1. Introduction

This thesis examines the co-evolutionary nature of human development on landscapes and the consequent shaping of species assemblages, which affect biodiversity conservation strategies in Southern Africa. A model is proposed to address the development nature of humans on the environment. Where this model may fit into current conservation biology principles and within the field of landscape ecology is discussed. This study then moves into a series of examinations of the landscapes of KwaZulu-Natal Province, South Africa, focussing on an assessment of avian diversity conservation, human development patterns, and human action in shaping avian communities, and an application of a co-evolutionary development model.

Techniques used include complementary-based reserve selection algorithms, ecological gradient analysis, pattern recognition programs, multivariate statistics, spatial statistics, geostatistics, and mathematical transformations of species assemblage data. Timely data products, such as the *South African National Land-cover database* (Fairbanks et al., 2000), the *1996 South African Population Census* (Stats SA, 1998), and the *1997 KwaZulu-Natal Sustainability Indicators Project* (Kok et al., 1997), which records the regions socio-economic and development status, were used to develop causal relationships. The 1997 *Atlas of Southern African Birds* (Harrison et al., 1997), representing the results from the largest biological inventorying project conducted in Africa, and its predecessor, the 1980 *Bird Atlas of Natal* (Cyrus and Robson, 1980) covering Natal and Zululand, are used as the biological relation to the biophysical and human development patterns.

A number of analyses are performed to describe attributes of the biodiversity hierarchy (Noss, 1990) that are affected by evolved human development patterns, including impact on avian distributions, avian diversity variation, and spatial autocorrelation. The organization scales of landscapes, communities, and species were studied in order to describe and attribute their dynamics to human disturbance gradients. Typically, effort is given to studying structure when assessing regions for biodiversity conservation, but this falls short of the main issue of functioning, which is a dynamic product of changes in structure. This research targets specific objectives of the Ecological Society of America's Committee on the Application of Ecological Theory to Environmental Problems by addressing requirements for understanding and monitoring changes in biodiversity associated with land-uses that are specifically associated with human dimensions of global change (National Research Council, 1994; Lubchencho et al., 1991). These include three ecological problems at two different levels of organization:

- **Community Level**
    - Community structure: What do the collective properties of communities, including various community indices, tell us about their functioning?
    - Biotic diversity: What are the patterns, causes, and consequences of spatial and temporal variation in species diversity?
- **Intra-ecosystems Level**
    - Landscape ecology: How do land-use patterns influence the ecology of component systems, including all levels of ecological organization up to the scale of the landscape itself?

The biodiversity databases used in this study are of a coarser resolution than could be implemented for local conservation assessment. The described research, however, may provide a valuable foothold for identifying commonalities in the biodiversity pattern-abundance, spatial expression of land-use/land-cover classes, and relevant information, for the multistage effort that would be required by such a local conservation assessment and planning effort. The application of a number of different analysis strategies on the same data sets provides greater opportunity for comparison and understanding than is available from the numerous unrelated case studies, which have been performed to date. Typically, these case studies employ a presence/absence species database with a standard land-cover map, are limited by geographical variability in biological, environmental and human response, treat human impacts in a limited fashion, and reflect on only a local subset of the possible universe of human-ecosystem responses. Though this study will be limited by many of the same considerations, the results provide a starting point from which to assess the validity of applying general systematic reserve selection schemes to the developing areas of Southern Africa.

1.1 Current Biodiversity Conservation Strategies

Conservation planning strategies rely on several contested methods (e.g., Mace et al., 2000) to provide the best case for conservation action. These include complementary-based reserve selection algorithms, gap analysis, species richness "hot spots", keystone species surrogates, and environmental surrogates.

In the last decade, the conservation community has made significant contributions to developing systematic reserve selection procedures (Bedward et al., 1992; Church et al., 1996; Csuti et al., 1997; Freitag and van Jaarsveld, 1995; Kirkpatrick, 1983; Lombard, 1995; Margules et al., 1988; Nicholls and Margules, 1993; Pressey et al., 1996; Rebelo and Siegfried, 1992). Conceptually, the need for systematic approaches to represent the protection of as many natural features (i.e., species, communities, or environments) as possible is well acknowledged. The use of the principles of complementarity, flexibility, and irreplaceability (see Pressey et al., 1993) for selecting priority regions and regional reserves makes for computationally elegant solutions. These protocols for priority conservation area selection, however, have several weak points: use of poorly surveyed taxa or habitat databases (Maddock and du Plessis, 1999); use of dangerously simple surrogate information (Faith and Walker, 1996a; Reyers et al., 2000); and more to the point, the efforts to date have generally not taken into account human influences, landscape pattern and processes. The systematic conservation techniques could also ignore interrelated attributes and feedback's that a more thoughtful and comprehensive approach might illustrate. In some cases, the spatial pattern of development in an area might be biodiversity "friendly" (e.g., Gadgil et al., 1993; Norgaard, 1994; Dahlberg, 1996; Fairhead and Leach, 1996; Zimmerer and Young, 1998; Shackelton, 2000) and have evolved with the resident human culture, but would not be acknowledged in formal protection based approaches. Increasingly, the shortcomings of the systematic reserve selection concepts to take into account the current or future biological sustainability of the areas selected, or to have the ability to spread the risk of species extinctions through proper spatial planning, is becoming evident.

Biological conservation strategies have traditionally centered on biological reserves, where a reserve is 'an area with an active management plan in operation that is maintained in its natural state and within which natural disturbance events are either allowed to proceed without interference or are mimicked through management' (Scott et al., 1993). The gap analysis school of biodiversity protection planning attempts to identify the gaps in representation of biological diversity in areas managed exclusively or primarily for the long-term maintenance of populations of native species and natural ecosystems. It is proposed that once identified, gaps be filled through new reserve acquisitions or designations, or through changes in management practices. The goal is to ensure that all ecosystems and areas rich in species are represented adequately in protected areas. Whereas the complementary reserve selection concept is an elegant and logical solution, though unrealistic, the gap analysis procedure is simple, scale dependent, and assumes that large tracts of land are still available for conservation. Large reserves (e.g., > 10 000 ha) are the most common strategy to maintain biotic communities over long periods in areas undergoing large-scale conversion from natural vegetation to agricultural and urban systems (Shafer, 1990; Noss et al., 1997). The gap analysis procedure can make only a partial contribution within South Africa since the vast majority of land is under communal or private tenure (see Christopher, 1982), highly fragmented in the ecologically important biomes (see Fairbanks et al., 2000), and the methodology does not provide for a representative (e.g., species, habitat) system. In areas of extensive habitat conversion, as found in parts of South Africa, the design of reserve systems is typically based on a model of reserves as isolated islands of habitat for native species (e.g., Rebelo and Siegfried, 1992; Lombard et al., 1997). The ultimate viability of a reserve system, however, is based on the size, shape, and connectedness of these remnant habitat areas (Forman, 1995; Fahrig, 1997), which should be designed within associated environmental processes (e.g., Cowling et al., 1999).

To be sure, the most important consideration, which is typically ignored, in any of these systematic methodologies is the role human societies, values, and economics play as threats and protectors to biodiversity. A logical framework for understanding human threats has not been considered in species or broad model approaches, but are root causes of the loss of biodiversity (Ehrlich and Wilson, 1991). Conservation planning needs to incorporate socio-economic variables, as well as the landscapes, ecosystems, and species of an area, to be relevant within developing countries. The case for integrated conservation planning in developing countries must take into account all factors inherent in and relevant to the landscape environment, which includes human needs. The importance of flexibility in conservation planning becomes important in discussing issues of persistence, since there are typically many different complementary networks, these can be exploited to reveal those networks that are currently sustainable based on their socio-economic, cultural, and landscape ecological situation.

1.2 Biodiversity Conservation Strategies in the Modern African Context

This thesis is concerned with the issue of sustainable biological conservation within southern Africa. In 1995, South Africa signed and ratified the *United Nations Convention on Biological Diversity* (UNCED, 1992), its objectives are: the conservation of biodiversity, the sustainable use of biological resources, and the fair and equitable sharing of benefits arising from the use of genetic resources. In 1997, the published response to this signing became the policy and strategy document *White Paper on the Conservation and Sustainable Use of South Africa's Biological Diversity* from the national government (South Africa, 1997). Internationally and nationally, it is acknowledged that if there is to be global cooperation to conserve biodiversity, recognition needs to be given to its uneven distribution around the world:

> 'Two-thirds of the world's biodiversity is located in developing countries, collectively termed "The South", and provides an important resource for the economic development of such countries. Biodiversity conservation thus carries a heavier burden for developing countries than for the biologically poorer "North", comprising the industrialized countries. Furthermore, it has largely been private companies in industrialized countries, which have benefited from the South's biological riches. Thus, it is argued by developing countries that issues such as the equitable sharing of benefits from the conservation and use of biodiversity, must be included in any global agreements concerning biodiversity.'
>
> \- *White Paper on the Conservation and Sustainable Use of South Africa's Biological Diversity*, 1997

Under this policy climate, rather than promoting the typical objectives for the preservation of biological diversity (i.e., ecological health or biological integrity), which cannot be (without much research and difficulty) formulated into scientifically defensible biological indicators, the principle goal of ecological management should be social, to maximize human capacity to adapt to changing ecological conditions (Reid, 1994; Goodland, 1995). Reid (1994) explains that in order to adapt to change, humanity needs both the diversity from which innovations can be created, and the productive ecological systems that provide biological and economic capital to invest in those innovations. Thus, maintaining biodiversity is a prerequisite for maximizing humanities ability to respond to changing conditions, as is maintaining the productivity of agricultural systems, the yield from forests and fisheries, clean water, and clean air (e.g., Daily, 1997). Conserving biodiversity should not only be seen as a luxury or competing land-use, but rather it is the embodiment of sustainable development within developing regions of the world.

The socio-economic situation in southern Africa can no longer promote large reserves without social concessions (i.e., Peace Parks). A large portion of the common, public, and private land is managed for renewable natural resources (i.e., livestock range, fuel wood, water, etc.), as well as, dryland and irrigated agriculture, exotic tree plantations, and urbanization. All of these activities lead to some level of landscape fragmentation. The use of a Biodiversity Management Area (BMA) system in these various landscapes could serve as a model to provide quality core habitat for many species (sensu Davis et al., 1996). These ecologically managed areas would be for those biological components that are negatively impacted by human activities. Their arrangement on the landscape would be based on ideals of persistence as well as representation, while acknowledging that human impacts and influences will be happening around them. In this respect, BMAs are extended to communal, private, and public lands and across multiple habitats. Human "quality of life" development should be allowed to go forward to the extent that they are compatible with the goal of maintaining native species and ecosystem diversity. The concept of a BMA is to monitor and manage in a hierarchical fashion from local ecosystem, to landscape, to regional levels in order to reduce risk.

The goal of conserving biological diversity is to ensure population viability or persistence over time within the required habitats. Sustainable conservation management must be seen in an integrated fashion, acknowledging components of population biology, landscape ecology, economics, and social needs. A major constraint to future biodiversity protection in South Africa is that state land will not go towards conservation, but will be provided for retribution to those landless individuals created by past British colonial and South African apartheid policies (South Africa, 1997). In any case, the amount of available state land is low, as the almost total transfer of land in the formerly White areas of South Africa from government to private ownership had occurred by the mid 1930's (Christopher, 1982). This is unique in colonialism, as it did not happen in other former British colonial areas outside of South Africa (i.e., Kenya, Australia, Canada, USA, etc.). The current land ownership and land development patterns strongly reflect the political and economic conditions of the apartheid era (Fairbanks et al., 2000).

In many regions, South Africa's biological conservation must also be viewed as managing natural remnants. Fragments of natural landscape that are available for conservation have two important considerations: isolation and human influence from within the landscape matrix. Isolation primarily affects the interior species. Therefore, patch size; shape, number, and configuration are critical, as are, corridor width, and connectivity. Patches must have characteristics adequate to support the interior species, and both corridors and patches must have a configuration that permits rapid recolonization when an interior species becomes locally extinct.

Management of the flow of objects from the matrix to fragments or formal reserves is the other focus. Human influence proceeds to minimize or eliminate these flows: there needs to be a balance of structure. Maintaining and creating large patches, and then surrounding these with a high density of corridors and small patches containing edges may be a possible solution (Forman and Collinge, 1995; Yu, 1996; Forman and Collinge, 1997). Recently, landscape ecologists and conservation biologists have distilled their experiences into a number of conservation principles that can be used as a basis for planning (Noss et al., 1997). These include: (1) species that are well distributed across their historical range are less prone to extinction; (2) large patches that support large populations support them for longer periods of time; (3) habitat patches that are continuous (less-fragmented) support long-term viability; (4) patches that are sufficiently close together allow dispersal and thus support long-term viability; (5) patches that are connected by corridors provide better dispersal; (6) patches of habitat that have minimal or no human influence are better; and (7) populations that naturally fluctuate widely are more vulnerable than stable populations.

Inevitably, this discussion leads to the appropriate integration of biodiversity protection with competing economic pressure and social value. These three broad themes generally play off each other in an area, which then evolves landscapes into complex mosaics that natural resource management institutions are faced with managing. Faith (1995) and Faith and Walker (1996b; 1996c) present a multi-criteria trade-off analysis as one type of an analytical framework to assess a region's sustainability (Figure 1.1). Regional sustainability as defined by Faith (1995), will reflect the region's success (or potential for success) in achieving effective trade-offs between conservation and development (or other criteria).

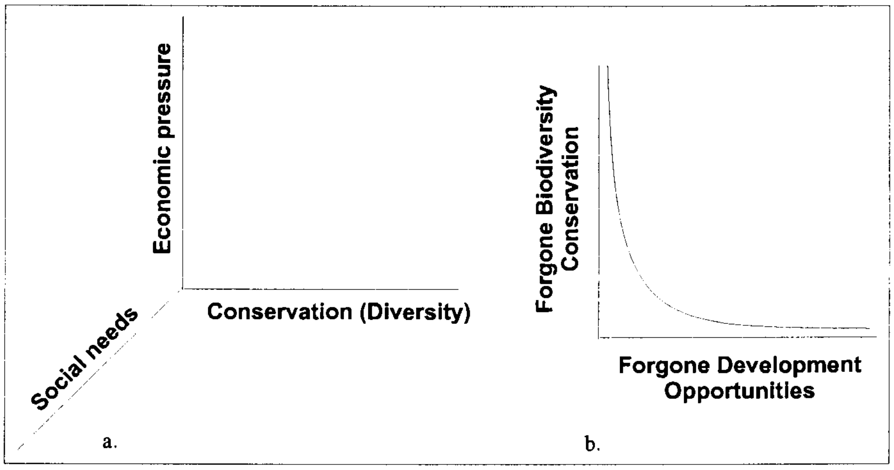

Figure 1.1: (a) The multiple interplay between the three broad themes in sustainable development analysis; and (b) a trade-off or regional optimization space curve. A given allocation of area to conservation or development will result in a total cost and total forgone biodiversity, so that the allocation can be plotted as a point in this space (Faith, 1995).

Faith and Walker's (1996b; 1996c) approach is simple, and probably dangerous to implement, but it does clearly present the competing goals commonly encountered. This dissertation takes these ideas a step further by setting them in a co-evolutionary construct within which to view conservation planning. One of the principle aims of a co-evolutionary dynamics model is to establish human-ecosystem interaction within an interpretative/interrogative framework. This analytical framework allows for the integration of complex environmental and socio-economic indicators to provide information needed to answer questions pertinent for sustainable biodiversity conservation. However, persistence will depend not only on land-use allocations (spatially) for sometimes competing land-uses, but also the degree to which appropriate implementation criteria and management for an area satisfies multiple goals.

1.3 Methodological Background

This section outlines the study site, data acquisition, and initial data processing used in this study.

1.3.1 Study Site

The study site used in this thesis corresponds to the KwaZulu-Natal Province within the Republic of South Africa (Figure 1.2). The province was chosen for its range of land-use/land-cover, contrasting development patterns representing third world southern African and first world Western influenced landscapes, availability of environmental and socio-economic data sets, and access to both detailed historical and contemporary bird distribution databases.

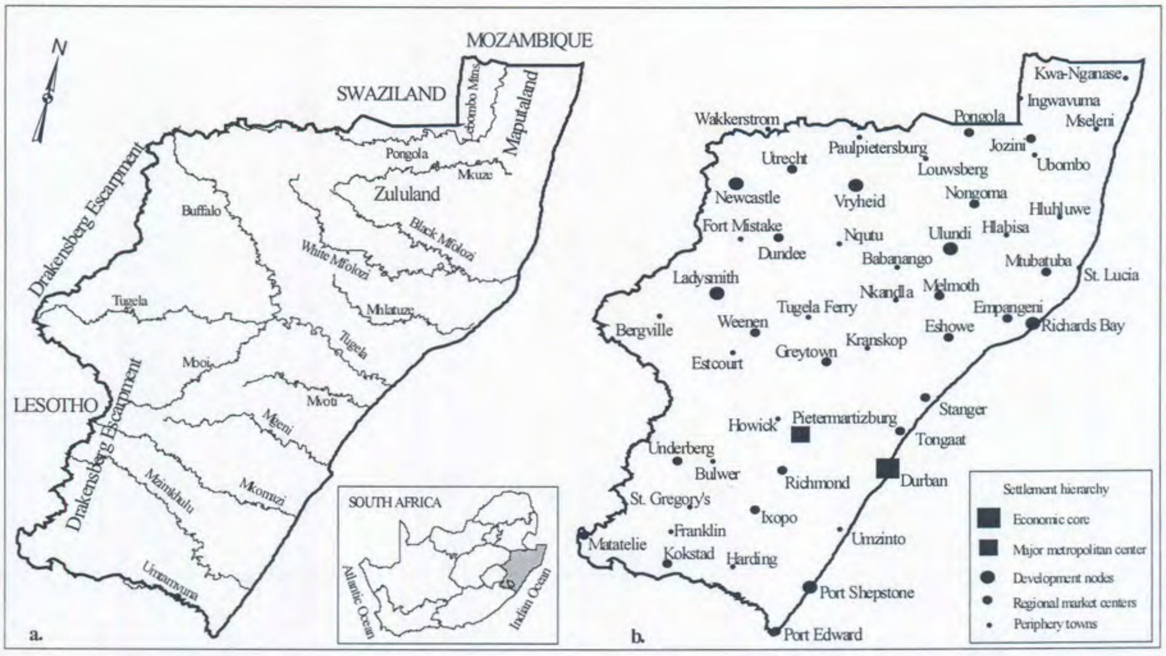

Figure 1.2: (a) Location of the KwaZulu-Natal Province study region within South Africa; and (b) major place names and their economic hierarchy within KwaZulu-Natal Province.

Analytical work conducted in Chapter 5 also utilizes data at the national South African extent.

KwaZulu-Natal Province is located on the east coast of South Africa and borders the countries of Lesotho, Swaziland, and Mozambique. KwaZulu-Natal covers just 7.6% of the land area of South Africa, but contains the largest population base (20.7%) of any province (Stats SA, 1998). The province is an important sub-tropical agricultural and tree plantation region, and over the last 20 years has seen increased development pressure in direct conflict with its active expansion of conservation based tourism (Thorrington-Smith et al., 1978; Armstrong et al., 2000).

Climatically, the province is characterized by the influence of the Indian Ocean's warm Agulhas current. This creates a wide coastal region of sub-tropical climate, with high humidity, high temperatures, and high summer rainfall. In southeast Africa the relief, which is in the form of a number of ascending steps, is such that, in general, the inland isotherms tend to run in a north-south direction, parallel to the coast. KwaZulu-Natal's western border is defined by the Drakensberg Escarpment, which forms a marked climatic gradient. There is a pronounced difference in temperature between the hot eastern coastlands and the cooler interior highlands, and at the same time, temperatures along the coast increase gradually northwards. The climatic transition from the coast to the westerly plateau is, however, gradual.

Rainfall at the coast ranges from about 760 to 1400 mm per annum, and is heaviest at the northern and southern districts of the area considered. Inland, on the seaward-facing escarpments, rainfall is about 1750mm per annum, but on the intervening surfaces, it is considerably less. Most of the rainfall is received during summer (September - March), but this characteristic is far more pronounced inland than at the coast. Consequently, the region has warm, wet summers and cool, dry winters.

The vegetation ranges from complex in the north-east, being made up of a number of different ecological associations, which include mangrove forest, swamp forest, dune forest, sand forest, coast forest, riverine woodland, and savanna woodland (Figure 1.3). To the south of this area and towards the Drakensberg Escarpment, there is a marked thinning out of this complexity. Bush clump grasslands and moist woodland dominant along the coast (south of St. Lucia), grasslands interspersed with afromontane forests occur in the southern-central interior and along the escarpment, dry thornwoodlands cover the western region of Zululand and a valley thicket complex dominants the incised river valleys (e.g., Tugela River).

1.3.2 Data Sets Used in Study

The multi-disciplinary nature of this study required several strategic databases and used many of the commonly available biophysical data layers. Among the processes that have been hypothesized to account for spatial patterns of species diversity are climatic extremes, climatic stability, productivity, and habitat heterogeneity (Brown, 1995; Wickham et al., 1997). Data were compiled from existing sources to represent these processes (Table 1.1); they included climate surfaces (Schulze, 1998) and a digital elevation model (Surveyor General 1993), as well as potential vegetation (Low and Rebelo, 1996), and land-use/land-cover types (Fairbanks et al., 2000) mapped in a raster-based geographic information system (GIS; ESRI, 1998). The GIS database has a raster cell resolution of 1 km by 1 km. Both geographic and projected Albers equal area cartographic systems were used.

1.3.2.1 Potential Vegetation

Vegetation type is a primary determinant of ecosystem type (Peters, 1992), playing a major role in determining the associated fauna. Two potential vegetation map products are available for South Africa: Acock's (1953) vegetation types, which is largely based on the agricultural potential of the vegetation, and Low and Rebelo's (1996) vegetation types, which is based on both structure and floristics, but is essentially a re-assessment of Acocks. The vegetation potential map of Low and Rebelo (1996) was mapped at a scale of 1:500 000. The 26 vegetation types that occur in KwaZulu-Natal were classified into eight functional community groupings (Table 1.2; Low and Rebelo, 1996; Cowling et al., 1997) for analysis (Figure 1.3).

