., increased exotic trees in grasslands, development of dams, urbanization, etc.) may largely be changing the majority of bird distributions altering biotic pattern that were at one time closely related to broad environmental gradients. Although landscape structure was demonstrably strongly related to several species assemblage types, one cannot conclude that it was a dominant factor given the large amount of unexplained variation. Therefore, the limited evidence gathered so far for this region containing woodland, grassland, forest and thicket suggests that one should not blindly accept the landscape structure hypothesis described in the introduction. Habitat configuration and subdivision undoubtedly play a role in regulating population dynamics, but the magnitude and nature of this role may vary geographically and over time in relation to changes in regional habitat conditions and other factors, and probably varies among species in relation to habitat selectivity, vagility, and scale.

The inclusion of the association analysis was able to further highlight several areas of concern that may have driven the changes found in the ordination analysis. Unfortunately, with the rather rapid development processes being conducted currently within post-apartheid South Africa, the comparisons between the 1970s and early 1990s would seem woefully out of date. Nevertheless, the use of the kappa index value and χ^2 test provided important results that could address precautions to future development options in the province (i.e., Lebombo Spatial Development Initiative). The areas that had changed bird inventories were generally targeted for development in the former KwaZulu homeland and Natal province (Thorington-Smith et al., 1978; Fair, 1975; South African government, 1975).

In the Maputaland region the changes were quite substantial and may in fact demonstrate how sensitive the birds of the region are to low levels of human disturbance. The cells with < 0.4

kappa values and χ^2 values not rejected were in areas developed since 1980. These include the Makhatini flats agricultural development region (sugarcane and cotton), which began large-scale farming in 1984 and had > 30 kms of irrigation canals installed and substantial bush clearing concluded by 1987. Also during the 1980s the road from Jozini to Kosi Bay was paved for greater traffic mobility. At the same time, the Tembe elephant reserve was created next to Ndumo in 1983, which seemed to have helped that grid cell area retain a similar bird inventory over the 10 year period. Probably the greatest change, however, to the area that precipitated the changes associated between the two bird surveys is the increase in human population. As recorded from the combined magisterial districts of Ubombo and Ingwavuma, the human population expansion occurred as follows: 1970- 108964; 1980- 148453; 1991- 260948; and 1996- 304222. Therefore, between 1979 and 1992 (between survey periods), there was a 75% increase in the human population within the Maputaland region.

Other areas of significant change include the Richards Bay development, where the harbor was partially completed by 1977 and fully completed in the 1980s with increased shipping, industrialisation and surrounding exotic forest plantations. The Newcastle, Vryheid, and Ladysmith areas were denoted by the government in 1975 to be development nodes (Fair, 1975; South African government, 1975), and therefore during the 1980s saw industrial expansion through mining, smelting and irrigated agriculture expansion.

5.6.1 Scope and Limitations

The scope of this study was restricted in several ways. These limitations identify additional research required before management recommendations can be suggested. First, the scale of the investigation placed lower and upper limits of resolution on the ability to detect habitat configurations and assess bird-habitat relationships (Wiens, 1989a,b). The extent of the landscapes was roughly 62500 ha; this defined the upper limit of resolution. Populations of the species undoubtedly are subjected to demographic influences operating over larger areas. These areas should also be related to more ecological defined types, rather than the use of an arbitrary grid cell. The use of the grid cell more than anything makes this study a test against a random sample structure and therefore any relationships found would be more than likely stronger using another sampling system (e.g., landscapes, catchments, vegetation types, etc.). The lower limit has been set by the resolution of the landscape structure variables, 1ha based on $100m^2$ raster. Patchiness occurs at many scales and patches can be defined in hierarchical fashion at progressively finer and finer scales (Kotliar and Wiens, 1990). Because landscape metrics are not invariant to scale (Turner et al., 1989), changing the minimum patch size would have significant effects on measures of landscape structure for specific patch types.

Second, the analysis presented is largely limited to a single scale. As the studies by Wiens and Rotenberry on shrubsteppe birds (Wiens and Rotenberry, 1981; Wiens and Rotenberry, 1985; Rotenberry, 1986; Wiens et al., 1987) demonstrate, habitat selection occurs at multiple scales, and habitats association often very among scales of investigation or analysis. This study is unable to infer about habitat associations at finer or even coarser scales.

Third, the classified habitat is based on structural characteristics that could be reliably mapped from satellite imagery. The broad vegetation definitions may not be important from an organism-centered or even community-centered perspective. Moreover, vegetation patches were somewhat arbitrarily and subjectively made discrete during the cover mapping and digitization process (Fairbanks et al., 2000). Vegetation structural differences were in many cases not abrupt (i.e., grassland-thicket or thicket-woodland transition). Thus, the final patch mosaics represented over-simplified representations of the actual spatial heterogeneity present in the grid cells.