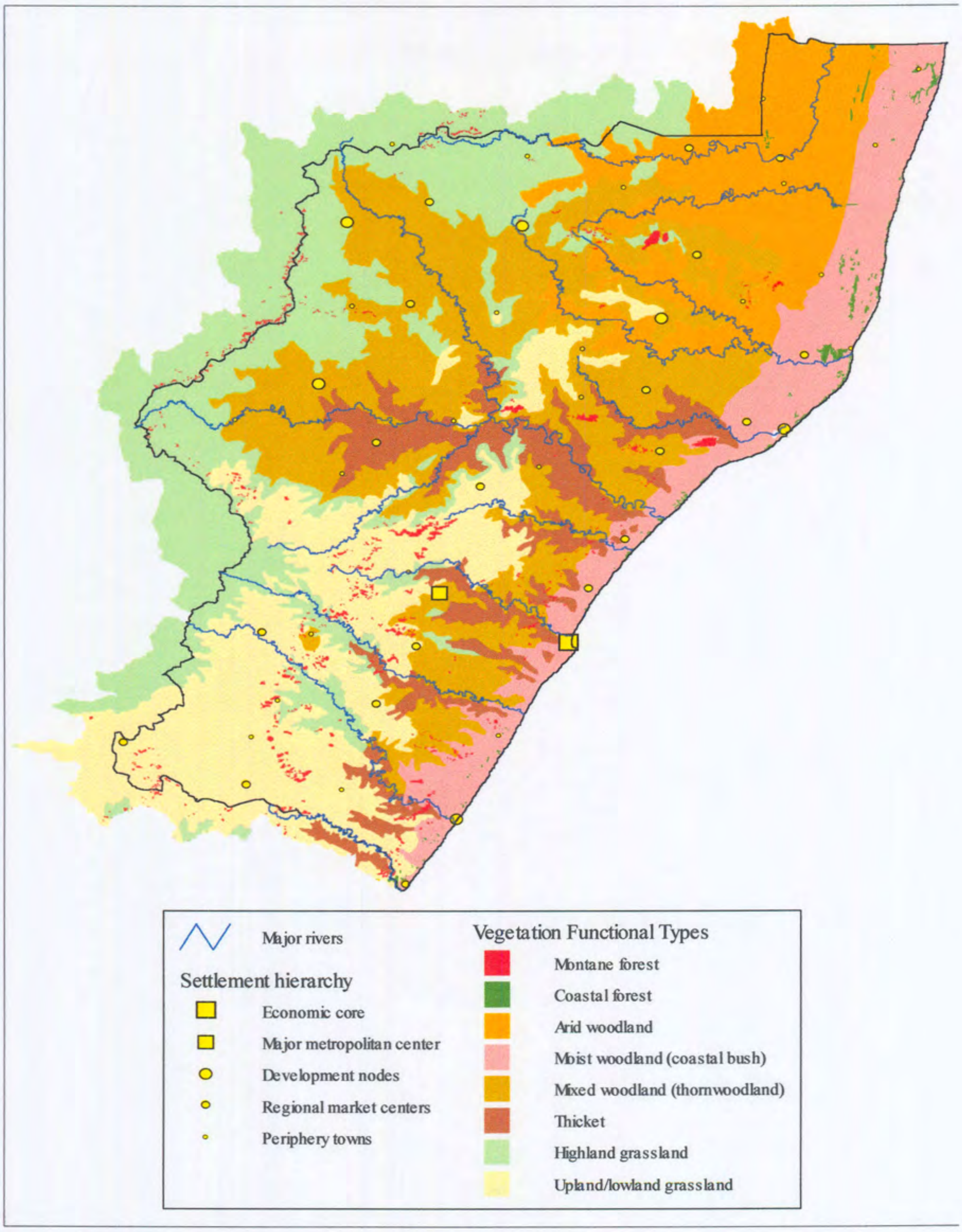

Figure 1.3: Functional vegetation types found within KwaZulu-Natal Province based on vegetation types described by Low and Rebelo (1996).

Table 1.1: Codes and definitions of explanatory variables, by variable subset, used in Chapters 3, 4, and 5.

Code	Definition
Topography	
DEMMEAN	Elevation (m)
DEMSTD	Elevation heterogeneity (std. deviation)
Climate	
GDMEAN	Number of days per annum on which sufficient water is available for plant growth
MAP	Mean annual precipitation (mm)
GTMEAN	Annual mean of the monthly mean temperature (°C) weighted by monthly grow days
NGTMEAN	Mean temperature (°C) during negative water balance
MAT	Mean annual temperature (°C)
HOTMNTHMN	Mean temperature of the hottest month, usually January (°C)
MINMNTHMN	Mean temperature of the coldest month, usually July (°C)
EVANNMN	Total annual pan evapotranspiration (mm)
PSEAS_MN	Precipitation seasonality from the difference between the January and July means (mm)
TSEAS_MN	Temperature seasonality from the difference between the January and July means (°C)
MXSEAS_MN	Maximum temperature seasonality from the difference between January and July (°C)
Land Types	
LAND†	Variety of defined landscapes from a maximum of 24
LANDVEG	Variety of combined landscape and vegetation types from a maximum of 217
LANDVEGF	Variety of combined landscape and functional vegetation types from a maximum of 126
VEG	Variety of defined vegetation types from a maximum of 26
VEGF	Variety of defined functional vegetation types from a maximum of 8
LCLUTYPES	Variety of defined land-cover/land-use types from a maximum of 29
LCLULAND	Variety of combined landscape and land-cover/land-use types from a maximum of 334

† Landscapes derived from analysis presented in Chapter 3.

Table 1.2: Functional vegetation classification of the 1:500 000 National Botanical Institute Vegetation of South Africa, Lesotho and Swaziland (Low and Rebelo, 1996).

Original potential vegetation types	Functional classification
Afromontane forest	Montane forest
Coastal forest	Coastal forest
Sand forest†	Coastal forest
Eastern thorn bushveld	Arid woodland
Lebombo arid mountain bushveld†	Arid woodland
Mixed lowveld bushveld	Arid woodland
Natal lowveld bushveld†	Arid woodland
Sour lowveld bushveld	Arid woodland
Subarid thorn bushveld	Arid woodland
Subhumid lowveld bushveld†	Arid woodland
Sweet lowveld bushveld	Arid woodland
Coastal bushveld grassland†	Moist woodland
Coastal hinterland bushveld†	Mixed woodland
Natal central bushveld†	Mixed woodland
Valley thicket	Thicket
Coastal grassland	Upland/lowland grassland
Moist upland grassland	Upland/lowland grassland
Short mistbelt grassland†	Upland/lowland grassland
Afro-mountain grassland	Highland grassland
Alti-mountain grassland	Highland grassland
Moist clay highveld grassland	Highland grassland
Moist cold highveld grassland	Highland grassland
Moist cool highveld grassland	Highland grassland
Moist sandy highveld grassland	Highland grassland
North-eastern mountain grassland	Highland grassland
Wet cold highveld grassland	Highland grassland

†Endemic vegetation types to KwaZulu-Natal

1.3.2.2 Topography

Topographic position has been found in other studies to significantly influence ecosystem variability patterns, especially the control of water movement (Kratz et al., 1991; Forman, 1995). A digital elevation model (DEM) of South Africa was available from the South African Surveyor General (1993) with a horizontal resolution of 400 m by 400 m and a vertical resolution of 20 m (Figure 1.4a). This was used to derive elevation information and a topographic landform index (ridge, valley, slope) using standard GIS routines (Figure 1.4b; Fairbanks, 2000). The percent slope surface was transformed to a surface representing flat-undulating (< 4%) and ridge landscapes (> 35%) and then a linear function scaled the slope data between the two extremes.

1.3.2.3 Climate

The principal controlling factor in southern African ecosystems is the soil water balance (Cowling et al., 1997; Scholes and Walker, 1993). The mean number of days per annum on which sufficient water is available to permit plant growth was considered a biologically meaningful index of water availability. Ellery et al. (1992) developed such a water balance index, which calculates the water budget from available climatology data. The index, called 'growth days' (GD) is defined as the sum of the monthly ratios of precipitation to potential evaporation, where the ratio is not permitted to exceed 1 in any given month (i.e., if rainfall is larger than evaporation, it is not carried over into subsequent months, but is assumed to have been lost as runoff). This is achieved by multiplying the monthly ratios by the number of days in the month and summing over the year. Intuitively it can be thought of as the number of days per year when soil moisture does not limit plant growth. The GD index was calculated on the 1 km by 1 km grid covering the entire country (Figure 1.4c), from monthly mean rainfall (1960-1990) and the monthly means of maximum and minimum daily temperatures (Dent et al., 1989). The annual mean of the monthly mean temperature weighted by the monthly growth days was recorded as growth temperature (GT), giving an indication of energy supply during the growing season (Ellery et al., 1992), while no growth temperature (NGT) is derived from the months weighted by no available growth days. The GT and NGT were calculated from available mean monthly temperature surfaces (Schulze, 1998). Other climatic variables considered for use included median annual precipitation, summed mean minimum and maximum rainfall for the driest and wettest quarters, mean annual temperature, and mean minimum and maximum temperatures for the coldest and hottest months. The seasonal variability with precipitation, temperature, and evapotranspiration were calculated from these raw datasets (Table 1.1).

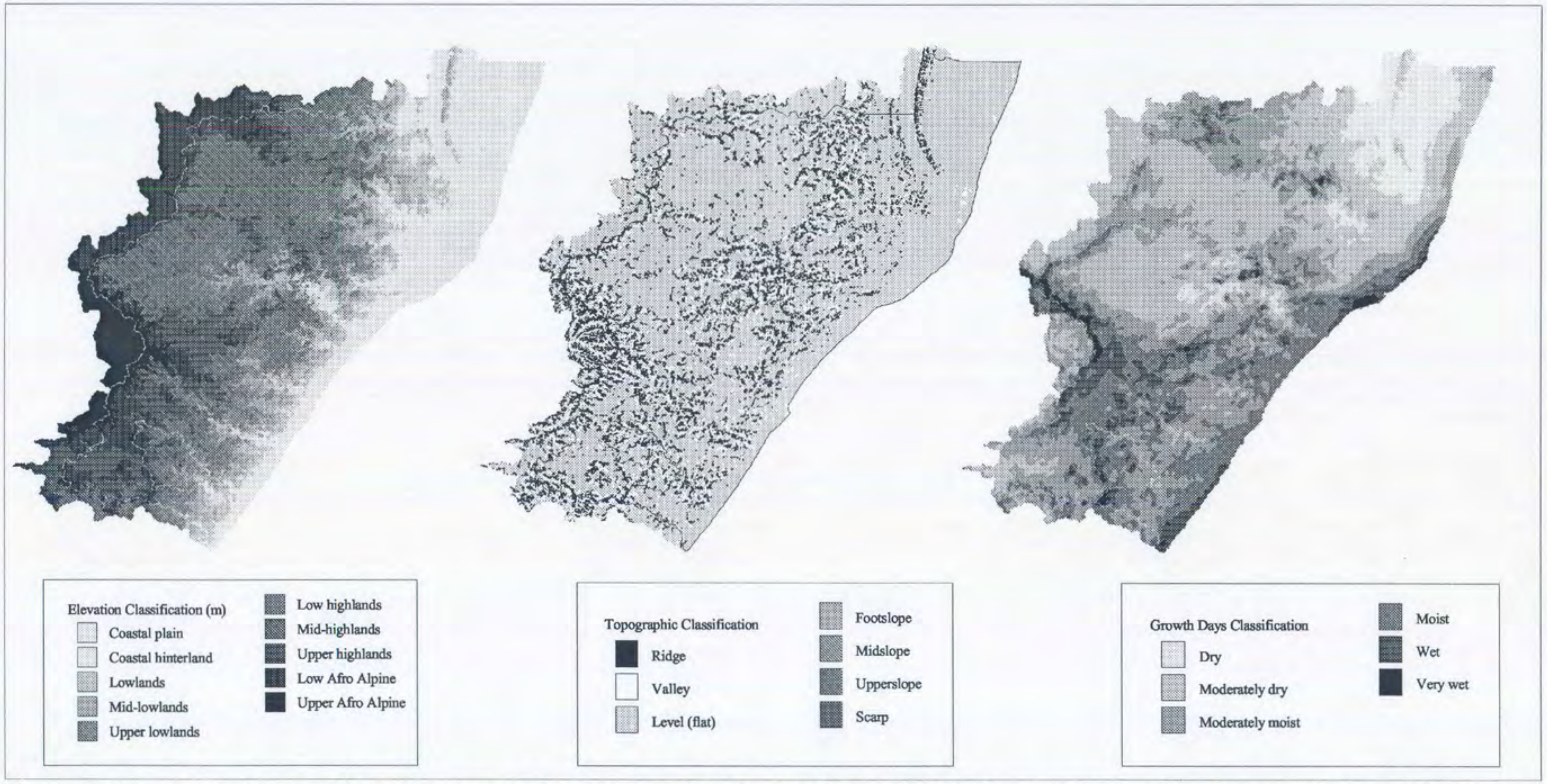

Figure 1.4: Examples of some of the environmental data layers used in thesis: (a) elevation; (b) topographic landform index; and (c) growth days.

1.3.2.4 Avian Distribution and Diversity

Biological atlases had their precedent made when Perring and Walters (1962) published the *Atlas of the British Flora*. Using a 10 km by 10 km gridded map, plant distributions were plotted on a presence/absence basis. This pointed the way for similar comprehensive and equally objective mapping of the breeding birds of Britain (Sharrock, 1976). This British tradition in naturalist field biology was adopted during the 1970s in South Africa by the Natal Bird Club. They developed a project whose aim was to map the distributions, by presence/absence per month, of all bird species occurring in KwaZulu-Natal during the decade 1970-79 (with emphasis on 1975-79), using the national quarter-degree grid (15 min x 15 min; ~24 km x 28 km, hereafter referred to as a grid cell). Each of these grid cells represents one of the maps in the 1:50 000 topocadastral map series produced by the South African Surveyor General (Figure 1.5). The objectives were to present occurrences of birds in KwaZulu-Natal, against which future changes in the avifauna could be measured. Data collection was conducted by means of fieldcards submitted by club members, Natal Parks Board, and the authors of the atlas. In 1980, Cyrus and Robson published the *Bird Atlas of Natal*, which represented a thorough account of the birds found in the province during the 1970s.

Starting in 1987, the Southern African Bird Atlas project (Harrison, 1992) was initiated by the Avian Demography Unit (ADU), University of Cape Town. The aims of their project were the same as for the Cyrus and Robson (1980) survey, but designed to cover the entire Southern African sub-region (South Africa, Lesotho, Swaziland, Namibia, Botswana, and Zimbabwe). The same procedures as used by Cyrus and Robson were adhered to (Nigel Robson was appointed as a science steering committee member), along with the continued use of the grid cell. The presence/absence of species was recorded during 1987-1992 (see Underhill et al., 1991; Harrison, 1992; Harrison et al., 1997 for details).

In the original forward to Cyrus and Robson (1980), Gordon Maclean (author of *Robert's Book of South African Birds*, 1984) explained that the greatest apparent shortcoming of any biological atlas is that it is out of date even as it comes off the press. This is as it should be, because it illustrates the dynamic nature of biological systems, especially in the face of anthropogenic impact. Therefore, an atlas becomes increasingly valuable as it highlights the changes that are constantly occurring. Baselines for future comparisons become more necessary every day, so an atlas of distribution in time and space becomes an invaluable tool in the hands of planners, geographers, and conservation biologists. KwaZulu-Natal forms less than one percent of the Afrotropical Region (Africa south of the Sahara), yet its economy in the late 1970s may have been the largest per unit area, and its rate of progress close to the highest on the whole continent. Maclean made note, at that time, that a measure of the natural resources of KwaZulu-Natal had become more critical than ever.

The Cyrus and Robson (CR) dataset comprises 33689 unique distribution records of 633 species covering 165 grid cells. The ADU dataset, clipped to cover the same number of grid cells, includes 40036 unique distribution records of 604 species of resident and visiting birds, which comprise 65% of the bird diversity recorded for the Southern African sub-region. The reporting rates for both datasets show observer bias in and around the Durban and Pietermaritzburg areas, and the Drakensberg and the Zululand game reserves (Figure 1.6). Nevertheless, for each survey period > 90% of the grid cells had at least one fieldcard returned for recording for each month of the year. In the case of the ADU survey the intensity of the recording during the 5-year survey (1987-92) allowed for an average of 105 fieldcards returned per grid cell. This level of reporting allowed the transformation of the number of times a species was recorded into relative abundance values, which were used to analyze avian assemblage structure in Chapter 5. Unfortunately, this type of data was not recorded within the CR atlas.

Investigations of the patterns in these bird atlases have been conducted using several biological and practical classifications. For each atlas, the birds were first grouped by life history class and then, for only the ADU atlas birds, grouped by primary ecological habitat requirement. Waterbirds were not analyzed separately as Guillet and Crowe (1985; 1986) had previously examined them. Wetland and waterbody sites are also already protected under the South African signing of the RAMSAR convention for wetland conservation (Cowan and Marneweck, 1996). Table 1.3 describes each of these datasets and provides the dataset name, as it will be referred to throughout the thesis. The conservation dataset is the only dataset not based on biological reasoning, but instead on the requirements of the local conservation authorities for planning purposes conducted in Chapter 4.

1.3.2.5 Land-cover/land-use Database

The South African National Land-Cover database (NLC; Fairbanks and Thompson, 1996; Fairbanks et al., 2000) was used to derive land-cover/land-use (LCLU) and transformation percentages for each grid cell. This national database was derived using photo-interpretation techniques from a series of 1:250,000 geo-rectified hardcopy satellite imagery maps, based on seasonally standardized, single date Landsat Thematic Mapper satellite imagery, captured principally during the period 1994-95 (Fairbanks and Thompson, 1996). It provides the first single standardized database of current LCLU information for the whole of South Africa, Lesotho, and Swaziland (see Fairbanks et al., 2000). For the purpose of this thesis, the 31 LCLU classes were reclassified into three categories: un-transformed, low intensity transformation, and high

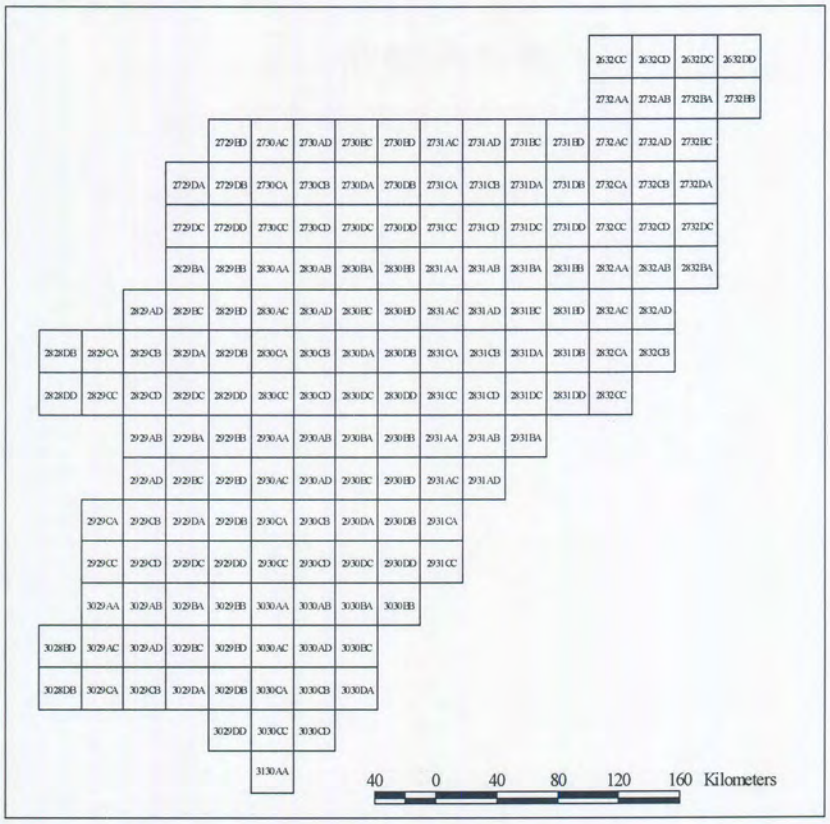

Figure 1.5: The 1:50 000 mapsheet system of grid cells for KwaZulu-Natal used to record bird distribution data during both survey periods.

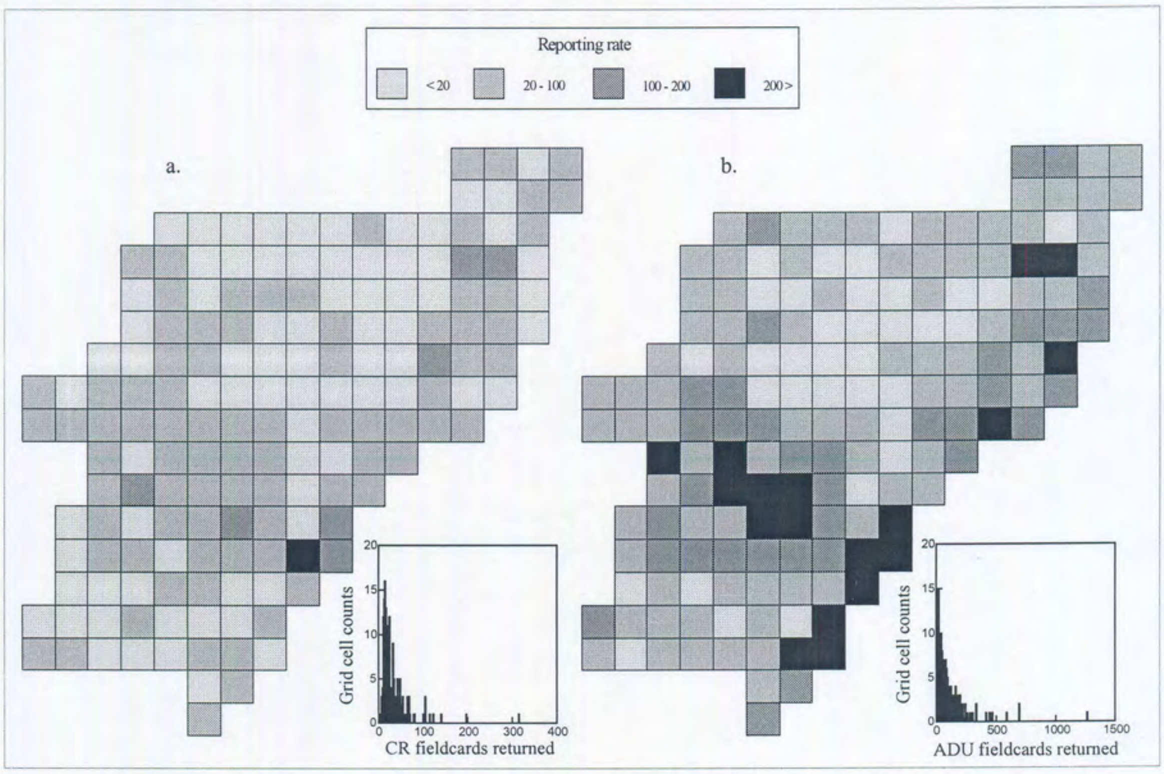

Figure 1.6: Spatial distributions of returned fieldcards and histograms distributions: (a) Cyrus and Robson (1980); and (b) Harrison et al. (1997).

Table 1.3: Bird datasets and descriptions used in this thesis.

Dataset	Description
Life History	
All birds	All birds found in each dataset. 633 in the Cyrus and Robson (1980) survey and 604 in the ADU (Harrison et al., 1997) survey.
Summer	Birds recorded during the months September-March.
Winter	Birds recorded during the months April-August.
Passerine	Birds classified as passerine in the descriptions provided by Harrison et al. (1997). Chiefly altricial songbirds of perching habits.
Non-passerine	Birds classified as non-passerine in the descriptions provided by Harrison et al. (1997). Relating to an order of arboreal birds including the rollers, kingfishers, hornbills, cranes, raptors, etc.
Breeding	Birds classified as breeding in South Africa and in particular to KwaZulu-Natal as provided by Harrison et al. (1997).
Non-breeding	Birds classified as not breeding in South Africa or KwaZulu-Natal as provided by Harrison et al. (1997).
Human influenced	Birds classified as being positively influenced, usually by habitat and therefore distribution, by human activity and/or land-use as described by Harrison et al. (1997).
Non-human influenced	Birds classified as either neutral to or negatively influenced by human activity and/or land-use as described by Harrison et al. (1997).
Ecological habitat	
Woodland†	Birds primarily associated with savanna woodland habitat.
Forest†	Birds primarily associated with indigenous evergreen forest (afromontane, coastal, and sand forest).
Thicket†	Birds primarily associated with thickets, bushland, and bush clumps.
Grassland†	Birds primarily associated with perennial grasslands.
Planning	
Conservation‡	Birds considered for representation in conservation efforts within KwaZulu-Natal (derived from personal analysis; Important Bird Areas of South Africa (1999); KwaZulu-Natal Nature Conservation Services).

† Relative abundances derived from the reporting rate in the ADU dataset were used instead of presence/absence measure.
‡ Only created from the more current ADU bird database.

intensity transformation land (Table 1.4; Figure 1.7a,b). Un-transformed class included all natural vegetation, e.g., forest, woodland, thicket, and grassland. Degradation, erosion, and subsistence agriculture dominated the low intensity category. These areas have a very low vegetation cover in comparison with the surrounding natural vegetation cover and were typically associated with rural population centers and subsistence level farming, where fuelwood removal, over-grazing, and subsequent soil erosion were noticeable within the satellite imagery (Thompson, 1996; Fairbanks et al., 2000). The high intensity transformed category consisted of areas where the structure and species composition were completely or almost completely altered, which includes all areas under crop cultivation, forestry plantations, urbanized areas, and mines/quarries. The LCLU classes are essentially a measure of transformation status in the context of threats to biodiversity (Figure 1.8).

Landscape pattern metrics

The developing field of landscape ecology has provided a strong conceptual and theoretical basis for understanding landscape structure, function, and change (Forman and Godron, 1986; Urban et al., 1987; Turner, 1989). Landscape ecology is largely founded on the notion that the patterning of landscape elements (patches) strongly influences ecological characteristics, including vertebrate populations. Therefore, the ability to quantify landscape structure is a prerequisite to the study of landscape function and change. For this reason, much emphasis has been placed on developing methods to measure landscape structure (e.g., O'Neill et al., 1988; Turner, 1990; Turner and Gardner, 1991; Li et al., 1993). While a number of investigators have quantified landscape structure in a variety of ecosystems (e.g., Krummel et al., 1987; Turner and Ruscher, 1988; Gustafson and Parker, 1992), few have examined the relationship between landscape structure and landscape function (e.g., Romme, 1982; Franklin and Forman, 1987; Baker, 1992; Baker, 1993).

The growing concern over the loss of biodiversity has challenged traditional local conservation strategy into developing better ways to examine and manage landscapes at a variety of spatial and temporal scales. Remote sensing developments have made it possible to analyze and manage entire landscapes to meet multi-resource objectives. As part of this study, in addition to LCLU proportions calculated per grid cell, a number of common landscape mosaic and class type pattern metrics were calculated (Table 1.5 and 1.6) for use in Chapters 5 and 6. The program FRAGSTATS (McGarigal and Marks, 1995) was used to calculate the spatial configuration of the LCLU within each grid cell and magisterial district. Landscape mosaic and class indices were calculated using the raster grid option. The LCLU data was converted to a grid cell resolution of 100 m, which is considered appropriate for the NLC database (Fairbanks and Thompson, 1996), development of pattern metrics (O'Neill et al., 1996), and the coarse-scale of this study.

Twenty-eight landscape mosaic indices of LCLU configuration were used that were considered appropriate for the land area of KwaZulu-Natal (Table 1.5) and 28 class level indices were calculated for each of the general vegetation types mapped (Table 1.6; woodland, forest, thicket, and grassland). These pattern indices quantify different aspects of configuration, although many are redundant and simply represent alternative formulations of the same formulation (McGarigal and Marks, 1995). The landscape boundary was considered the edge of the grid cell or magisterial district for the purpose of calculating all the metrics. The implications of this procedure means that the true sizes of patches will decrease because of the closing

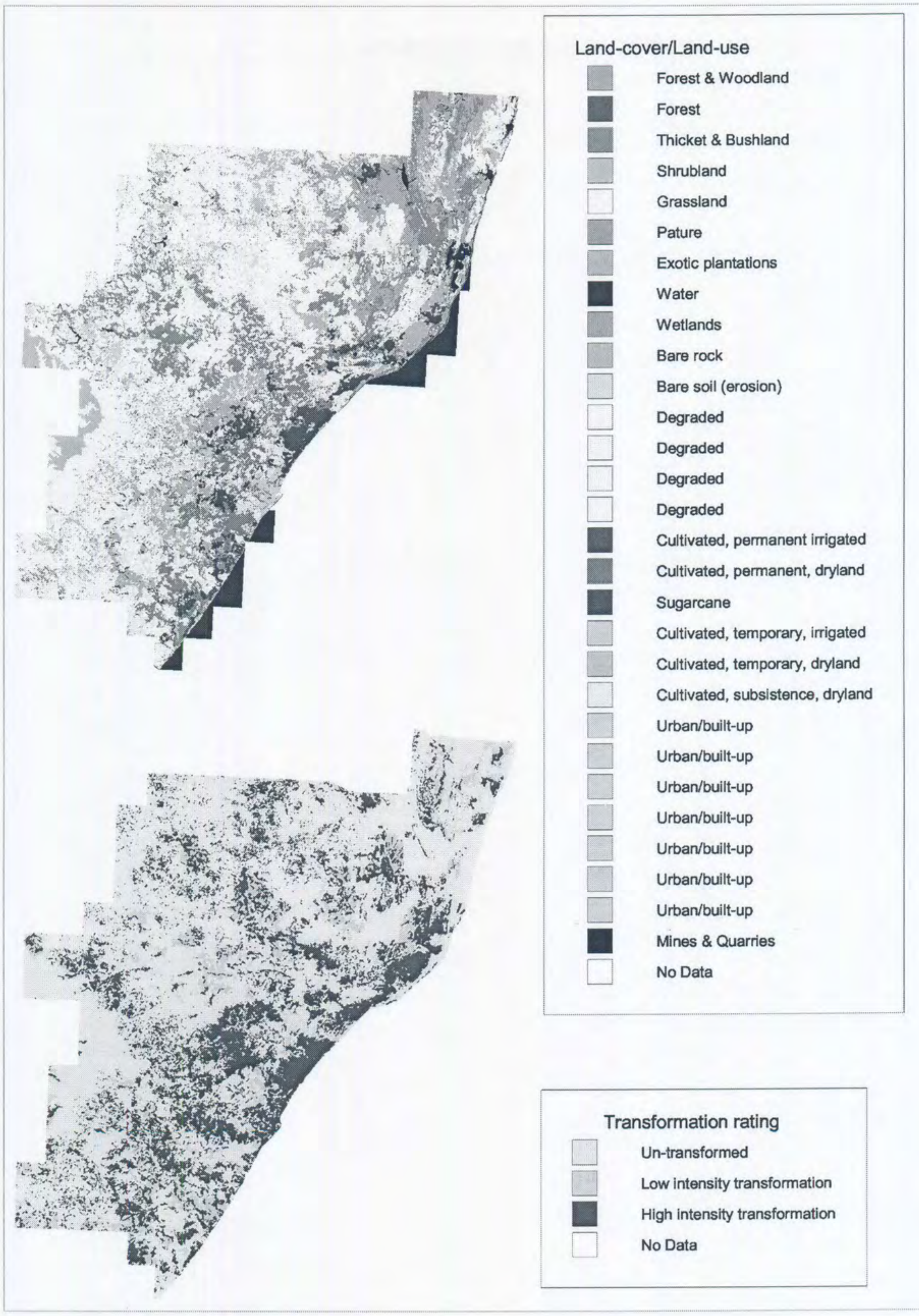

Figure 1.7: (a) Simplified map of land-cover/land-use distribution across KwaZulu-Natal province; and (b) three level transformation map derived from Table 1.4.

Table 1.4: Land-cover/land-use classes used in the South African National Land-Cover (NLC) database and the re-coded transformation classes used for this study.

NLC code	Original NLC Classes	Transformation Classes
1	Forest and Woodland (savanna)	Un-transformed
2	Indigenous Forest	Un-transformed
3	Thicket, Bushland, or Bush Clumps	Un-transformed
4	Low Shrubland and/or Fynbos	Un-transformed
5	Herbland	Un-transformed
6	Grassland	Un-transformed
7	Improved Grassland (pasture, recreational fields)	High intensity
8	Forest Plantations (exotic tree spp.)	High intensity
9	Waterbodies	Un-transformed
10	Wetlands	Un-transformed
11	Bare Rock & Soil (natural)	Un-transformed
12	Bare Rock & Soil (erosion surfaces)	Low intensity
13-17	Degraded Vegetation (NLC codes 1,3,4,5,6)	Low intensity
18-22	Cultivated lands (variations of commercial permanent/temporary crops, irrigated/dryland, and sugarcane)	High intensity
23	Cultivated lands (dryland subsistence)	Low intensity
24	Urban/built-up land (residential)	High intensity
25-28	Urban/built-up land (residential small holdings by subdivided vegetation; NLC codes 1,3,4,5,6)	Low intensity
29	Urban/Built-up land (commercial)	High intensity
30	Urban/Built-up land (industrial/transport)	High intensity
31	Mines and Quarries	High intensity

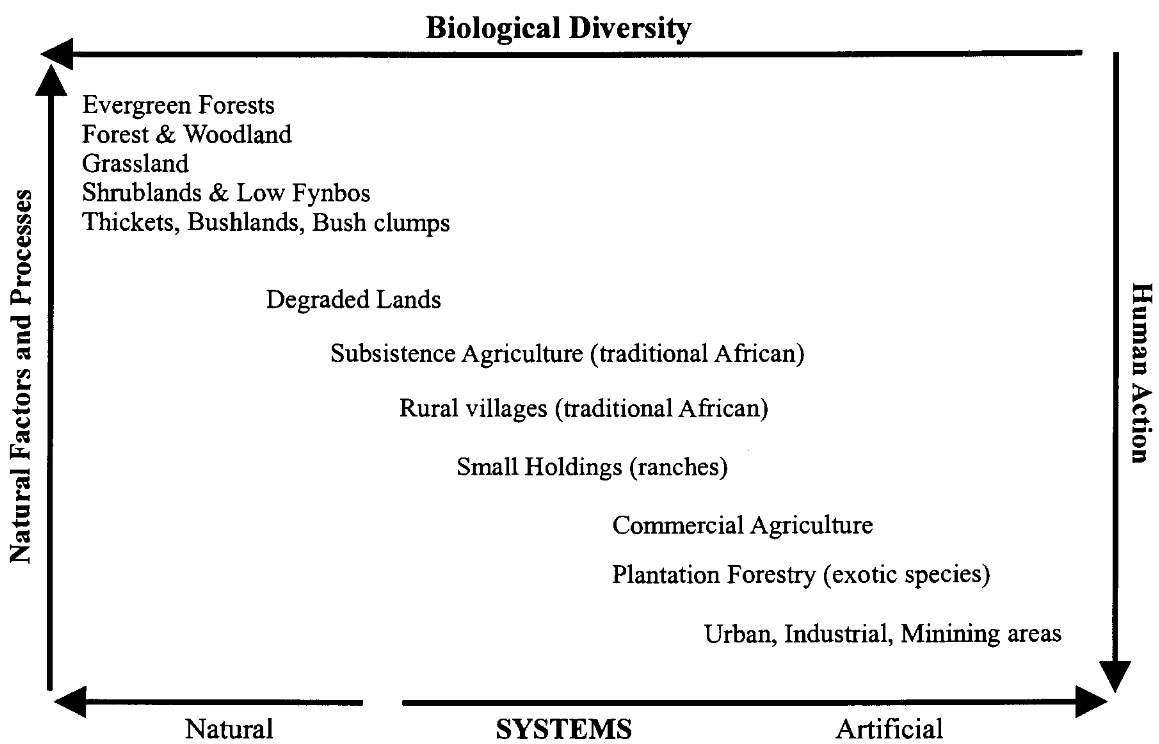

Figure 1.8: Conceptual model of the impacts of increasing levels of human developed land-use on biodiversity and natural processes (modified from Reid et al., 1993).

Table 1.5: Codes and definitions of explanatory landscape mosaic indices used in Chapters 5 and 6, by variable subset.

Acronym	Description[†]
Landcover	
POPTOT96	Total population from 1996 census
POPDEN96	Population density from 1996 census
FOR_PER	Percent woody cover
GRS_PER	Percent grass cover
WET_PER	Percent wetland and waterbody cover
LOWI_PER	Percent subsistence agriculture cover
PLNT_PER	Percent exotic plantation and woodlot cover
DRY_PER	Percent commercial dryland agriculture cover
IRR_PER	Percent commercial irrigated agriculture cover
URB_PER	Percent urbanization cover
M_PER	Percent low intensity transformation
T_PER	Percent high intensity transformation
T_TOTAL	Percent total transformation cover (i.e. combined low and high intensity transformation)
ROAD_INDEX	Percent road density cover
Patchiness	
LPI	Largest patch index (%) - percent of landscape composed of the largest patch
NP	Number of patches
PD	Patch density (no./100 ha)
MPS	Mean patch size (ha) – average size of patches in landscape
PSSD	Patch size standard deviation (ha) – absolute measure of patch size variability
CI	Contagion index – measure of clumpiness of patches within the landscape (contiguity across landscape).
Shape	
MSI	Mean shape index – mean patch shape complexity; equals 1 when all patches are circular and increases as patches become non-circular
AWMSI	Area-weighted mean shape index – similar to MSI, but patch shape index weighted by patch area
FD	Fractal dimension – measure of shape complexity as a departure from simple Euclidean geometry
MPFD	Mean patch fractal dimension – mean patch shape complexity; approaches 1 for simple geometric shapes (e.g., circle, square) and 2 for complex shape; adjusted to correct for bias in perimeter
AWMPFD	Area-weighted mean patch fractal dimension
Interior	
MCAPP	Mean core area per patch (ha) – sum of core areas divided by the number of patches
PCASD	Patch core area standard deviation (ha) – square root of the sum of the squared deviations of each patch core area from the mean core aras per patch, divided by the number of patches of the same type
MAPDC	Mean area per disjunct core (ha) – sum of the disjunct core areas of each patch, divided by the number of disjunct core areas
DCASD	Disjunct core area standard deviation (ha)
DCACV	Disjunct core area coefficient of variation (ha)
Isolation	
MNND	Mean nearest-neighbor distance (ha) – sum of distance to nearest patch divided by number of patches
NNSD	Nearest-neighbor standard deviation
MPI	Mean proximity index – sum of patch area divided by nearest edge-to-edge distance squared between the patch and the focal patch of all patches of the corresponding patchy type whose edges are within 500 m
II	Interspersion index (%) – measure of patch type adjacency against all other patch types (i.e., maximally interspersed and juxtaposed to other patch types)
Richness	
CR	Class richness
CRD	Class richness density
Heterogeneity	
SHDI	Shannon diversity index
SDI	Simpson diversity index
MSDI	Modified Simpson diversity index
Evenness	
SHEI	Shannon evenness index
SEI	Simpson evenness index
MSEI	Modified Simpson evenness index

[†]See McGarigal and Marks (1995) for a complete description and definition of each index.

Table 1.6: Codes and definitions of explanatory class level pattern indices used in Chapter 5, by variable subset.

Acronym	Description[†]
Patchiness	
LAND%	Percentage of the landscape composed of the corresponding patch type
LPI	Largest patch index (%) - percent of landscape composed of the largest patch
NP	Number of patches
PD	Patch density (no./100 ha)
MPS	Mean patch size (ha) – average size of patches in landscape
PSSD	Patch size standard deviation (ha) – absolute measure of patch size variability
PSCV	Patch size coefficient of variation (%) – relative measure of patch size variability
Shape	
MSI	Mean shape index – mean patch shape complexity; equals 1 when all patches are circular and increases as patches become non-circular
AWMSI	Area-weighted mean shape index – similar to MSI, but patch shape index weighted by patch area
MPFD	Mean patch fractal dimension – mean patch shape complexity; approaches 1 for simple geometric shapes (e.g., circle, square) and 2 for complex shape; adjusted to correct for bias in perimeter
AWMPFD	Area-weighted mean patch fractal dimension
Interior	
CADI	Core area density index (%) – percentage of the landscape composed of core areas of the corresponding patch type
TOTAL_CA	Total core area (ha) – total amount of core area of the corresponding patch type; core areas were defined by eliminating a 100 m wide buffer along the perimeter of each patch
NCA	Number of core areas – number of core areas, as defined above
CAD	Core area density (no./100 ha) – density of core areas, as defined above
MCAPP	Mean core areas per patch (ha)
PCASD	Patch core area standard deviation (ha) – square root of the sum of the squared deviations of each patch core area from the mean core aras per patch, divided by the number of patches of the same type
PCACV	Patch core area coefficient of variation (ha)
MAPDC	Mean area per disjunct core (ha) – sum of the disjunct core areas of each patch, divided by the number of disjunct core areas
DCASD	Disjunct core area standard deviation (ha)
DCACV	Disjunct core area CV (ha)
TCA%	Total core area index (%) – total percentage of the class type that is core area
MCA%	Mean core area index (%) – average percentage of a patch that is core area
Isolation	
MNND	Mean nearest-neighbor distance (ha) – sum of distance to nearest patch divided by number of patches
NNSD	Nearest-neighbor standard deviation
NNCV	Nearest-neighbor coefficient of variation
MPI	Mean proximity index – sum of patch area divided by nearest edge-to-edge distance squared between the patch and the focal patch of all patches of the corresponding patchy type whose edges are within 500 m
II	Interspersion index (%) – measure of patch type adjacency against all other patch types (i.e., maximally interspersed and juxtaposed to other patch types)

[†]See McGarigal and Marks (1995) for a complete description and definition of each index.

of the patches by an artificial study area boundary. Since there is nothing simple that can be done about this, conclusions drawn from the analysed data are appropriately tempered. Several core area indices were calculated based on a specified edge width, which, for the purpose of this study, was defined as 100 m wide buffer along the perimeter of each patch. This width represents a somewhat arbitrary decision based, in part, on avian studies by Temple (1986), McGarigal and McComb (1995), and studies by Laurance and Yensen (1991) and Laurance (1994). Edge related metrics were not calculated for this study because of confounding using the arbitrary grid cell and geopolitical magisterial district as sampling units. The use of the equal area grid cell, however, did reduce the effects of area in the metric calculations for the analysis, eliminating the need for regression area correction suggested in other landscape pattern metric studies (e.g., McGarigal and McComb, 1995). However, this technique was used in Chapter 5 to remove the area effects confounding the magisterial district metrics.

1.3.2.6 Road Effects Database

In addition to LCLU threats, one of the most widespread forms of alteration of habitats and landscapes over the last century has been the construction and maintenance of roads (Trombulak and Frissell, 2000). Road networks affect landscapes and biodiversity in seven general ways: (1) increased mortality from road construction; (2) increased mortality from vehicle collisions; (3) animal behavior modification; (4) alteration of the physical environment; (6) alteration of the chemical environment; and (7) increased alteration and use of habitats by humans (from Trombulak and Frissell, 2000). These networks cover 0.9% of Britain and 1.0% of the USA (Forman and Alexander, 1998), however the road-effect zone, the area over which significant ecological effects extend outward from the road, is usually much wider than the road and roadside. Thus, while the LCLU database provides a reasonable estimate of areas with high current vulnerability to biodiversity loss due to existing anthropogenic land transformation; road-effect zones can be used to provide another estimate of the threat to avian biodiversity.

Some evidence on the size of the road-effect zone is available from studies in Europe and North America. Reijnen et al. (1995) estimated that road-effect zones cover between 12-20% of The Netherlands, while Forman (2000) illustrated that 19% of the USA is affected ecologically by roads and associated traffic. The road-effect zone for KwaZulu-Natal was determined using a similar method to that used by Stoms (2000) in which the spatial extent of road effects can be used as an ecological indicator that directly represents impacts on biodiversity. For this, the road-effect zone was used as a measure of the area potentially affected by roads. The affected distances were estimated from the reviews mentioned above, as well as from local published studies (Milton and MacDonald, 1988), and unpublished data, which demonstrated that more than 80% of the transformed area of KwaZulu-Natal Province occurs within 2 km of a road, with approximately 61% of the untransformed areas occurring within the same distance (Pers. Com. Grant Benn, 1999). Therefore, national routes and freeways were assumed to affect biodiversity for a greater distance from the roadway (1 km on each side) than dirt roads (50 m; Table 1.7).

Road segments from the South African Surveyor General (1993) 1:500 000 map series files (Figure 1.9) were buffered to the distance related to its class. The roads in protected areas were excluded from this analysis as the road-effect in nature reserves is of little concern in this study. A road disturbance index was calculated within each grid cell by summing the total area of the buffered roads and converting to a percentage of that grid cell.

Table 1.7: Buffer widths assigned to road classes for calculating road effect zone (after Stoms, 2000).