All three limitations were originally pointed out by McGarigal and McComb (1995), and are inherent to all landscape ecological investigations as they deal with the issue of "measured heterogeneity" vs. "functional heterogeneity" (Kolasa and Rollo, 1991). Measured heterogeneity may or may not correspond to something functionally meaningful to a particular species or group of species (Wiens, 1989a; Wiens 1989b). Thus, results based on measured heterogeneity may lead to erroneous conclusions. This study had no *a priori* knowledge of what the functionally relevant scale would be, so even though the scale was set based on available data the bird assemblages were designed to make-up for any scale limited functional configurations and were meaningful from a land management perspective.

5.7 Summary

This study was the first systematic quantification, synthesis, and mapping of avian-environment gradients across a large, contiguous region of southern Africa based on two periods of biological atlas data. The goals of faunal atlases are sound and there is a need for continued national biological surveys of taxa (Balmford and Gaston, 1999). However, the uncritical use of these data to determine conservation priorities (Scott et al., 1993; Williams et al., 1996), as well as to understand the environmental mechanisms behind biodiversity patterns (O'Connor et al., 1996; Bohning-Gaese, 1997) could prove problematic. Distribution and abundance may change over time; therefore, ideally their estimate should be conducted within a sufficiently short period. This is a potentially serious problem with biological atlas surveys, on which estimates of distribution are often based, because such studies are forced to accumulate observations across several years. The results are frequently used to develop "hot spot" indices, provide data for reserve selection analyses or are used as inputs into macroecology studies. Biological atlases effectively show the compound errors in richness over time diverging from ecologically meaningful community assemblage indices. Thus, that contemporary biological atlases may already present transformed distribution and diversity patterns can easily be overlooked.

Atlasing projects, however, do provide a unique opportunity to explore at a macro-scale, contemporary species distribution-abundance relationships with human disturbance, and especially how human disturbance may be providing contradicting effects in commonly used ecological indices. While this analysis underscores the value of sound species-related distribution data and emphasizes the necessity for survey research in conservation biology (Haila and Margules, 1996), equal emphasis must be placed on the role of human influence in shaping extant biological communities. Although largely transformed areas may currently harbor many species, these areas may not be able to sustain natural ecological processes and viable populations (Baudry, 1993; Hobbs, 1993; Freemark, 1995).

Understanding the influence of landscape structure on spatial and temporal patterns of species is an important component of developing prescriptive management recommendations to conserve biological resources. Wiens (1992), and Flather and Sauer (1996), however, note that much of what has been reported in the literature is of a descriptive nature, documenting patterns of association such as has been reported here. There is a great danger from inferring causation from correlations, especially as associated to the scale of this study. However, Flather and Sauer (1996) also note that careful interpretation and analysis of extant data sources serves an important heuristic function (Carpenter, 1990), can lead to insights into the factors affecting patterns in the distribution and abundance of species (Brown, 1984), and can provide a regional context for interpreting and guiding future local studies (Wiens, 1992).

This chapters findings support a conceptual model of multi-scaled controls on bird distribution, and the related notion that local community structure is the result of both regional and local scale abiotic/biotic processes, landscape structure and human action. Broad-scale climate and topography were the primary controls to the differences in bird composition within the KwaZulu-Natal province. The study also showed that the broad scale environmental relationships are not stable over time and bird assemblage changes may be related to longer climatic cycles and land-cover change processes. The use of ordination analysis provided a good exploratory tool for untangling this ecological complexity. Even though the landscape measures explained a portion of the variation in bird variation, this analysis demonstrates the potential limitations of using a simple pattern association with presence/absence or relative abundance data. It is suggested that investigators use several analytical approaches and use the consistency in results among approaches to gauge confidence in the conclusions. This study tried to adhere to this approach using spatial correlation, geostatistics, ordinations, and temporal association analysis. Each provided key pieces to understanding the changes in bird distributions and structure.

Despite strong ecological contrasts within the KwaZulu-Natal province, the analyses presented here succeeded in synthesizing species-environment relations. These findings suggest that apparent conflicts among local bird studies can be explained by real ecological differences among places. Indeed, the results in this chapter provide a broader context for considering gradient and classification studies conducted at a finer, local scale within a landscape. This analysis also places crucial questions on the roles of establishing isolated nature reserves and their ability to persevere bird community persistence. In Baillie et al. (2000) several theoretical points regarding bird populations were examined and are supported by this chapter's result. These include: (1) Habitat deterioration may not only lead to population declines within that habitat but also in adjacent habitats of good quality; and (2) if dispersal is an important process then protecting only isolated areas may be insufficient to maintain the populations within them, which provides support to the landscape ecology principles involving conservation of the wider landscape through connectivity.

Macro-economic policies fueled by globalization and human population growth are rapidly changing the landscapes of southern Africa, which in turn affect wildlife populations (and consequently the results of longer term surveys). Consequently, we cannot just identify and manage for "species diversity", as measured by richness and diversity indices, alone as they ignore species assemblage structures (Soulé and Simberloff, 1986). Results suggest that the detrimental effects of development on bird species populations may cause the erosion of persistence of South African bird assemblages, while biological atlasing may artificially inflate the species richness recorded in a study region.