South African Surveyor General Description	Buffer width (m)
National route	1000
Freeway	1000
Arterial	500
Main	250
Secondary (connecting and magisterial district roads)	100
Other (rural road)	50
Vehicular trail (4 wheel drive route)	25

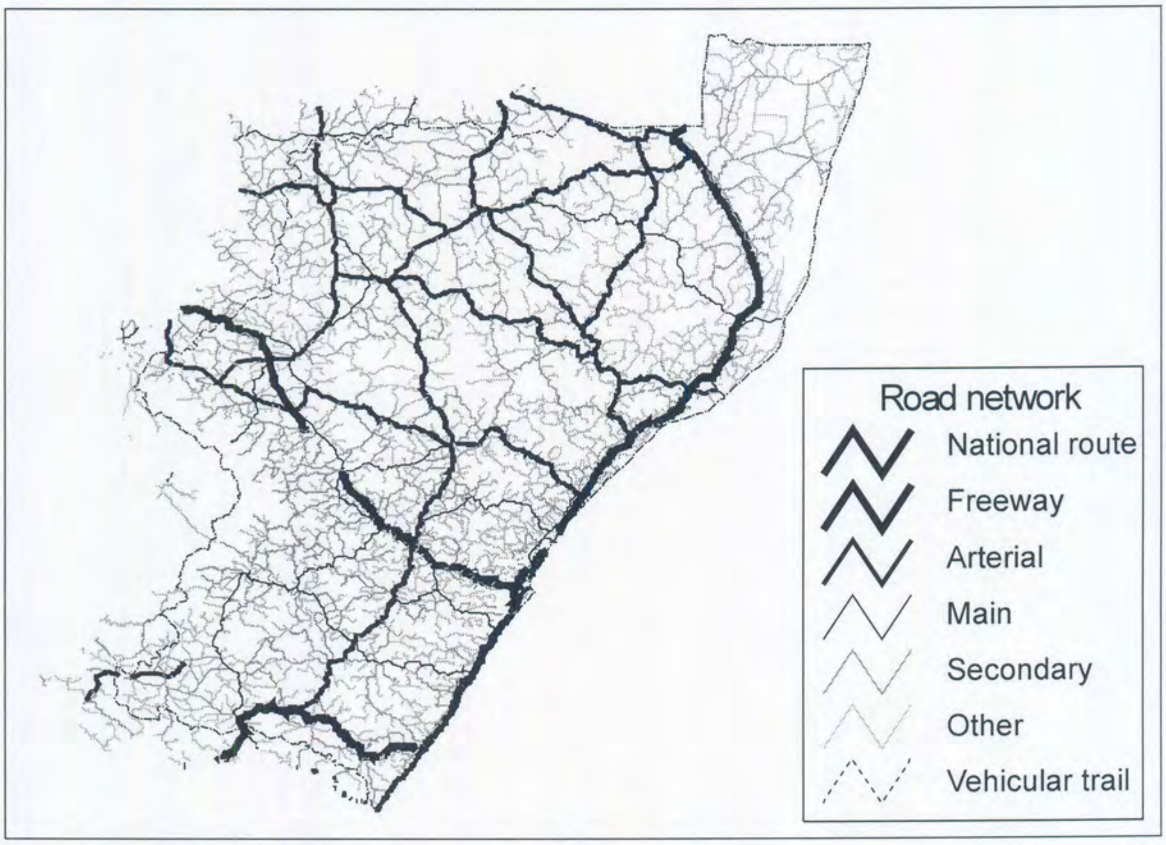

Figure 1.9: The 1:500 000 KwaZulu-Natal road distribution network.

1.3.2.7 Socio-economic Indicators

Three databases of available social and economic indicators were examined for variables that would cover the entire province using the latest magisterial district definition (Table 1.8) and distributions from the 1996 Census (Figure 1.10). By limiting the data to the 1996 boundaries used in the 1996 South African Census (Stats SA, 1998) a whole host of historical census and economic data was made unacceptable for this study. This is rather unfortunate, however, the radical changes in districting that have accompanied the disbanding of the apartheid state have seen the magisterial districts and boundaries change five times since the 1991 census. The 1996 census ushered in the first reliable geographic results of the countries demography. Boundary

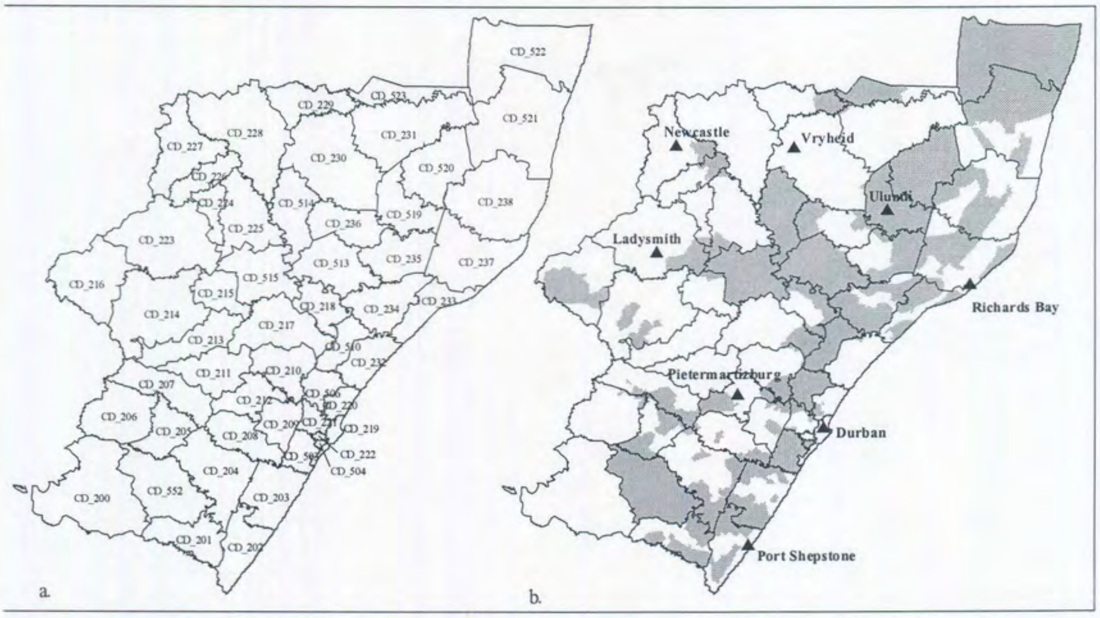

Figure 1.10: (a) Magisterial districts used for the 1996 Census; and (b) magisterial districts in relation to the former KwaZulu and Transkei homeland boundaries (pre 1994; shaded gray).

Table 1.8: Codes and names of magisterial districts in KwaZulu-Natal Province.

HSRC code	Magisterial district	HSRC code	Magisterial district
CD_200	Mount Currie	CD_226	Dannhauser
CD_201	Alfred	CD_227	Newcastle
CD_202	Port Shepstone	CD_228	Utrecht
CD_203	Umzinto	CD_229	Paulpietersburg
CD_204	Ixopo	CD_230	Vryheid
CD_205	Polela	CD_231	Ngotshe
CD_206	Underberg	CD_232	Lower Tugela
CD_207	Impendle	CD_233	Mtunzini
CD_208	Richmond	CD_234	Eshowe
CD_209	Camperdown	CD_235	Mthonjaneni
CD_210	New Hanover	CD_236	Babanango
CD_211	Lions River	CD_237	Lower Umfolozi
CD_212	Pietermaritzburg	CD_238	Hlabisa
CD_213	Mooi River	CD_503	Umbumbulu
CD_214	Estcourt	CD_504	Umlazi
CD_215	Weenen	CD_506	Ndwendwe
CD_216	Bergville	CD_510	Mapumulo
CD_217	Umvoti	CD_513	Nkandla
CD_218	Kranskop	CD_514	Nqutu
CD_219	Durban	CD_515	Msinga
CD_220	Inanda	CD_519	Mahlabathini
CD_221	Pinetown	CD_520	Nongoma
CD_222	Chatsworth	CD_521	Ubombo
CD_223	Kliprivier	CD_522	Ingwavuma
CD_224	Glencoe	CD_523	Simdlangentsha
CD_225	Dundee	CD_552	Umzimkulu †

† This district is managed by the Eastern Cape Province but has been included as part of KwaZulu-Natal for this study.

problems with the ex-homelands, especially in KwaZulu-Natal, were finally removed, yet the spatial landscape characteristics of their former presence was not.

The socio-economic data was drawn from the *1996 census* (Stats SA, 1998), 1996 *KwaZulu-Natal Service Needs and Provision* (Human Sciences Research Council, HSRC; Schwabe et al., 1996), and the *1997 KwaZulu-Natal Development Indicators* (Human Sciences Research Council, HSRC; Kok et al., 1997) databases. The last two databases are unique in South Africa, as KwaZulu-Natal province is the only region to have rather recent social surveys conducted for each magisterial district based on development indicators (i.e., need for water, sewer, etc.) that provide information on basic needs and tensions. Appendix A provides the descriptive breakdown of the eighty-four socio-economic and environmental indicators used in Chapters 5 and 6.

1.3.2.8 Provincial Protected Areas Database

KwaZulu-Natal Nature Conservation Service provided a spatial database of their provincial protected areas (Figure 1.11). The protected areas database describes the boundaries of provincial reserves, digitized from 1:50 000 maps. Table 1.9 provides the names and basic descriptions of the protected areas. The spatial distributions of private conservation areas and game farms were not available for the analyses.

1.4 Differing Aspects of This Study

The compilation of a series of studies described in this thesis is unique from most traditional landscape ecological and conservation biology studies in at least three major respects. The first is the coarse-size of the geographical sampling unit from which the species distribution information is derived; the second is the quantification of coarse-scale avian turnover related to environmental and landscape pattern gradients; and the third is the pattern analysis of socio-cultural and economic data in relation to evolved landscape pattern.

Typically, most quantitative bird analyses have used plots or transect as sampling units. The aim of such studies is to characterize local avian-vegetation relationships (e.g., Wilson, 1974, Forman et al., 1976; Cody, 1985; Opdam et al., 1985; Opdam et al., 1984). Small plot based samples have been used in coarse-scale avian analysis for many years (e.g., Wiens, 1973; Rottenberry and Wiens, 1981; Wiens, 1989a; McGarigal and McComb, 1995). The sampling schemes rely on subjective choices to find representative "homogeneous" vegetation plots in a much larger vegetation community type or landscape within which a birds presences and relative abundances are recorded.

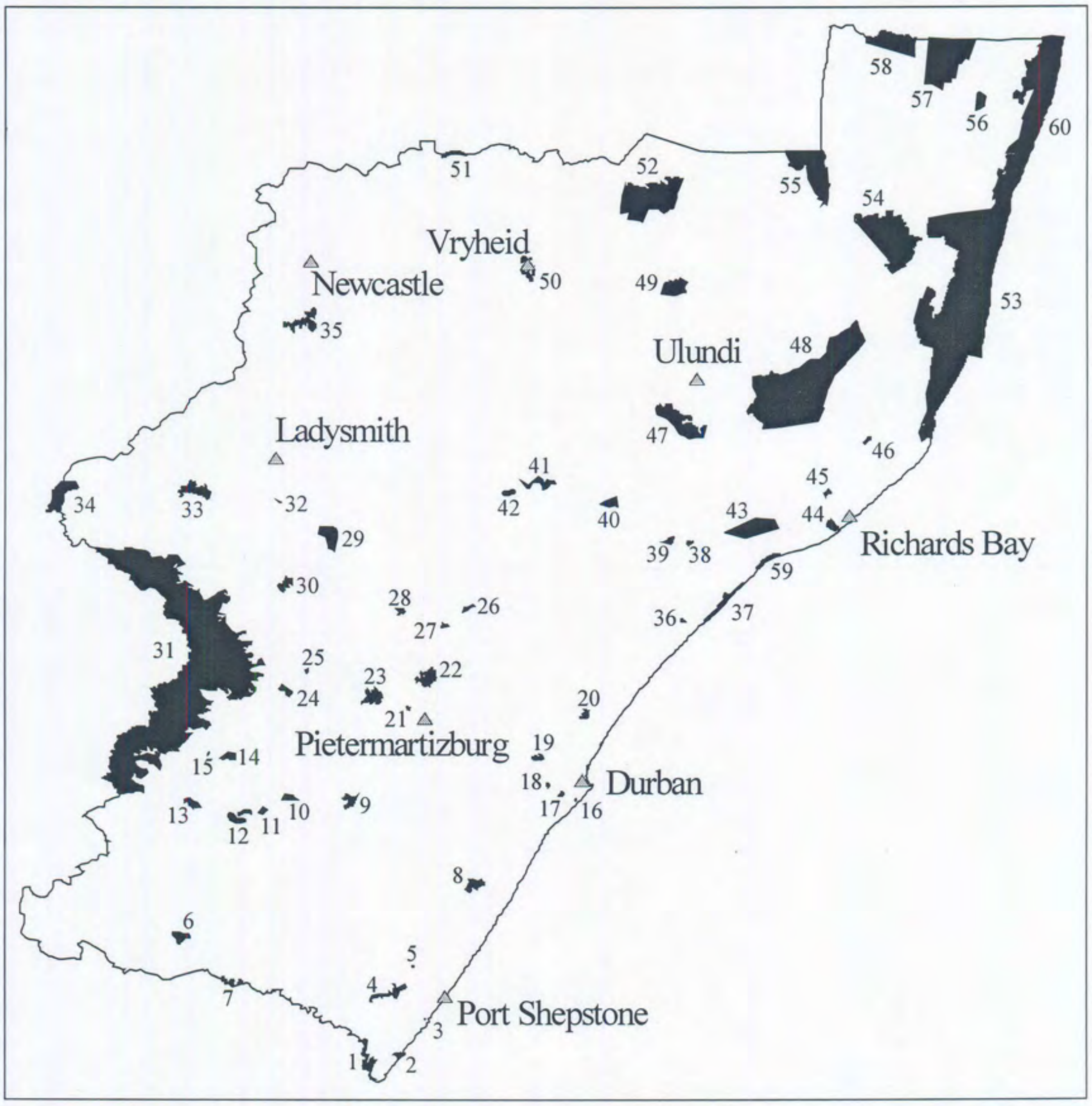

Figure 1.11: Protected areas of KwaZulu-Natal Province managed by KwaZulu-Natal Nature Conservation Services.

When approached from the regional scale, the plot sampling strategy leads to scale problems (Wiens, 1981) and to substantial under representation of less common species due to the shorter survey periods (Preston, 1948). The plots can usually provide ecologists with an idea of how species grade with the environment on a fine scale, but comprehensive bird species information for a vegetation type or landscape is always limited by time and sampling effort. The effort described in this thesis is a trade-off of spatial precision for more comprehensive community inventory in coarse mapsheet units. This study also has the added advantage of not having to worry about high frequency spatial and temporal effects (Preston, 1960).

Table 1.9: Names and descriptions of the protected areas managed by KwaZulu-Natal Nature Conservation Services.

Map Code	Name Description	Map Code	Name Description
1	Umtamvuna Nature Reserve	31	Natal Drakensberg Park
2	Mpenjati Nature Reserve	32	Tugela Drift Nature Reserve
3	Skyline Nature Reserve	33	Spoienkop Dam Nature Reserve
4	Oribi Gorge Nature Reserve	34	Royal Natal National Park
5	The Valleys Widlife Sanctuary	35	Chelmsford Dam Nature Reserve
6	Mount Currie Nature Reserve	36	Harold Johnson Nature Reserve
7	Bruce's Valley Natural Heritage Site	37	Amatikulu Nature Reserve
8	Vernon Crookes Nature Reserve	38	Dlinza Forest Nature Reserve
9	Soada Forest Nature Reserve	39	Entumeni Nature Reserve
10	Greater Ingwangwana River	40	Nkandla Nature Reserve
11	Greater Ingwangwana River	41	Qudeni Forest reserve
12	Greater Ingwangwana River	42	Tugela Gorge
13	Coleford Nature Reserve	43	Ngoye Forest Reserve
14	The Swamp Nature Reserve	44	Richards Bay Game Reserve
15	Himeville Nature Reserve	45	Enseleni Nature Reserve
16	Bluff Nature Reserve	46	Lake Eteza Nature Reserve
17	Stainbank Nature Reserve	47	Opathe Nature Reserve
18	Paradiase Valley Nature Reserve	48	Umfolozi-Hluhluwe Game Reserve
19	Krantzkloof Nature Reserve	49	Ngomi Forest Reserve
20	Hazelmere Public Resort Nature Reserve	50	Vryheid Mountain Nature Reserve
21	Doreen Clark Nature Reserve	51	Pongola Bush Nature Reserve
22	Albert Falls Nature Reserve (dam)	52	Itala Game Reserve
23	Midmar Dam Nature Reserve	53	Greater St. Lucia Wetland Park/Marine Reserve
24	Umgeni Vlei Nature Reserve	54	Mkuzi-Pumulanga Game Reserve
25	Fort Nottingham Heritage Site	55	Pongolwane Biosphere Reserve
26	Umvoti Vlei Nature Reserve	56	Sileza Forest Reserve
27	Karkloof Nature Reserve	57	Tembe Elephant Park
28	Blinkwater Nature Reserve	58	Ndumo Game Reserve
29	Weenen Nature Reserve (dam)	59	Umlalazi Nature Reserve
30	Wagendrift Nature Reserve (dam)	60	Maputaland Biosphere Reserve

1.5 Format

This thesis is presented as chapters that document a set of studies that are stand-alone papers. Several of the chapters have been published or are in press (Chapters 3, 4, and 5) and the remaining Chapters (2, 5, and 6) are prepared for submittal. The chapters, however, are designed around the central theme of conservation within human dominated systems, and thus the whole is much greater than the parts. Chapter 2 provides the reader with a background and justification to the theory of co-evolution and its integration within landscape ecology. The argument sets up the analytical framework to be used in the subsequent chapters to show the need for this type of approach for biodiversity conservation in developing nations. Chapter 3 details the creation and critiques the use of a landscape model for conservation area identification. Chapter 4 defines a methodology and procedures to use environmental gradient analysis in conjunction with complimentary-based reserve selection algorithms to analyze and prioritize avian conservation areas. The effort in Chapter 5 looks at multi-scaled spatial effects on avian diversity and community structure. The study determines how changes in landscape structure (both composition and configuration) affect bird populations in the spatially and temporally dynamic landscapes at the extents of South Africa and of KwaZulu-Natal Province. Chapter 6 provides pattern analysis of human dominated landscapes evolved in association with socio-economic variables. The emphasis is on the co-evolutionary model outlined in Chapter 2 and aimed at assessing the ideal reserve system for birds developed in Chapter 4. Thus, Chapter 6 brings together lessons and results developed in all the previous chapters to lend support to a revision of biodiversity threat models and analysis. The thesis work is then rounded off with conclusions providing a broader message on the impact of the results and delivering final thoughts on the stated effort.

2. Developing a Co-evolutionary Landscape Ecology Framework to Address Sustainable Biodiversity Conservation

To understand the crisis with respect to the destruction of biodiversity we urgently require an analytical framework, which takes into account socio-cultural values, economic systems, and the biophysical theater in which this tragedy takes place. The growing rates of this destructive process further urge the development of a conceptual framework aimed at understanding the responses of ecosystems to habitat destruction, with associated landscape change. Such information will be available by the integration of both field and theoretical studies. What needs to be articulated for defined regions of the world are the principles upon which the actual biodiversity threats have evolved. By developing an appropriate framework based on co-evolutionary thought and landscape ecology principles, the likelihood of potential landscape changes across a variety of systems may be assessed to guide conservation planning efforts.

Understanding the form, behavior, and historical context of landscape dynamics is crucial to understanding ecosystems and subsequent biological diversity at several temporal and spatial scales (O'Neill et al., 1986; Noss, 1990; Forman, 1995). This understanding and analysis should not be limited to the physical or natural history of landscapes, but must include landscapes within an anthropogenic context first noted by Sauer (1925). In essence, sustainability research with respect to biodiversity conservation could be better addressed by way of a co-evolutionary landscape ecology framework.

There have been numerous calls for the study of landscape or ecosystem diversity and function for conservation purposes (e.g., Noss, 1983; Forman, 1989; Franklin, 1993; Forman, 1995; Walker, 1995; Risser, 1995; Folke et al., 1996). Because conservation of species diversity depends on conservation of the habitats and landscape ecosystems in which species live (Noss 1990; Franklin 1993), a greater attention should be given to understanding and examining the economic, social, and cultural diversity of human groups in landscapes within regions. Fundamentally, landscapes can be viewed as the critical spatial scale at which biodiversity is minimized, as it is the scale where macro and microeconomic policies converge.

This chapter argues that problems related to biodiversity loss, landscape resilience and ecosystem integrity have at their root a co-evolutionary response. A conceptual development and proposed research agenda to enhance the theoretical and application framework for biodiversity conservation planning within developing country landscapes is expressed.

2.1 Sustainability and Resilience

As the scale of the world's socio-economic situation continues to grow there is increasing demand for land and its resources. A firmer knowledge of changes in the diverse landscapes of developing countries must aid the urgent need to join environmental management that is sound with economic development that is viable in the long-term. The imperative for conservation-with-development has been labeled "sustainable development" (Goodland, 1995). Much publicized mandates for sustainable development echo forth as a *sine qua non* of conservation in the developing countries of the world, a seeming panacea for the world's environmental problems. Nonetheless, sustainable development has remained a general concept and one that is subject to unending debate (Redclift, 1987; Dovers and Handmer, 1993; Meffe and Carroll, 1997). Indeed the more exact meanings of sustainability are typically lacking. The most widely used definition of sustainability states: 'A sustainable condition is one in which there is *resilience* for both social and physical systems, achieved through meeting the needs of the present without compromising the ability of future generations to meet their own needs' (WCED, 1987).

Stability is substituted in the original statement for the operative term, resilience (Holling, 1973; 1986), which is required of a system to return to a "stable" state. For sustainability, the concept of ecosystem resilience becomes crucial for biodiversity conservation. Resilience represents the ability of ecosystems to recover from or adjust easily to disturbance, and the speed with which they return to an attractor state (Pimm, 1984), which can be deemed "stability." Following the work of Holling (1973; 1986), resilience can be used to identify the existence of functions within systems that, at any given moment, are offset from any one of a number of locally stable attractor states. Resilience in this sense is a measure of the perturbation that can be absorbed before an ecosystem in the domain of one attractor state is dislodged into that of another attractor state (Folke et al., 1996). It is essentially the capacity of the system to buffer disturbance. The essential condition for the resilience of a system in order to persist is determined by spatial heterogeneity and the associated biotic diversity, based on Elton's (1958) original hypothesis that ecological stability should depend on biological diversity. There have been many conceptual and empirical advances, and debates (e.g., Woodwell and Smith, 1969; Pimm, 1984; Holling 1986; Tilman, 1996; Tilman et al., 1996) on the importance of diversity within systems.

At the landscape scale, biotic processes, interacting with abiotic ones, can control structure and variability. This is also the scale range where human land-use transformations occur, so that the area where plant and animal controlling interactions unfold is the same area where human activities and population interact with the landscape. The landscape concept is appropriate for sustainable planning because it is sufficiently large to contain a heterogeneous matrix of LCLU elements that provide a context for mosaic stability (Forman 1990; 1995).

2.2 Biodiversity Protection Strategies

Efforts to conserve biodiversity remain largely rooted in the concept of species, a most ephemeral part of an ecosystem. Species-based approaches address only a small part of biological diversity because they ignore different levels of organization and the functional linkages among these levels (Noss, 1983; Pimm, 1991; Maddock and du Plessis, 1999). Broadening our view of biodiversity into one of ecosystem hierarchy and diversity highlights that the species diversity of an ecological system is a systems-related attribute (Noss, 1990; Jizhong et al., 1991). A focus on ecosystem diversity underscores the inherent value of the systems, apart from which the myriad of species cannot survive.

To be sure, the most important considerations, which are typically directly ignored, for any of the conservation methodologies outlined in Chapter 1 are the role human societies, values and economies play as threats and protectors of biodiversity. Conservation based public agencies and academic conservation biology tends to disassociate themselves from the human-side of the analysis and only focus on their biological domain science. Humans' are a part of natural systems and by their evolutionary nature disturb "natural" habitat (e.g., through habitat loss, fragmentation) and altercate key resources (e.g., water, soil, climate), which in turn affects the species, community assemblages and food webs in the hierarchy (Figure 2.1). A logical framework for understanding the interactions of human threats has not been considered in species or broad model approaches of conservation planning, although they are the dominant causes of biodiversity loss (Ehrlich and Wilson, 1991).

2.3 Critique and Reconstruction of Problems

The multi-dimensional and multi-disciplinary field of sustainability encompasses the traditional academic disciplines of ecology, economics, sociology, developmental studies, and philosophy (Norgaard, 1988; van Jaarsveld, 1996). It strives to integrate social, economic and environmental goals into a single manageable framework capable of directing regional and global development towards a more just and equitable future (Munasinghe, 1993).

Several problems continue to hamper the scientific communities ability to address sustainability and the integration of the environment, society and economics. The following problems currently challenge sustainability and biodiversity conservation:

- The fallacy of "natural" nature. There is little point in regretting the history that has made humans or exotic species part of the ecosystem they now inhabit (e.g., Cronon, 2000).
- The view that there is an achievable end state.

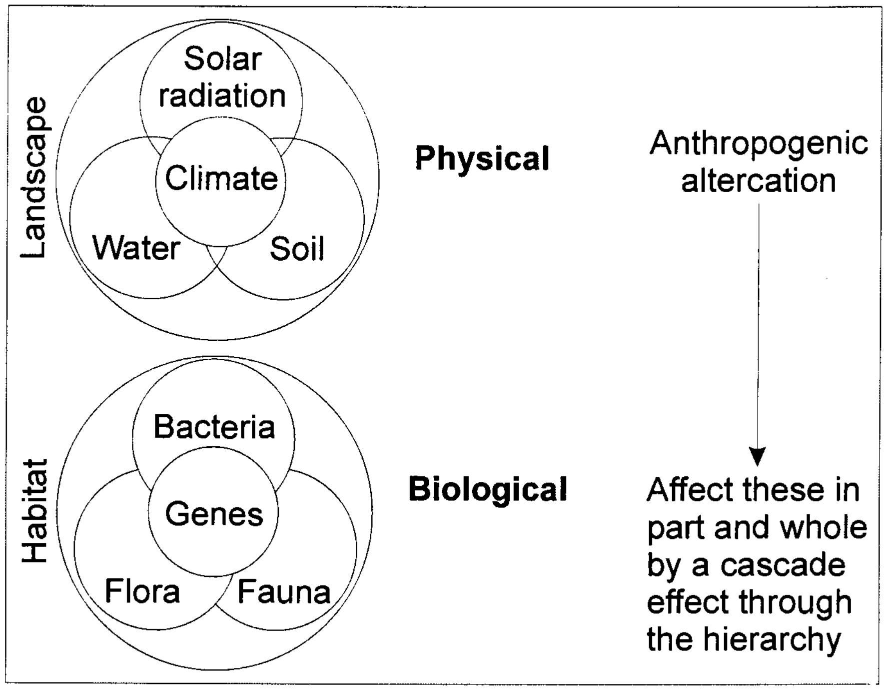

Figure 2.1: Key resources appropriated through human action and the biota that are affected through a hierarchical cascade.

- The role of isolation, i.e., one discipline or segmented disciplines driving development and conservation. Problems tend to be isolated, rather than acknowledging their true connective nature.
- The drive toward one correct analytical framework, when there are more than one way of looking at solutions.

A continuation of previous ideas and opening new ways of thinking and viewing our current crisis with biodiversity loss needs to be explored. The following proposed profile of reconstruction should continue the debate:

- The development of shared learning.
- A co-evolutionary understanding of development and the biodiversity crisis in especially developing countries.
- The continued acknowledgement and support of the role of resilience with the adoption of adaptive environmental management (e.g., Holling, 1996). This follows on the realization that most ecosystems are in various levels of dis-equilibirium and that policy must remain flexible and evolutionary.
- The need to develop models of macro/micro scale interaction in order to build realistic conservation impact scenarios for planning and policy assessment (e.g., Dale et al., 1994).

- The continued acknowledgement of spatial variation and scale as important factors in understanding environmental systems (e.g., Wiens, 1989b)

One of the principle aims of a co-evolutionary dynamics model is to establish human-ecosystem interaction within an interpretative/interrogative framework. We must develop a critical, evaluative methodology, which stresses a multiple interpretative framework and is consistent with the need for a multiple modelling strategy. This is an acknowledgement of the impossibility of any single model adequately encompassing the diversity of social and environmental phenomena, which comprise co-evolutionary systems.

Essentially all model characterizations of human-ecosystem processes are of necessity both incomplete and proximate; thus we need a variety of model scenarios not only at different temporal and spatial scales, but also at different levels of social and natural aggregation. We need a research framework, not only capable of encompassing qualitative and quantitative observational sets, but moreover, one in which empirical data can be situated within an interpretive frame of reference. By proposing a co-evolutionary landscape ecology framework we are looking for systematic ways of linking disparate bodies of knowledge, currently resident in discrete academic boxes. The conceptual structure must be able to facilitate and allow interrogative dialogue between qualitative and quantitative data sets. To truly understand what is needed for sustainable biodiversity conservation, a scheme should encompass three distinct areas of knowledge acquisition interlinked and focussed on supplying information and knowledge for shared learning (Figure 2.2). This framework avoids reductionist methods, which stress the importance of arriving at a single unambiguous model as the basis of prediction. In contrast the goal is directed at the representation of human-ecological systems with a view to a more complete understanding of biodiversity threat and uniquely tailored regional action. Therefore, we need more, rather than fewer representations so as to create a more effective dialog.

Monitoring indicators should be able to provide information on long-term LCLU patterns of the locale, along with attendant social and political constraints within which resource management strategies were implemented. The relationship between power structures and the land provides new information on the rates of resource exploitation, human demography, and the differential resilience of specific landscape units to support biodiversity. The nature of this framework should be able to generate a series of scenarios arriving, not at any single predictive

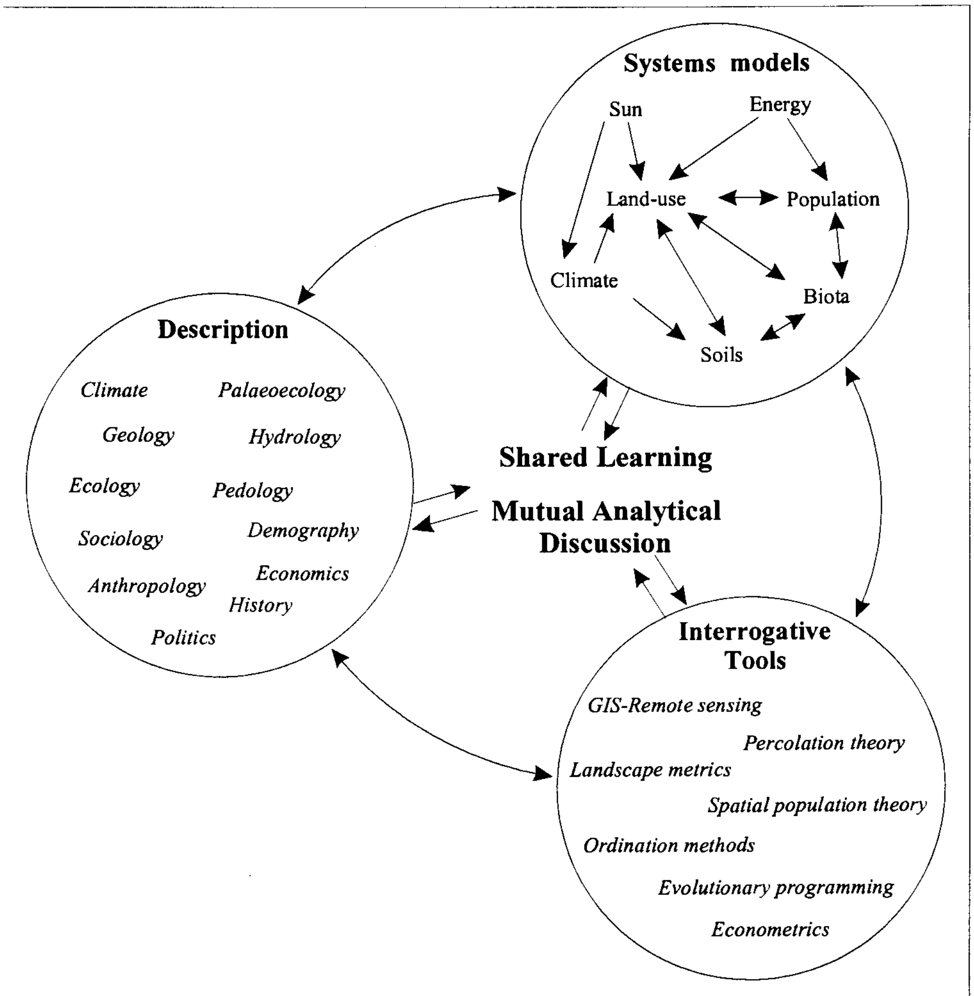

Figure 2.2: A shared learning framework for assessing human-ecosystem sustainability dynamics.

model of unsustainability, but at a series of potential evolutionary pathways to which the landscape or region is prone. In a sense, it is a mapping of the 'possibility spaces' within which human settlement and ecosystem functioning can persist, and within which is nested a probability space of human action.

Limited resources for the protection of the environment and the rising competition between land-use developments in developing countries call for appropriate conceptual frameworks and relevant methods for facilitating and analysing trade-offs and compromises. The methodology must encompass economics, socio-cultural and environmental attributes in a disaggregated fashion to understand a regions overall vulnerability with respect to sustainability. Van Jaarsveld (1996) offered one way of looking at the highly disaggregated data that are typically acquired from each of these sectors. It was suggested that the development of highly aggregated indexes may have significant political advantages in communicating with the public and policy-makers, but they do not provide an ideal or adequate framework within which political action should be prioritized. Instead a framework should be developed that would require an evaluation of disaggregated data, and leaving the researcher with the problem of dealing with, and interpreting, complex environmental, social and economic data matrixes in the absence of a simplistic 'cause-effect' understanding of interactions between these variables or their social values. In biodiversity conservation planning in developing nations, there is a need for analyses that are able to answer questions of viability or security of conservation practices in the face of anthropogenic land-use changes driven by global economic policy. An integration of complex environmental and socio-economic indicators should provide the information needed to answer questions pertinent for sustainable biodiversity conservation.

2.4 Evolutionary Pathways

2.4.1 Co-evolutionary Framework

There need be little doubt that the landscapes we have today (homogeneous and heterogeneous, 'wild' and humanized, fine-grained and coarse-grained), and hence the ways in which cultures interact with nature, have been strongly influenced by historic economic instruments. Increasingly aspects of social organization as well as the paths of knowledge and technology advance affect the pathway landscapes assume (i.e., pattern and process). Norgaard (1988; 1994) presents this aspect of viewing these interactions between economics and other factors by borrowing from evolutionary, and in particular from co-evolutionary, explanations of change, portraying development as a process of co-evolution between knowledge, values, organizational, technological, and environmental systems (Figure 2.3). In Norgaard's (1994a; 1994b) portrayal, each of these systems is related to each of the others, yet each is also changing and affecting change in the others. Deliberate innovations, chance discoveries, random changes, and chance introductions from other societies occur in each system which affect the fitness and hence the distribution and qualities of components in each of the other systems. With each system putting selective pressure on each of the others, they co-evolve in a manner whereby each reflects the other. This type of thinking is consistent with landscape ecological theories which incorporate the interaction of humans and species immigrations, emigrations, and populations effecting pattern and process leading to state changes (Forman, 1995). Co-evolution explains how everything is tightly locked together, yet everything is also changing. This approach could be used as a conceptual underpinning to understand current and future biodiversity threats and to assess the sustainability of protected areas.

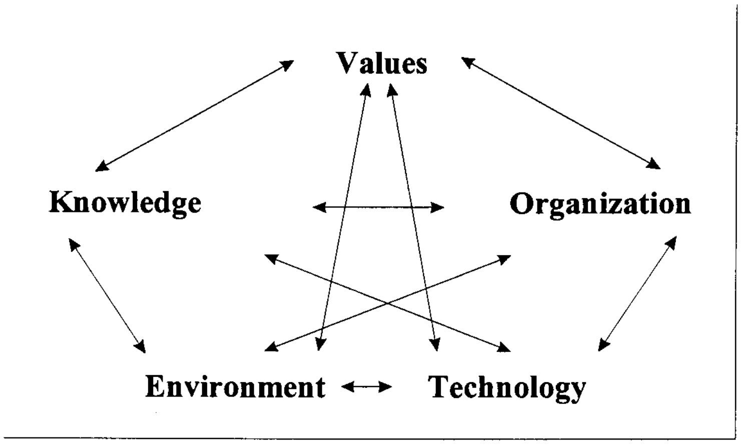

Figure 2.3: A co-evolutionary view of development (Norgaard, 1994).

2.4.2 Non-linear Dynamics

Discoveries in the natural and physical sciences have demonstrated the evolutionary pathways traced by non-linear systems, and their convergence towards a variety of stable, quasi-stable and unstable states. These trajectories are reached through a sequence of bifurcations, during which the system undergoes qualitative change (Laszlo, 1987). A fundamental aspect of human-environment relationships is the opposition or tension between temporal rhythms, which are embedded in natural processes and those resident in societal structures; the asymmetries between them provide the context for abrupt discontinuous transition through bifurcation (Figure 2.4). In this presented case the bifurcation is symmetric and represents the pathways of spatial landscape change. Since humans are an intimate part of landscapes the process of landscape pattern evolution begins with habitat perforation or dissection leading to fragmentation, shrinkage of fragments and finally a lengthy process of attrition of the remaining fragments (Forman, 1995). The land-use types that replace the natural habitat add to the diversity of the landscape till at some point the attrition of the natural remnants is so great that the homogenizing forces of human development at some defined analytical scale renders the landscapes simple again.

Human-environment systems are a prime example of the operation of non-linear dynamical processes. They are governed by interlinked sets of non-linear processes, which resist obvious disaggregation into systemic subsets- something which conventional reductionist methodologies force upon them. An important property of such complex systems is the role played by feedback mechanisms, which amplify or reinforce human physical and social processes. For example, the development of economic core areas and a poor periphery appears to be the process of cumulative and circular causation.

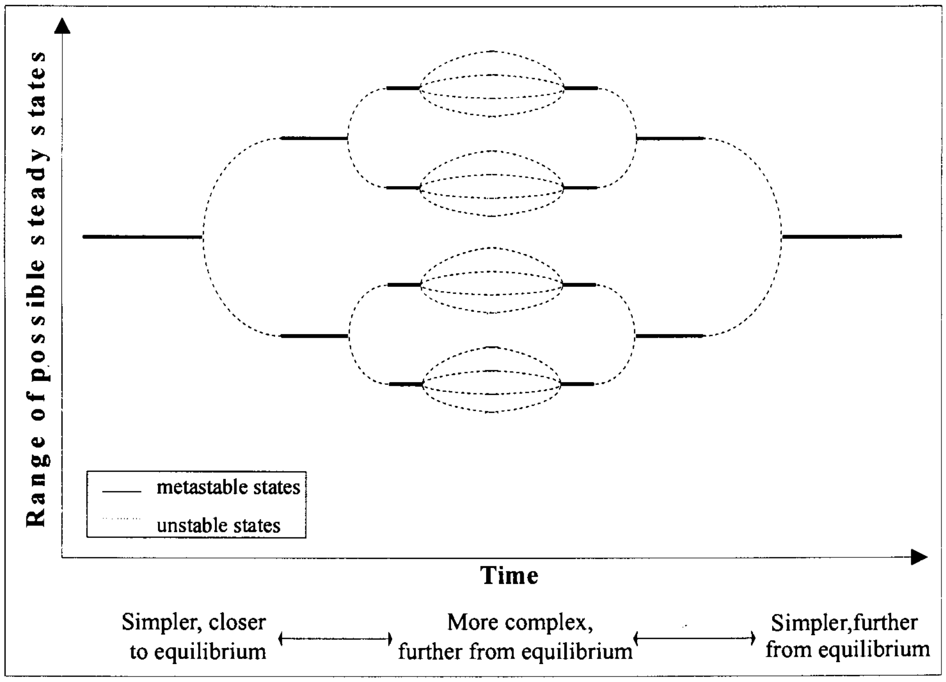

Figure 2.4: Bifurcation diagram of the probable development of landscape pattern.

The existence of external economies, economics of scale, and agglomeration in core areas, compounded by the provision of transportation networks, serve to enhance and capitalise upon existing advantages of relative locations.

In the language of dynamical systems, two elementary concepts are important: the notion of phase space and the other is concerned with the concept of attractors or basins of attraction (for more detail see Waldrop, 1994). First, phase space can be thought of as a geometric representation of the universe of possibilities possessed by a system- in a sense, the allowable territory within which it operates- an arena in which a phase portrait of the evolutionary history of the system can be constructed. Second, is their long-run behavior, which is manifest by a particular attractor; a region of the phase space to which all points ultimately converge. It is effectively the 'signature' of the system.

With respect to human-modified landscapes under discussion here, what we are faced with is an empirical situation in which a number of different attractors are co-present. In a sense they inhabit an operational space constrained by non-linear causality on account of the multiple periodicities represented by the wide variety of temporal rhythms, which define natural ecological phenomena and their constant modification by human social groups who themselves are defined by alternative periodicities (i.e., economics). Research in a number of fields has shown that non-linear feedbacks can amplify these rhythms causing either catastrophic collapse (Holling, 1986) or the emergence of spontaneous structure (Allen, 1993), with the system evolving to a new qualitative state.

2.4.3 Landscape Socio-ecodynamics

To elaborate the process within the context of landscapes, imagine that the systems of Figure 2.3 - values, knowledge, social organization, and technology - are made up of different ways of valuing, knowing, organizing, and doing things. Similarly the landscape (environmental) system consists of different types of species and other particular ecological factors which it starts with before human contact (Figure 2.5). From a starting pre-human landscape geography (T_0) a perturbation (unstable state) occurs whereby a particular human social organization arrives randomly, allowing that landscape to co-evolve (T_1) to a new characteristic look (pattern, process, use) with relative stability. Sauer (1925) originally referred to this process as landscape morphology, where a landscape environment could take a multitude of pathways making prediction difficult. In effect changes within any one of the components from Figure 2.3 acts to evolve the landscape development process conceptualized in Figure 2.4 and simplified in Figure 2.5. The process of experiments, discoveries, chance mutations, and introductions within each of the systems (Figure 2.3) drives co-evolution across all of the systems simultaneously and thus creating bifurcation on the landscapes. The landscape bifurcations described in Figures 2.3, 2.4, and 2.5 helps us to understand how policy overriding economic, social and environmental systems (Figure 2.6) can cause critical instabilities (bifurcation) and thus instigate a new co-evolutionary pathway within a landscape. Policy is a fundamental determinant of the way natural resources are exploited and/or conserved and how human systems are organized. In South Africa the separate development policies of the Ex-Apartheid State created spatial separation and development pathways for local indigenous African versus colonial Europeans. The landscape character of the created African tribal homeland system versus the Western industrial development model of White South Africa are still clearly evident today (Fairbanks et al., 2000). The commonly held implications of this can be the asynchronous rhythms between the natural world, societal reproduction and consumption patterns which challenges the sustainability of landscape biodiversity conservation. Munasinghe and Cruz (1995) note that linking specific causes with particular effects is especially difficult where many conditions are changing simultaneously. However, it is usually possible to identify a small number of linkages affecting high priority environmental concerns.

Through the process of co-evolution, the world's landscapes can be thought of as having become a patchwork quilt along a gradient of loosely to strongly interconnected, co-evolving social and ecological systems. Within each landscape the ecological system evolved in response to cultural pressures and tended to reflect the values, worldview, and social organization of local peoples. At the same time, the cultural system in each landscape evolved within the constraints imposed by the ecosystem and hence tended to mirror the fertility, species composition, stability, and management options presented by the ecosystem.

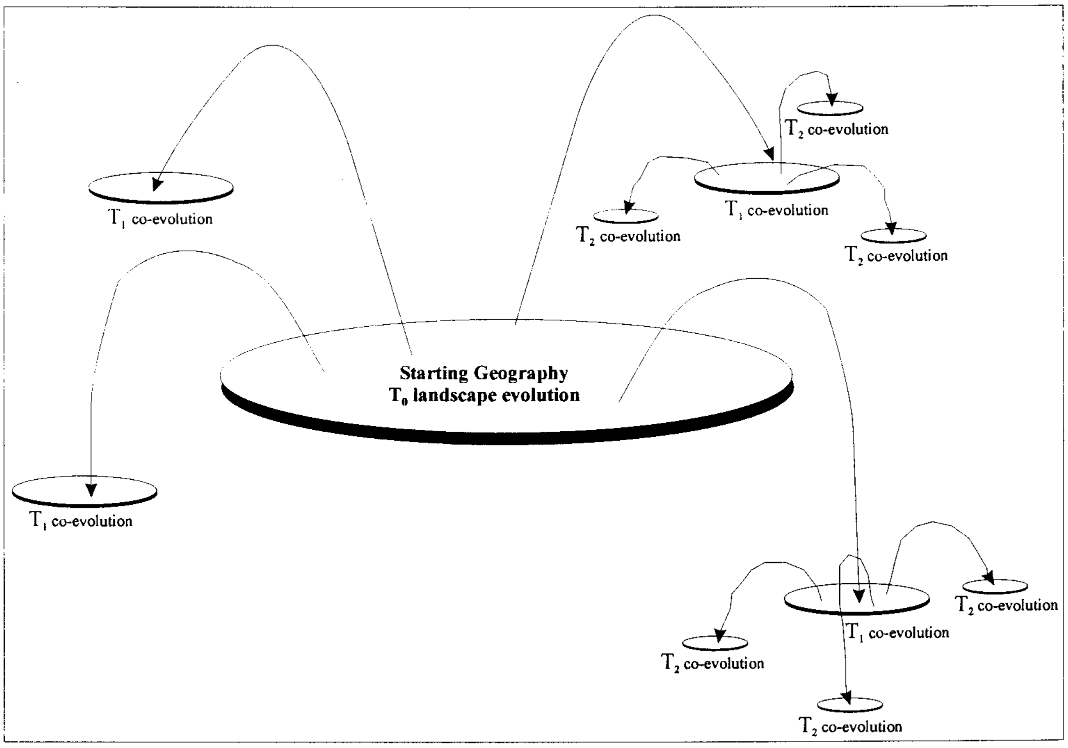

Figure 2.5: Conceptual diagram describing the process of co-evolution within landscapes.

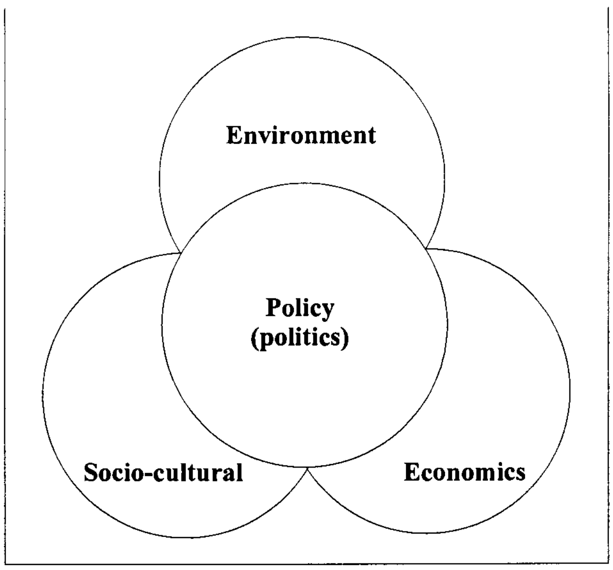

Figure 2.6: The interaction among the major sectors affecting sustainable development. Policy-political action oversees and drives decisions and actions taken in the other sectors.

Therefore, each landscape takes on unique characteristics particular to the non-random biological and cultural structuring occurring within the landscape mosaic. This reading of a landscape can provide us with a valuable framework for examining developing countries. Developing nations area able to illustrate co-evolution more clearly than technologically advanced nations (Norgaard, 1994). Information about the path a landscape or region has co-evolved along may let us interpret future actions. Future landscape paths could be assessed in terms of objectives such as sustaining biodiversity both in the unprotected landscape matrix and formally protected areas.

2.5 Landscape Ecology Principles to Ensure Sustainability

The real world is represented by finely fragmented habitats interwoven with human-altered environments. This is especially true in southern African landscapes where nomadism, colonialism and the ever rising human population have affected every part of the region in some way, shape or form (Puzo, 1978). The vast majority of biotic inhabitants that occur across the remnant pockets of the original environment are important. The species that can survive in the habitat fragments come together to determine the integrity and resilience of ecosystems to a range of environmental perturbations. In essence biodiversity loss has a direct impact on the ability of interdependent ecological-economic systems to maintain functionality, and thus in a policy sense, sustainability. In South Africa, for example, the vast majority of the natural landscape is fragmented by land-uses (Fairbanks et al., 2000), which presents logistical problems for conservation planners using species-based reserve selection designs (Lombard et al., 1997; Wessels et al., 2000). African conservation analysis frequently still maintains the false expectation that large pristine tracts of 'natural' habitat to support irreplaceable species will be available in seas of poverty (Western, 1989; Adams and McShane, 1996).

Landscape ecology has been broadly defined as the study of the effect of landscape pattern on ecological processes (Turner, 1989). In a clearer sense landscape ecology is the study of how landscape structure affects (the processes that determine) the abundance and distribution of organisms. The object of landscape ecology is not to describe landscapes, but to explain and understand the processes that occur within them. Certainly, the most challenging aspect is to extend this discipline to the analysis of pattern in a socio-economic context, given the need to find more sustainable forms of landscape management.

The application of the principles of landscape ecology in the formulation and solving of problems is of interest here. Human influences in landscapes tend to eliminate gradual changes and to produce abrupt boundaries, however the diversity of human cultural groups and their subsequent economic development levels based on a combination of policy, historical, and environmental factors effect landscapes and biotic diversity in a variant of ways. Landscape metrics employed to quantitatively measure the spatial patterns of boundaries and patches within a natural landscape (Turner, 1989) could be linked to socio-economic and cultural systems to assess the health of ecological systems (O'Neill, 1999; O'Neill et al., 1999) for biodiversity conservation.

The ecological structure, function, and potential change of landscape mosaics need to be understood within the socio-cultural and economic structures of a region to adequately address sustainable conservation action. The spatial arrangement of local ecosystem level components and land-uses within a landscape within a region will have an affect on the areas ecological integrity. To understand an area's conservation potential one must understand an areas current and future landscape function, but within human economic and social systems. Thus, landscapes should be perceived as the tangible matrix of the total human ecosystem (sensu Naveh, 1997), and therefore as concrete systems in their own right and not just as ecosystems on km-wide stretches.

2.5.1 Hierarchy, Scale, and Landscape Metrics

This argument to consider the evolution of human-ecosystem interactions within a complex, co-evolutionary context governed by metastable states, means that the resulting ecodynamics of pattern and process can be viewed from a hierarchical perspective (O'Neill et al., 1986). A key concept is that ecosystem processes operate over a wide spectrum of rates, and these can be assembled into discrete classes. The structure imposed by these differential rates allows the system to be decomposed into organizational levels, with each level being segregated on the basis of response times (i.e., higher levels associated with slower rates, and lower ones by more rapid rates). Within such a scheme, ecosystem structure is viewed as a series of weakly coupled sets within a hierarchy of process rates involving biotic interaction and abiotic factors. The non-linear couplings in these processes are further complicated by human action, whether as the result of un-coordinated stochastic events or by a series of policy-directed interventions (Giampietro, 1994).

Scale is critical, for as spatially heterogeneous areas, landscapes may exhibit stability at one spatial scale, but not at another. Thus, the scale at which observations are made profoundly influences the research and analytical interpretation process (Turner, 1989; Wiens, 1989b). In this case a variety of local and regional studies would be ultimately required to confidently provide conservation planning and management strategies.

Analysis of landscape pattern makes use of measurements of the connectedness, diversity, shape complexity, and size of land-cover patches to study ecological condition at local to regional scales (Turner and Gardner, 1991). These metrics (O'Neill et al., 1988; Ritters et al., 1995) have been used to assess landscape condition (Krummel et al., 1987; Wickham et al., 1999), infer ecological process from pattern (Milne, 1992; Fahrig, 1997), and show how landscape configuration can impose constraints on biological populations (Pearson et al., 1993; Flather, 1996; Flather and Sauer, 1996). From a regional perspective, land-cover patterns may be considered as either forcing or constraint functions for sub-regional dynamics, or as integral parts of strictly regional models (Allen and Starr, 1982). Information about land-cover patterns has proven useful for both local and regional assessments of ecological condition (Vos and Opdam, 1993).

Landscape metrics are a set of tools that can be used to measure pattern, which can be correlated to ecological processes, biodiversity persistence, and define 'spatial signatures' which describe the co-evolutionary response of landscapes (O'Neill et al., 1996; Wickham et al., 1996). Therefore, by using a monitoring framework to quantify spatial patterns and their changes (O'Neill et al., 1999) we can quantify their effect on ecological processes and then combine these indicators with biodiversity elements, socio-economic, and cultural information to provide a integrated conservation solution.

2.5.2. Measuring the Ecological Effects of Landscape Pattern

Physical location, transportation costs, social climate and policy often determine the profitability of an economic activity. In turn, economic activity is the primary determinant of landscape pattern and change, and therefore the resiliency of ecosystem function. Co-evolution of human-ecosystem dynamics develop positive feedback loops which enforces landscape pattern 'signatures.' This allows remotely sensed imagery, GIS, and landscape ecological metrics to be combined into a powerful approach for interrogation and interpretation of the pattern, which can then be back related to social, economic, and environmental indicators. For example, let us assume that we wish to evaluate the status of the landscape pattern for several defined co-evolutionary landscape regions. We could ask how far the present landscapes deviates from an ideal landscape for sustaining all hierarchical levels of species diversity with complete habitat cover (high dominance) in large (un-fragmented) and complex patches. We might also ask how far the landscape deviates from a total state of ecosystem decay with many human land-use and natural land-cover types (low dominance), in dissected (fragmented) and simple patches.

In statistical parlance, the 'response' variables in landscape ecology are abundance/distribution/local process variables, and the 'predictors' are variables that describe landscape structure. However, in order to understand present co-evolution from past interactions the 'responses' are variables that describe landscape structure, and the 'predictors' are the economic, socio-cultural, and environmental indicators. Gradient analysis may provide a promising analytical approach to understanding the effects of multiple stressors on ecosystem functioning (Whittaker, 1967; McDonnell and Pickett, 1993) by integrating the complexity of multiple stress effects across the landscape (McDonnell et al., 1995). The gradient approach relies on the assumption that graduated spatial environmental patterns govern the structure and functioning 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 monitored. 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

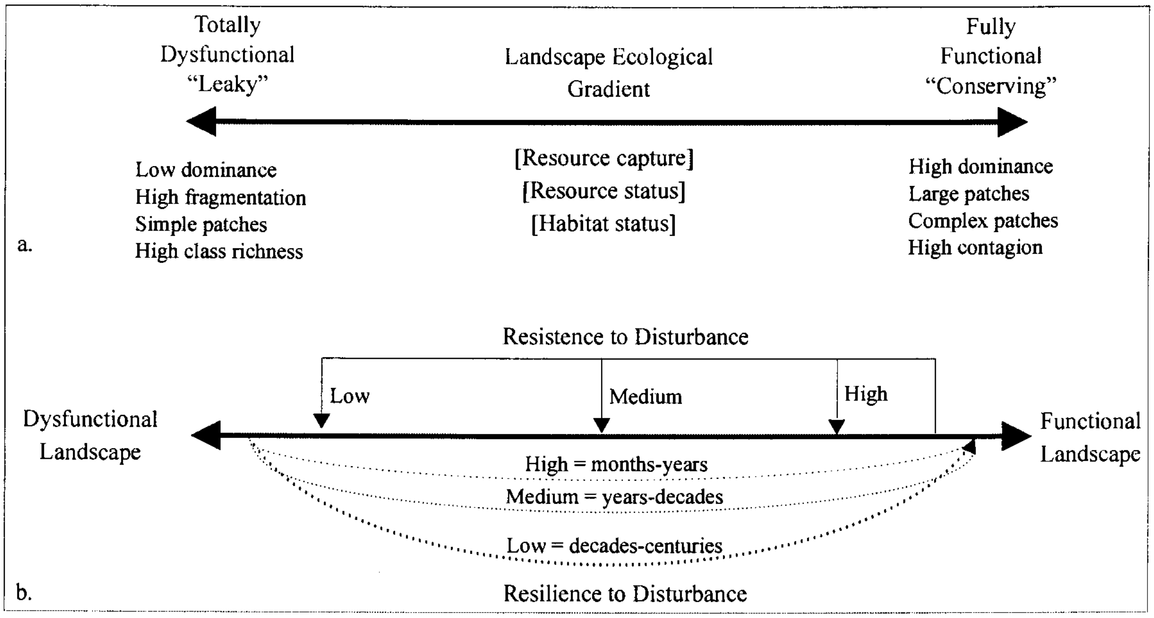

Figure 2.7: Landscape functionality as: (a) a continuum from functional to dysfunctional, and in relation to (b) resistance and resilience to disturbances (modified from Ludwig, 1999).

biotic responses to these gradients (ter Braak and Prentice, 1988; Jongman et al., 1995). Therefore, how well a landscape functions to conserve resources and maintain biodiversity could be viewed as a continuum (Figure 2.7a). Ludwig (1999) proposed a conceptual model that deemed landscapes as "fully functional" when they conserve resources to maintain rich and diverse environments that provide many habitats suitable for a high species richness. At the other end of the spectrum, a landscape may be very dysfunctional where all resources 'leak' from the system, resulting in a landscape with poor resources and no habitats suitable for species. The concept of stability (resistance and resilience) can then be applied to how disturbances affect landscape functionality. Resistance refers to the ability of the system to remain unchanged when disturbed, while resilience refers to the ability of the system to rapidly return to an assumed equilibrium state. Using these definitions (Figure 2.7b), a landscape has low resistance if a disturbance causes a highly functional system to become dysfunctional. A landscape with high resistance will only slightly shift down the continuum under the impact of the same disturbance. Highly resilient landscapes will rapidly recover, for example, in a matter of months or a few years, to a displacement down the continuum caused by a disturbance. Landscapes with low resilience may take centuries to recover from this same disturbance. This conceptual model could show promise in being able to assess various landscape environments and the drivers that have 'pushed' them into different 'states' or pathways (McIntyre and Hobbs, 1999).

2.6 Socio-Ecosystem Interaction

Following on the argument developed so far, this chapter proposes an enhancement of the theoretical framework for biodiversity conservation planning by integrating both anthropogenic and ecosystem integrity goals into a decision framework guided by co-evolutionary theory and landscape ecology methods. The basic principle encompasses a larger approach to biodiversity protection, by protecting levels of biodiversity linked by process and spatial organization. This is the underlying concept for integrated approaches to the management of land resources (e.g., Noss, 1990). The implementation of landscape level plans in routine environmental policy and planning is complex, but if we understand that environmental change is a co-evolutionary process that acknowledges pluralistic systems then suitable frameworks can be developed for protecting biodiversity based on each regions particular issues rather than on a general model.

In studies of the causes and consequences of tropical deforestation in Rondonia, Brazil, Southworth et al. (1991) and Dale et al. (1993; 1994) indirectly developed a co-evolutionary model. The authors acknowledged land-use change as one of the major factors affecting global environmental conditions and that to address the problem, spatially combined explicit ecological information and socio-economic factors. This aspect is particularly needed within developing countries. In Figure 2.8, a framework is presented for developing a methodology that integrates the idea of co-evolution by addressing the state of human social and economic welfare, the biodiversity profile and the landscape ecological attributes of a defined region. Ethical stewardship of the environment requires that society monitor and assess environmental change at the national scale with a view toward the conservation and wise management at the local scale (O'Neill et al., 1997; O'Neill et al., 1999). Most social and economic indicators are measured at regional levels, while some of the most important environmental and social changes occur at a landscape scale (e.g., Forman, 1995). The landscape scale is important because political decisions to manage natural resources are made at broad scales, such as catchments. Decisions about how to change land cover may be made by individual landowners, but their impacts are seen cumulatively, as a change in spatial pattern on the landscape. These decisions are usually also a reflection of global, national and regional policy, economic or social situations that draw attention to a hierarchical reading of these co-evolutionary systems. Resulting data from 'representative' reporting zones (e.g., political districts, catchments, etc.) of economic, socio-cultural and environment- reflecting the true state of society and nature- are recorded and analyzed hierarchically (Figure 2.8) within some defined multidimensional data reduction method.

For example, in sub-Saharan Africa women and children invest enormous energy in obtaining domestic energy from fuelwood and herding cattle. Dasgupta (1993) has described the complexities of interactions among population growth, poverty, and environmental deterioration. Men are typically part of a migratory labor system whereby they leave the rural tribal areas for temporary work on the mines and in industry. Monies are sent back to their wives for food and cattle purchase, which is equated as wealth accumulation (Hall, 1987). As the human and cattle population grows in these areas grazing range is placed under greater pressure leading to land degradation. An examination of KwaZulu-Natal, South Africa illustrates this pattern noted by Dasgupta (1993) and Ehrlich et al., (1995) whereas areas of low male to female population ratios in developing countries have a higher percentage of degraded land (Figure 2.9). In KwaZulu-Natal this can be depicted as a systems model (Figure 2.10), which has been documented historically (Cole, 1960) and linked anthropologically (Hall, 1987). Therefore, along with economic geography models, culture should also be assigned a central role in any theory

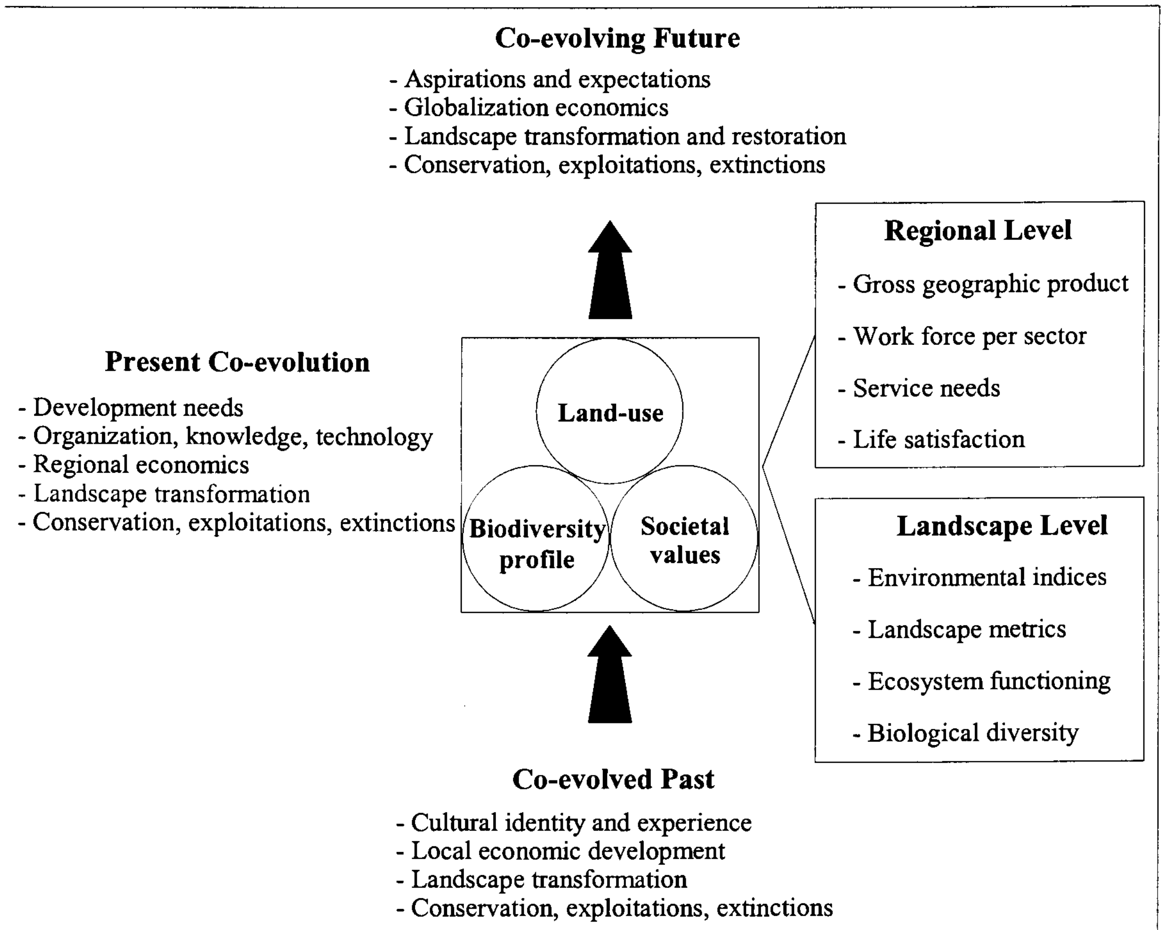

Figure 2.8: An overview of the hierarchical indicator reading framework for analysing co-evolutionary dynamics.

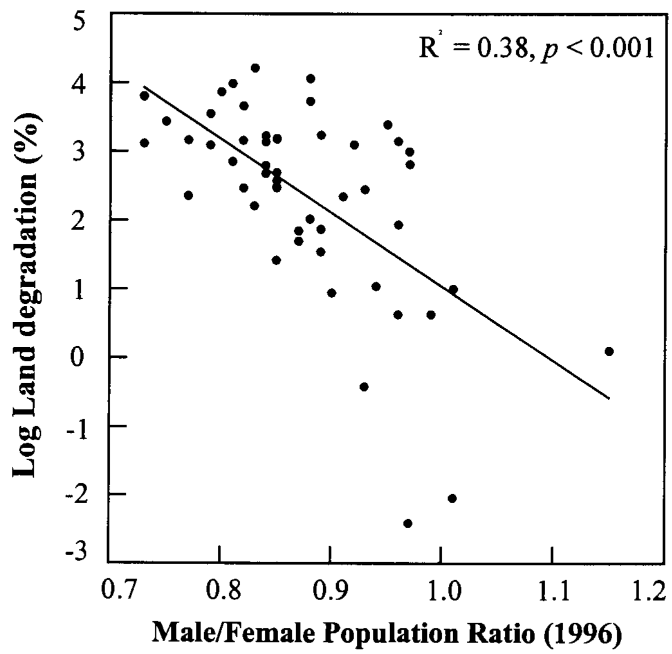

Figure 2.9: Linear regression relationship of male/female population ratio to percentage degraded land per magisterial district in KwaZulu-Natal (N=52). Human population data from 1996 census and land degradation assessment from the South African National Land-cover Database (Fairbanks et al., 2000).

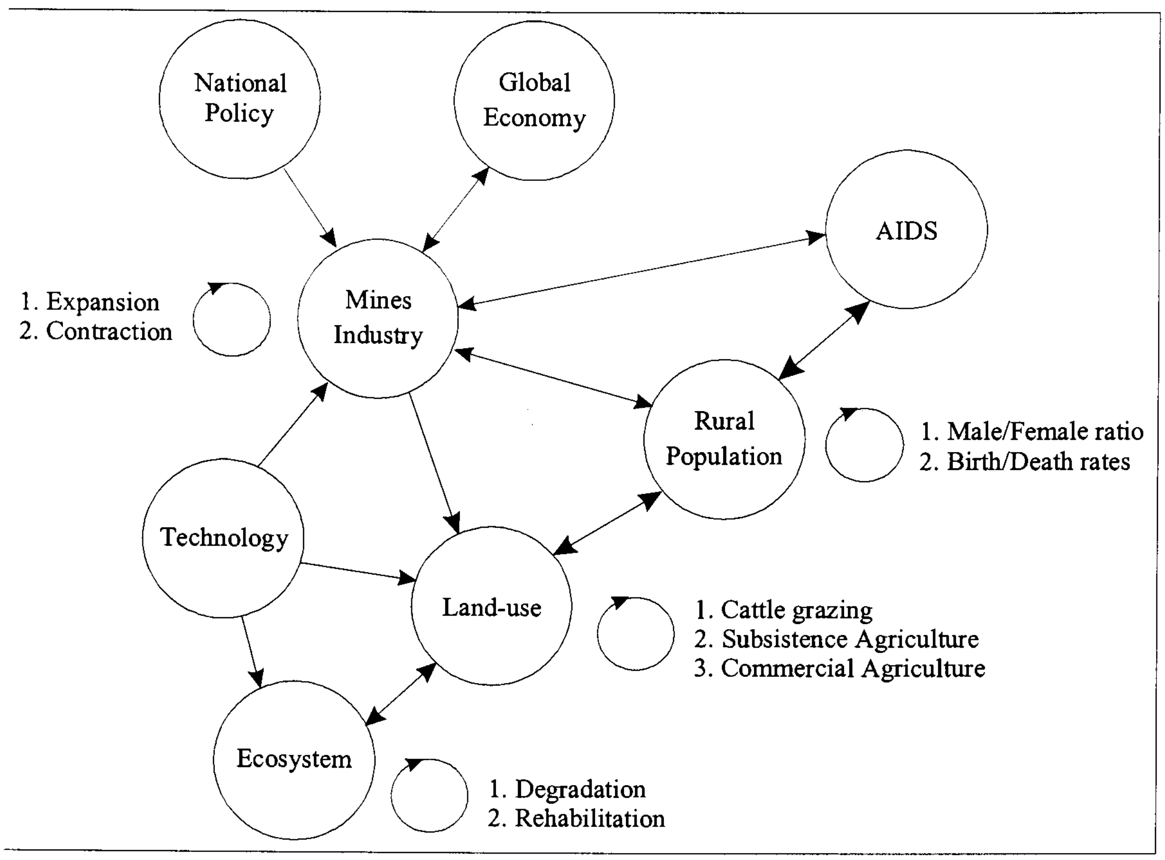

Figure 2.10: Economic core and poor rural periphery systems model of landscape development within rural African communities in South Africa.

purporting to characterize the process of land-use intensification and landscape pattern development among rural African communities.

2.7 Co-evolutionary Implications for Sustainable Biodiversity Conservation

The primary implication of the foregoing discussion is the need for a conceptual retooling and use of multiple analytical methods if we are to come to a more complete understanding of the future development of human-ecosystem interactions on biodiversity conservation. The proposed framework fundamentally changes our ideas with respect to evolution, human-ecosystem interactions and long-term predictability. This argument also draws attention to how much deeper an understanding can be made of developing nations through transdisciplinary research and shared learning.

The implications of the role of non-linear phenomena in generating long-term dynamics is a pre-requisite for understanding the evolutionary processes which structures landscapes and subsequent biodiversity loss. This type of thinking effectively renders evolutionary models which support linear, simple trajectories redundant (see Turner et al., 1996; Wear et al., 1996), stressing the fact that human-ecosystem dynamics within landscapes seen as long-term history can more usefully be conceptualized as a series of transformations of structuring and restructuring over time. Essentially, if human-ecological systems are prone to complex co-evolutionary pathways and the kind of 'structured disorder' associated with chaos, then this has significant consequences for biodiversity conservation and general land management policy decisions (e.g., Holling, 1986).

In developing countries simple systematic conservation planning may fall short in informing conservation planners and policy makers as to the future persistence of ecosystems, landscapes, and species populations. A new model of co-evolutionary landscapes incorporating social, cultural, economic, as well as environmental indicators (species, habitats, landscapes, landscape metrics) is needed to understand and develop conservation management plans which incorporate the goal of persistence (sustainable biodiversity). Although preserving biodiversity through formal protected areas is an important short-term step, it will not be sufficient to solve the problem of biodiversity loss (Western, 1989; Shafer, 1994). Reserves are embedded within the larger environment, and most reserves alone cannot deal with ecological attributes that cover larger scales (e.g., broad climate, global climate change). Thus, conservation efforts should firstly be planned at the scale of the regional landscape to assess the available landscape matrix of 'natural' fragments. Small reserves will lose their distinctive species if they are surrounded by a hostile landscape (Askins, 1995; Baillie et al., 2000). Reserves, as islands in a sea of change driven by interconnected economic and social systems, may not be a basis for sustainable biodiversity conservation.

Moving toward a model of a co-evolving patchwork quilt of discursive communities conceptually presents social systems as systems against a responsive environmental backdrop. These landscapes will change over time through mergers and divisions as the social and environmental systems co-evolve. The strategy is to use the available social, economic and environmental data in an analytical framework that helps promote sustainable landscape and regional social, economic and environmental systems.

Conservation International (1998) revealed that just seventeen nations collectively claim more than two-thirds of all known species worldwide, making conservation efforts in these 'megadiversity' countries essential for the survival of Earth's natural heritage. Not surprisingly, fifteen of the countries singled out are considered developing. These countries are also home to a major portion of the planet's cultural diversity, perhaps even a larger percentage than for biodiversity. Positive human welfare is directly related to sustainability of the environment and is the critical link in the chain towards a comprehensive conservation (persistence) goal. It should be apparent, that human welfare has to be met at the same time as biodiversity conservation, for they are not mutually exclusive.

3. Identifying Regional Landscapes for Conservation Planning

Landscape ecology has made a significant contribution to conservation biology (Noss, 1983; Noss, 1990; Hansson and Angelstam, 1991; Forman, 1995). However, much of the landscape ecological research that investigates biological conservation problems has not occurred within appropriately defined landscapes, rather relying on arbitrary ecoregion delimitations (as discussed Host et al., 1996; Wright et al., 1998). For planning purposes, a representative landscape approach to conservation could potentially be used as a spatial surrogate to ensure the long-term maintenance of biodiversity. The maintenance of processes that sustain ecosystem structure and functioning is essential for achieving persistence goals for systems of conservation areas (Baker, 1992; Noss, 1996). If a landscape approach to conservation biology is to be effective, the landscape units need to be properly defined. At present, the only ecologically defined system that exists within South Africa is for the Kruger National Park (Gertenbach, 1983). This is understandable considering the relatively recent international emergence of landscape ecology as a discipline (Wiens, 1992), the importance placed on species systematics and inventorying in southern Africa (Huntley, 1989), and the emphasis placed on poorly sampled species databases for reserve selection (e.g., Rebelo and Siegfried, 1990; Lombard, 1995; Freitag and van Jaarsveld, 1997). The first step in developing a successful landscape level conservation plan is identifying and locating the landscapes of a region.

The goals and objectives of environmental management frequently require the classification of regions based on measurable environmental characteristics. Delineation of ecological landscapes is useful in a variety of contexts, for example, in the assessment of the regional representation of conservation areas (Margules et al., 1988; Bedward et al., 1992; Franklin, 1993; Pressey et al., 1994), defining zones for sustainable ecological management (Forman, 1995), and as a framework for assessing the diversity of species and processes within landscapes (Lapin and Barnes, 1995).

An ecological framework that can integrate multiple environmental characteristics diminishes problems of duplication among government land resource agencies, and it can assist in the exchange of information and research results. Towards this end, the utility of ecoregional classifications, developed for the conterminous United States (Omernik, 1987; Gallant et al., 1995; Omernik, 1995) and Canada (Wiken, 1986), have been successfully demonstrated (e.g., U.S. Environmental Protection Agency: Environmental Monitoring and Assessment Program).

There are two broad approaches to classifying landscapes: human landscape-based classification approaches mainly applied in European countries (Blankson and Green, 1991;

Green et al., 1996), and biophysical approaches (Christian and Stewart, 1953; De Agar et al., 1995; Bailey, 1996; Bernert et al., 1997) which combine climate, soils, vegetation and landform into observable and definable land units (e.g., Omernik, 1987). Methods vary from visual assessments using elements like scenery, to quantitative procedures, which group areas with similar values for a set of mapped variables (Benefield and Bunce, 1982; Blankson and Green, 1991; Host et al., 1996; Bernert et al., 1997). These methods are not completely objective, as variables for consideration have to be chosen, but are less judgmental than visual methods.

We used the biophysical approach, because the aim was to identify natural landscapes and then assess their conservation status by examining both the degree of protection and the amount of human-induced transformation that has occurred. This study presents a landscape classification system for the province of KwaZulu-Natal (South Africa) by using biophysical data and a combination of principal component analysis, clustering and spatial overlay techniques. A preliminary analysis is also undertaken to illustrate the important role that this kind of information can and should play in identifying conservation worthy areas.

3.1 Methods

3.1.1 Explanatory variables

The variables used were those commonly used in the description of ecological regions (Omernik, 1987; Omernik, 1995; Bailey, 1996). The set of variables was broad, and included those describing the physical (topography, landform, geology and climate) and biological environments (vegetation) and was integrated into a geographic information system (GIS). Only the topography, landform and climate variables were used in the classification analysis, the geologic and vegetation maps were not used directly in the demarcation of landscapes (as proposed by Omernik, 1987; Bailey, 1996). Rather, they are used to derive a typology of attributes within the landscapes that allows the landscapes to be described according to the vegetation types and geological substrates found in each unit. This adds considerably to the conservation planning objective by not subjectively combining the unit boundaries of vegetation and geology with landscapes to create arbitrary units (Host et al., 1996) and thus mask the landscape heterogeneity into a coarser ecoregional unit (Wright et al., 1998).

3.1.2 Approach

A systematic approach was developed for delineating landscapes (Figure 3.1) within the KwaZulu-Natal province that could be applied to any geographical region. To prevent landscapes

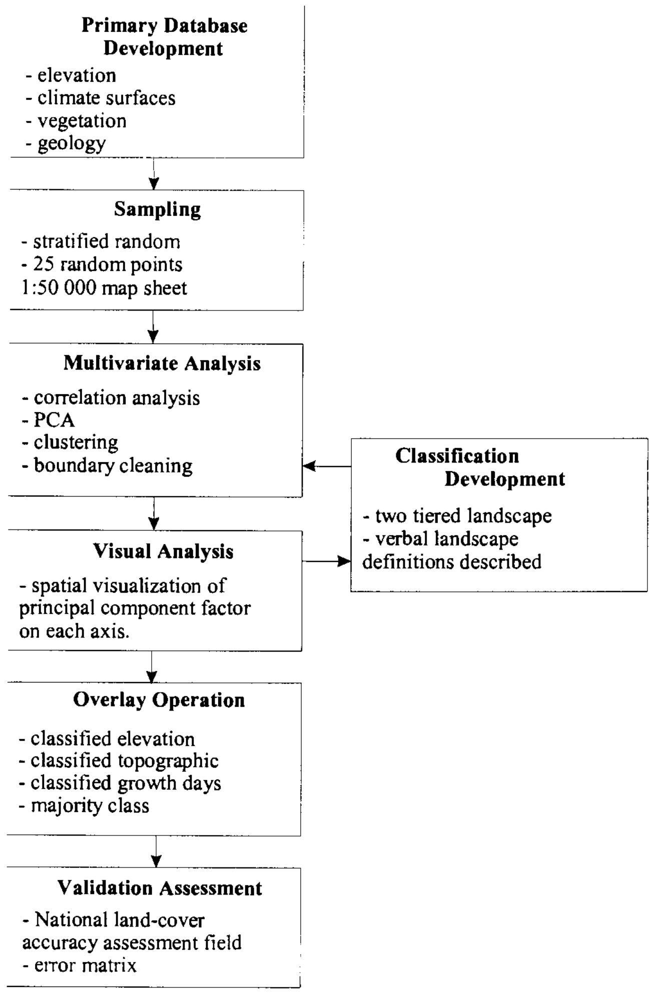

Figure 3.1: Analysis framework used to classify and identify the landscapes.

occurring along the KwaZulu-Natal border from being defined by arbitrary political boundaries, the study area was extended across the borders using catchment boundaries (DWAF, 1996). This overlap will also allow for easier edge-matching of future landscape classifications developed by neighboring provinces.

The analysis was raster grid cell based. The analysis cell size was partly determined by the largest cell size of the already rasterised data sets and a logical cell size for future integrative work, in this instance 1 km^2. All data sets were converted to Lamberts Azimuthal Equal-Area projection for analysis. To reduce the amount of data to be analysed, a stratified random sampling of data sets was conducted. The 165 South African Surveyor General 1:50 000 map sheets covering KwaZulu-Natal were used to stratify a random sample selection, with 25 cells being chosen from each sheet (i.e., a total of 4675 samples).

Pearson correlation coefficients were used to examine multicolinearity and thus minimise the duplication of variable information, and make decisions with regard to variables being recorded in the field. Principal component analysis (PCA) was performed on the resulting variables, which allows the important descriptors to be standardized against each other for interpretation into spatial objects (see Legendre and Legendre, 1998).

Pattern and cluster analysis was undertaken on the PCA results in ArcView GIS (ESRI, 1998) using bivariate map plots of the axes factor scores produced by the PCA analyses and then applying a natural breaks clustering classification technique. This method identifies breakpoints by looking for groupings and patterns inherent in the data using Jenk's optimization, which minimizes the variation within each class (Jenks, 1963). Using these techniques the data sets responsible for the greatest amount of variation, as identified by the PCA, were classified. The classified data sets were then subjected to class boundary cleaning by smoothing transitions between classes. This procedure removes class border roughness which is caused by inaccuracies in the coarse resolution data (ESRI, 1998).

Landscapes were constructed by combining the classified terrain and climatic data sets in a stepwise manner using Arc/Info GRID GIS (ESRI, 1998), and smoothing the intermediate derived data sets with a 3x3 grid cell neighborhood majority class filter. This transformation reassigned pixel values based on the most prevalent class membership within a 3x3 grid cell moving window. Scarpace et al. (1981) found that majority filtering actually increased classification accuracy by reducing 'random' noise in classification results. When applying this method over large regions the errors average out, so the landscape estimates are probably quite accurate even if the cell by cell estimates may be less accurate.

A validation exercise was performed using the South African National Land-Cover Database accuracy assessment points (Fairbanks and Thompson, 1996). The overall accuracy of the landscape classification map was tested using 530 stratified random field locations. Actual class membership for the sample locations was assigned on majority area coverage of a class within a cell. A combination of using the extra attributes collected in the field (e.g., topography, position, and vegetation) per point and inspection of the fixed ground photography of the area around a point was used to determine actual landscape class membership. This helped to ensure that the derived landscape types were recognisable ecological units for conservation analysis and planning.

3.1.2.1 Landscape Conservation Analysis

A crucial consideration in maximizing the protection of biodiversity is the assignment of priorities for protection in the face of real-world constraints (Pressey et al., 1996). The concepts of irreplaceability (Pressey et al., 1994) and vulnerability (Pressey et al., 1996) were developed to explicitly define conservation value and priority for representative areas. In its simplest form, irreplaceability is a measure of the likelihood that an area will be needed to achieve a conservation goal; vulnerability is a measure of the imminence or likelihood of the biodiversity in an area being lost to current or impending threatening processes. Thus, irreplaceability is a measure of conservation value whereas conservation priority is the value of an area combined with some assessment of the urgency with which it should be conserved (Pressey, 1997). Areas of high irreplaceability and high vulnerability are highest priorities for conservation action (Pressey et al., 1996). Focusing conservation resources on such areas will maximize the extent to which representation goals will be achieved on the ground.

To demonstrate the value the landscapes add to the analysis of conservation goals, by helping identification of conservation worthy regions, we conducted an analysis of the derived landscapes with the South African National Land-Cover database (Fairbanks and Thompson, 1996; Fairbanks et al., 2000) and a protected area database for KwaZulu-Natal. The land-cover database contains spatial information on natural land-cover and identifiable human land-use mapped from Landsat TM imagery at 1:250 000 scale (Fairbanks et al., 2000). The land-use classes are essentially a measure of transformation status in the context of threats to biodiversity. The protected area database described the boundaries of provincial reserves, digitized from 1:50 000 maps.

The land-cover data was used to assess the vulnerability of the landscapes to future human transformation based on the diversity of land-uses in each landscape. The rationale being that landscape types with several land uses are more vulnerable to future transformation than areas of single land uses because of their unique and favorable environment (e.g. available positive water balance and heat units) to a variety of human development potential (this will, however, depend on the available land cover classes being transformed). The level of irreplaceability was determined using a linear weighted combination of the extent of transformation, representation in protected areas, and rarity (measured as the relative areal contribution of each class):

$$\text{Irreplaceability} = \textstyle\sum_3 (\text{Rarity*weight}) + (\text{Transformation*weight}) + (\text{Representation*weight})$$

The classification of the measures was derived using the natural breaks classification technique (Jenks, 1963). The vulnerability and irreplaceability scores were scaled from 0-100% as calculated from classifications and weights (Table 3.1) as defined by KwaZulu-Natal Nature Conservation Services (KZNNCS).

Table 3.1: Landscape rarity, transformation, and protection classification rules based on frequency classification with accompanying importance ratings.

% of Total (Rarity)	Weights	% Transformed	Weights	% Protected	Weights
< 1.7%	1	> 50%	1	< 10%	1
1.7 - 5%	0.75	34 - 50%	0.75	10 - 25%	0.66
5 - 7.6%	0.5	18 - 34%	0.50	> 25%	0.33
> 7.6%	0.25	< 18%	0.25		

3.2 Results

3.2.1 Landscape Classification

Median minimum rainfall for driest and wettest quarters, growth temperature, mean annual temperature, mean maximum temperature for January, and mean minimum temperature for July were highly correlated ($r > 0.50$; $p < 0.05$) with elevation (Table 3.2) and were dropped from further analysis. Elevation alone is a good predictor of orographic precipitation and temperature gradients. Similarly, median annual precipitation was highly correlated with growth days ($r > 0.50$; $p < 0.05$) and was dropped from further analysis (Table 3.2). Growth days have been found to be a better predictor of water balance for determining the effectiveness of rainfall for biomass production in southern Africa (Ellery et al., 1992; Fairbanks, 2000).

The PCA results (Table 3.3) showed that the elevation model accounted for most of the variation, and therefore the primary gradient for the region, on axis one (0.84), similarly for the topographical landform index on axis two (0.975) and growth days on axis three (0.966). These three variables were therefore used for construction of the landscapes and the topographic heterogeneity variable was dropped from any further analysis. By using local a priori knowledge, visual interpretation and examination of the ordering of the factor scores on each axis with the clustering technique we determined elevation could be meaningfully classified into two hierarchical levels of ten detailed and four coarse classes (Table 3.4). The topographic landform index was retained at seven classes and lumped to two classes at a coarser level (Table 3.4). The growth days index was reclassified into 30 and 60 day ranges to produce a six level and three level hierarchical classification (Table 3.4).

Table 3.2: Pearson correlation matrix for environmental variables used in landscape classification (n = 4675). Correlations highlighted in bold violate the $r > 0.50$ multicolinearity limit defined for this study. †

	demsd	dem	tli	dm	wm	mdp	gd	gt	mat	maxj	minj
demsd	1.0	0.37	0.03	-0.13	**0.50**	0.35	0.36	-0.43	-0.39	-0.43	-0.26
dem		1.0	0.19	**-0.52**	**0.70**	0.22	0.31	**-0.94**	**-0.98**	**-0.84**	**-0.92**
tli			1.0	0.01	0.05	0.06	0.05	-0.08	-0.05	-0.10	0.05
dm				1.0	-0.04	**0.53**	0.49	0.28	0.43	0.17	**0.63**
wm					1.0	**0.79**	**0.78**	**-0.74**	**-0.72**	**-0.73**	**-0.55**
mdp						1.0	**0.91**	-0.38	-0.27	-0.45	-0.02
gd							1.0	**-0.56**	-0.43	**-0.67**	-0.12
gt								1.0	**0.98**	**0.97**	**0.82**
mat									1.0	**0.91**	**0.91**
maxj										1.0	**0.67**
minj											1.0

†Variable names: topographic heterogeneity (demsd); elevation (dem); topographic landform index (tli); driest quarter precipitation (dm); wettest quarter precipiation (wm); median annual precipitation (mdp); growth days (gd); growth temperature (gt); mean annual temperature (mat); mean maximum temperature January (maxj); mean minimum temperature July (minj).

Table 3.3: Factor weights, eigenvalues, and total variance explained derived by the PCA analysis on the chosen topographic and climatic variables. Values in bold denote the significant variable identified for each axis.

Variables†	Axis 1	Axis 2	Axis 3
DEMSD	0.77	-0.15	0.30
DEM	**0.84**	0.25	0.06
GD	0.21	0.04	**0.97**
TLI	0.06	**0.97**	0.03
Eigenvalue	1.34	1.03	1.02
Total Variance Explained (%)	43.46	25.28	16.63

†Variable names: topographic heterogeneity (demsd); elevation (dem); topographic landform index (tli); growth days (gd).

The first data combination involved the overlaying of the detailed level I elevation classification with the level I topographical landform index classification producing 20 unique combinatorial classes from the input data. All combinations of classes potentially could have yielded 70 unique classes, but in this case, only 20 unique elevation-landform types were derived. This combination was then overlaid with the level I growth days index. The combined data set derived 104 classes out of a potential 120, but several classes were shown to be small and spurious in nature (≤ 3 grid cells). The majority class filter was processed over the data surface and a final 97 class landscape map was produced. These 97 classes represent the landscapes of KwaZulu-Natal at the highest level of detail by being derived from the level I classification hierarchies of the input data. The 97 classes were then hierarchically collapsed to the coarser 24 class landscape level II classification for ease of use and illustration (Figure 3.2).

Table 3.4: Elevation, topographic landform index and growth days index classification hierarchies.

Elevation range (m) from PCA axis 1	Level I	Level II
0 - 162	Coastal plain	Coastal
162 - 352	Coastal hinterland	Coastal
352 - 558	Lowlands	Lowlands
558 - 754	Mid-lowlands	Lowlands
754 - 948	Upper lowlands	Lowlands
948 - 1138	Low highlands	Highlands
1138 - 1353	Mid-highlands	Highlands
1353 - 1610	Upper highlands	Highlands
1610 - 1986	Low Afromontane/Escarpment plateau	Afromontane
1986 - 3484	Upper Afromontane/Lesotho Alpine	Afromontane
Topographic landform index		
	Level/flat	Undulating/flat
	Valley	Undulating/flat
	Foot slope	Mountainous/hilly
	Mid-slope	Mountainous/hilly
	Upper slope	Mountainous/hilly
	Scarp	Mountainous/hilly
	Ridge/crest	Mountainous/hilly
Growth Days ranges (days)		
60 - 90	Dry	Dry
90 - 120	Moderately dry	Dry
120 - 150	Moderately moist	Moist
150 - 180	Moist	Moist
180 - 210	Wet	Wet
210 - 247	Very wet	Wet

3.2.2 Validation

The coarser Level II landscape classification was analysed using conventional error matrices for predicted versus actual class membership at field checked locations. Three summary statistics, percent correctly classified (PCC), 95% confidence limits and the Kappa statistic, were generated from the matrix for comparing the performance of the landscape model. PCC provides an intuitive measure of classification accuracy. The Kappa statistic is a measure of overall agreement based on discrete multivariate analysis described by Bishop et al. (1975), which has been promoted for use in the remote sensing community (Congalton et al., 1983; Foody, 1992).

Overall the level II landscape classification accuracy is good at 86.8% PCC (83.8 - 89.7% at 95% confidence), considering the coarse data resolution, with predictable confusions along landscape borders and within areas where the coarse data were not able to describe local structural anomalies. The Kappa statistic implies that our classification is 85.3% better than the accuracy that would result from a random class assignment. This means that a high repeatability of the same classification results could be acquired by another knowledgeable analyst using

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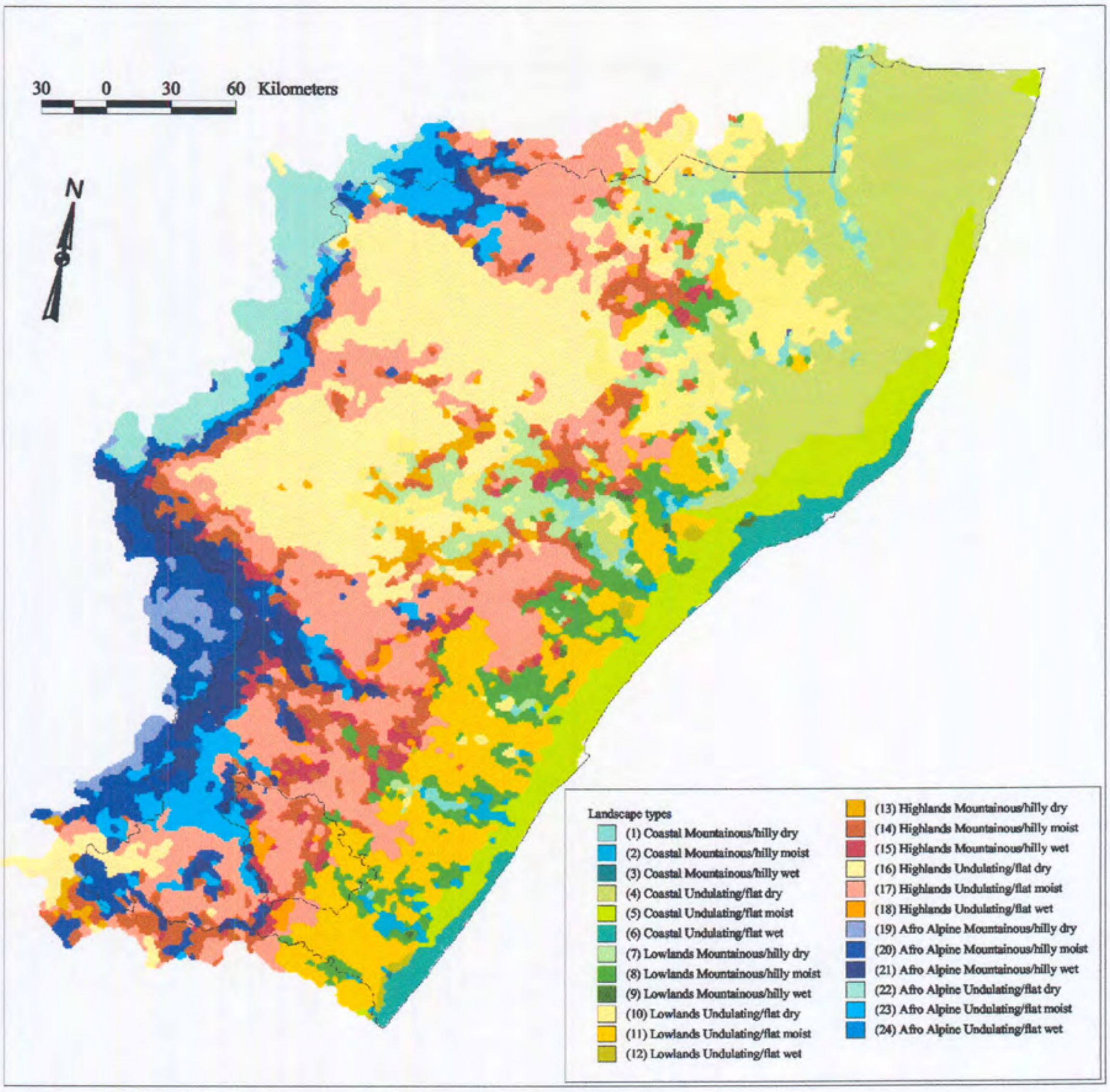

Figure 3.2: Landscape classification (Level II; 24 classes) of KwaZulu-Natal Province, South Africa.

our methodology and having local *a priori* knowledge.

3.2.3 Landscape Conservation Analysis

Landscape rarity, current transformation status, and current protection provided by conservation authorities are presented in Table 3.5. Figure 3.3 illustrates the current human-induced transformation status on the level II landscapes. The majority of the transformation has taken place in the coastal and highland regions. Figure 3.4 demonstrates the bias the provincial protected area network managed by KZNNCS has in its protection of landscapes versus the landscape vulnerability status. In this case, the Maputaland coastal region and the Drakensberg

Table 3.5: Calculations of percent rarity, current transformation percentage and percent protected in managed nature reserves. The legend for the landscape numbers is given in Figure 3.2.

Level II	% of Total	% Transformed	% Protected
1	1.2	24.2	4.2
2	0.6	0.2	1.0
3	0.01	25.2	0.0
4	12.7	29.9	13.3
5	5.9	62.5	13.9
6	1.7	50.0	5.8
7	4.1	21.2	6.3
8	4.0	30.0	0.5
9	0.1	39.3	1.4
10	6.2	34.2	1.5
11	7.6	52.9	1.5
12	0.2	66.1	0.0
13	1.4	18.6	0.7
14	6.7	25.1	2.0
15	1.6	33.1	10.9
16	13.9	30.8	0.8
17	15.0	40.3	0.9
18	0.4	56.2	1.9
19	1.6	34.6	14.8
20	5.1	12.5	20.2
21	3.0	2.5	51.7
22	3.3	11.9	2.6
23	3.7	12.5	4.1
24	0.2	8.2	7.8

Escarpment are well conserved (areas with Malaria and high rocky areas), but the landscapes denoting the lowlands and highlands (highly valued agricultural lands) are severely under protected. This illustrates a much noted paradox in conservation's history: pieces of land have been put aside in an *ad hoc* manner, often on economically marginal land or to conserve a few charismatic species (Pressey, 1994).

Irreplaceability and vulnerability (Figure 3.5) reveal the landscapes with high values for both as areas of high priority for conservation action. The majority of these areas have undulating/flat terrain with moist-wet climates in the coastal, lowland, and highland regions (e.g. 5, 6, 12, 17, and 18). These priority landscapes are dominated by mixed woodland and upland grassland ecosystems (Table 3.6), which are habitats considered in serious threat to development throughout South Africa (Fairbanks et al., 2000). By using the modest IUCN protection rule of 10% minimum area and a hypothetical division of vulnerability status at 50% (see Figure 3.4), only three landscape types (4, 5, and 15) are minimally protected with greater than 50% vulnerability (Figure 3.6). In the case of landscape type five, which lies along a north-south coastal gradient, only the far northern section receives adequate protection. By using a combination of analytical graphs and spatially plotting these results, landscapes like type five can be identified by their skew

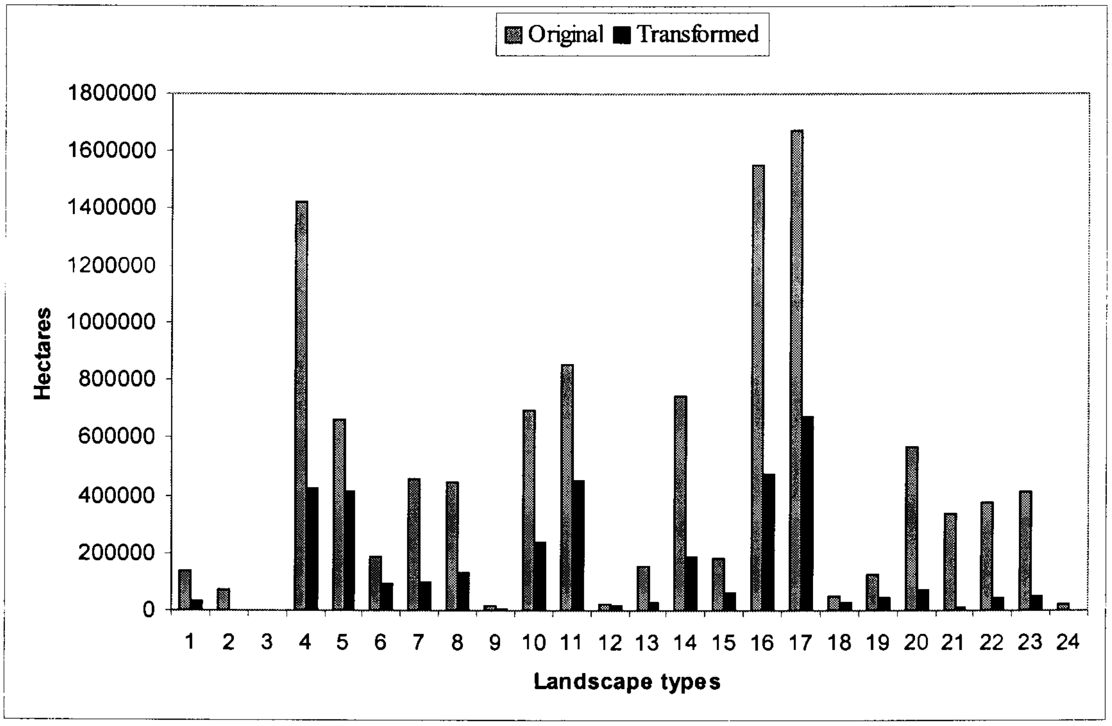

Figure 3.3: Preliminary assessment of the level of transformation within the second level landscapes relative to their areal coverage (see Figure 3.2 for number code descriptions).

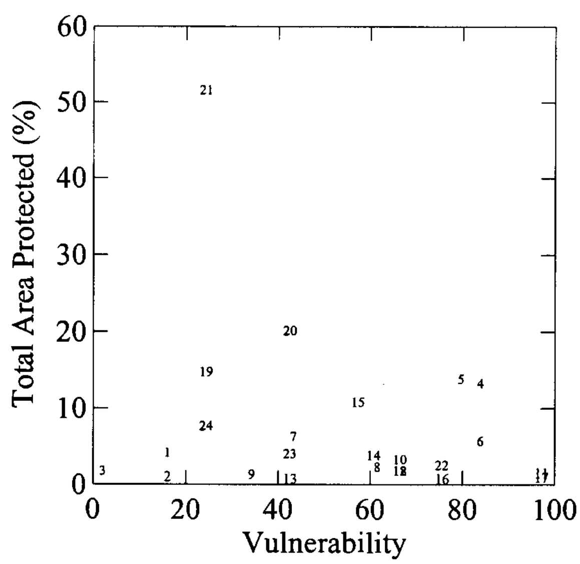

Figure 3.4: Scatter plot of current protection status vs. vulnerability for each landscape type (see Figure 3.2 for number code descriptions).

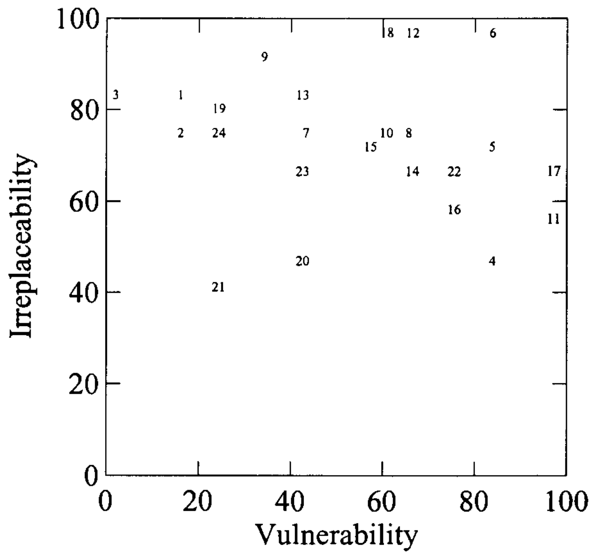

Figure 3.5: Preliminary scores for irreplaceability (conservation value) and vulnerability to threatening processes for the landscapes. Landscape types in the upper right-hand corner are conservation priorities (see Figure 3.2 for number code descriptions).

Table 3.6: The values represent the percentage of each level II landscape type that is comprised of each functional vegetation type. Values in bold represent vegetation types with >10% affiliated area with level II landscape types.

Level II	Forest†	Arid Woodland	Moist Woodland	Mixed Woodland	Thicket	Upland Grassland	Highland Grassland
1	0.5	**47.3**	0.3	**26.9**	**24.2**	0.0	0.8
2	1.7	0.0	**31.7**	**37.0**	**25.6**	3.9	0.0
3	**12.5**	0.0	0.0	0.00	0.0	**87.5**	0.0
4	0.9	**62.7**	**26.2**	7.2	2.8	0.0	0.1
5	1.9	0.0	**76.9**	**10.3**	**10.6**	0.2	0.0
6	3.6	0.0	**88.0**	1.0	2.7	4.7	0.0
7	0.2	**32.0**	0.0	**26.9**	**23.5**	4.6	**12.8**
8	1.2	5.5	5.4	**43.6**	**28.9**	**12.0**	3.4
9	**27.6**	0.0	5.3	**37.6**	8.8	**20.6**	0.0
10	0.0	**33.3**	0.0	**38.4**	**11.2**	2.7	**14.3**
11	0.7	1.7	5.3	**44.6**	**20.6**	**22.5**	4.5
12	3.3	0.0	9.5	**49.2**	4.1	**33.9**	0.0
13	0.0	2.1	0.0	**41.7**	**21.7**	**17.6**	**16.8**
14	1.1	2.2	0.0	**22.4**	4.6	**36.4**	**33.4**
15	8.0	1.3	0.0	7.9	2.8	**61.1**	**18.9**
16	0.1	1.3	0.0	**66.1**	4.9	8.5	**19.1**
17	0.4	1.2	0.0	**13.9**	1.1	**46.2**	**37.2**
18	2.4	2.6	0.0	1.0	1.8	**86.9**	5.4
19	0.1	0.0	0.0	0.0	0.0	0.8	**99.1**
20	0.4	0.1	0.0	1.5	0.0	**28.2**	**69.7**
21	2.2	0.7	0.0	0.0	0.0	**34.6**	**62.5**
22	0.1	0.0	0.0	0.0	0.0	0.1	**99.8**
23	0.8	0.0	0.0	0.9	0.0	**45.0**	**53.3**
24	1.8	0.0	0.0	0.0	0.0	**79.3**	**18.9**

†Note: Forest is a combination of *Montane* and *Coastal Forest.*

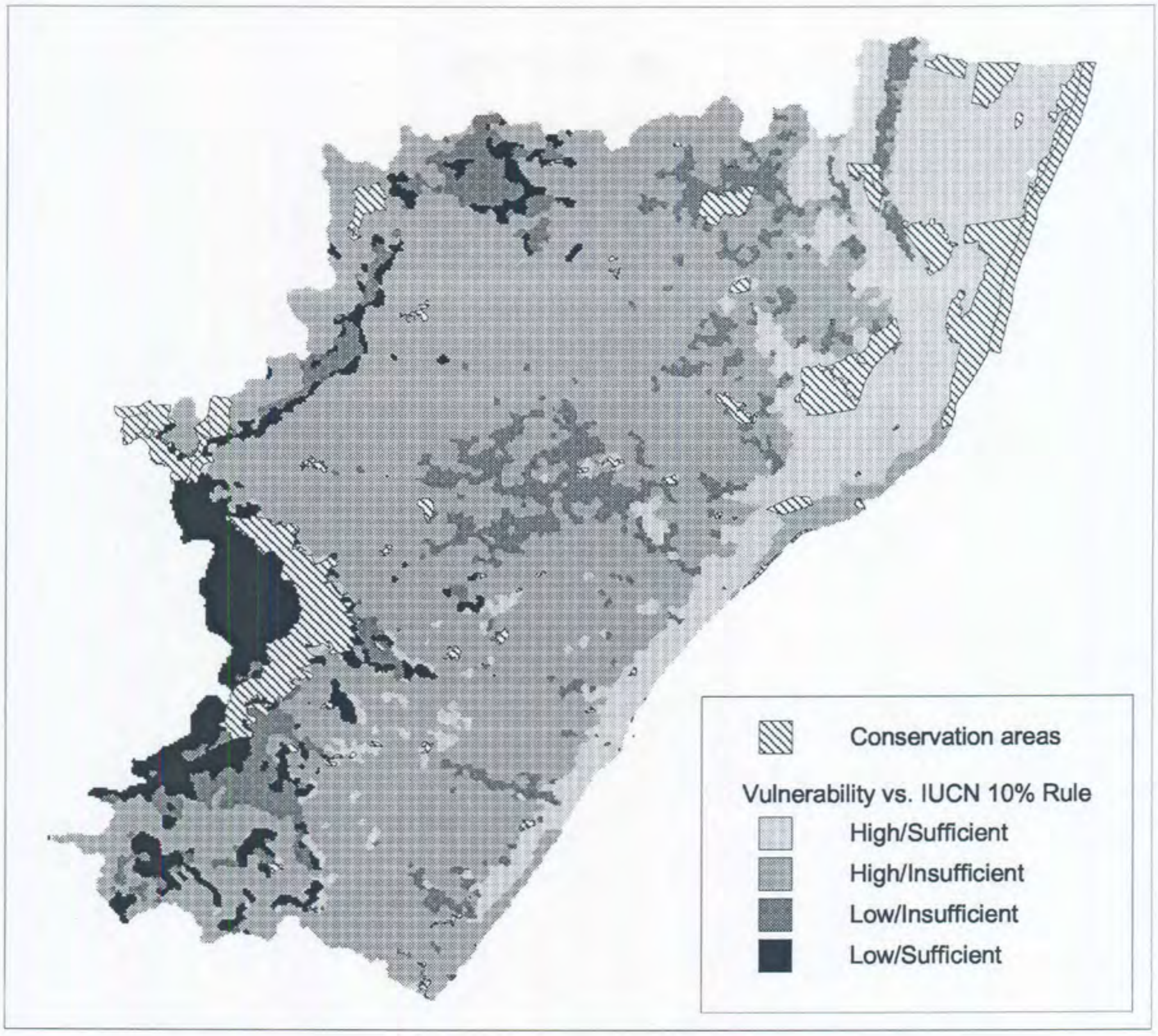

Figure 3.6: Landscape types classified by a 50% vulnerability status boundary and using the proposed IUCN 10% target for minimum protection of habitats.

representation and critical contribution to a provincial conservation goal.

Landscape types (6, 8, 10, 11, 12, 14, 16, 17, 18, and 22) represent the bulk of the province and have been historically ignored by the conservation authorities and targeted for development. They primarily contain fertile habitats of mixed woodland and upland and highland grasslands (Table 3.6). The almost total transfer of land in the formerly white areas of South Africa, from government to private ownership, is possibly unique in the annals of European colonisation. The state by the mid 1930's had lost control over resources, which in countries such as Australia, Canada or the USA were retained by the authorities because of their unsuitability for agriculture (Christopher, 1982). The strong tradition of land ownership rather than leasehold in South Africa and the absence of state interest in land through a leasehold system has developed a strong demand for land and an attempt to make a living in areas often highly unsuitable for the purposes of farming (Christopher, 1982; Schoeman and Scotney, 1987). Demand for land has further driven land prices to levels far in excess of its value as an agricultural commodity, and thus confounded past and present conservation efforts.

In practice, conservation managers rely on species distribution data as an aid to developing conservation plans. However, it would seem more reasonable to adopt the Noss (1990) hierarchy framework for identifying important areas for conservation based on a combination of landscape priority-species or vegetation priority-species. An example using the landscape priority assessment (from Figure 3.5) and a vegetation priority assessment (see Appendix B for Reyers et al., in review) were conducted with the bird atlas database (Harrison et al., 1997). Landscapes are ranked in order of importance based on dividing the graph (Figure 3.5) into four quadrants based on the 50% boundaries on each axis and then defining the following ranked values for the landscapes (Cartesian quadrants read clockwise; based on suggestions from the C-Plan website, http://www.ozemail.com.au/~cplan/background_1.html):

I. Very high priority for conservation in formal or secure reserves. (Rank 1)

II. High conservation values but not threatened, maybe consider off reserve management. (Rank 3)

III. Low priority for conservation. (Rank 4)

IV. These areas may contain features that are already represented in reserves, but which are still at risk. (Rank 2)

The priority vegetation type ranks were conducted in a similar manner (Appendix B), with the KwaZulu-Natal province containing four ranked vegetation types based on a national level assessment (Appendix B). The spatial distributions of the landscape and vegetation priority ranks are contained in Figure 3.7. Each ranked class on each map is used sequentially in turn to define the search areas for rarity and richness-based reserve selection algorithms (Rebelo and Siegfried, 1992; Howard et al., 1998; Reyers et al., 2000). The results of using the hierarchy of ranked landscapes and vegetation to determine complementary sets of bird species for conservation are provided in Figure 3.8.

Clearly, from the examples given, the goal of conservation is not only to ensure minimum landscape, habitat and species protection, but also to represent geographic gradients and to enable longer-term ecological and evolutionary processes to persist. This is not in conflict with the

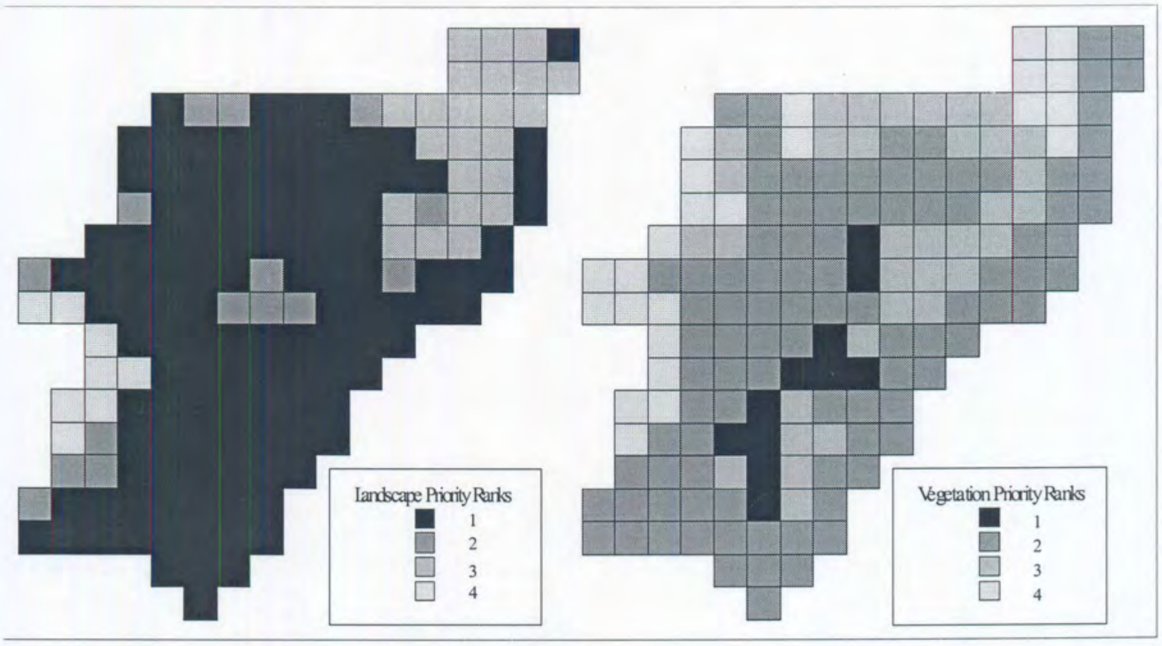

Figure 3.7: Priority ranks for landscapes and vegetation types as inclusion to rarity and richness-based reserve selection algorithms.

importance of habitat loss for the immediate persistence of biodiversity, but long-term persistence goals also need to be considered in designing and implementing reserve systems, especially in response to global change.

3.3 Discussion

This analysis represents one of the few times that a landscape or ecoregion classification has been properly assessed for accuracy and fitness for use in the field, and thus evaluated for use in systematic conservation planning. Using indirect methods, Wright et al. (1994) and Host et al. (1996) also assessed the value of larger ecoregional units (e.g., Omernik, 1987) and a machine driven ecosystem classification with mixed success. The use of ecoregion classifications for conservation planning is questionable given the very coarse scale of the units, the mixing of 'potential' and actual data sets (e.g., potential vegetation, climate zones, land-use pattern, soils, etc.), and the reliance on boundaries drawn by a consensus of experts, which may not provide a repeatable methodology. Rather, a data driven and parsimonious approach based on ecologically important structural and climatic variables derived at a larger landscape scale may allow for a better understanding of the pattern and processes required for biodiversity preservation. This type of landscape model can then be independently assessed with potential vegetation and edaphic

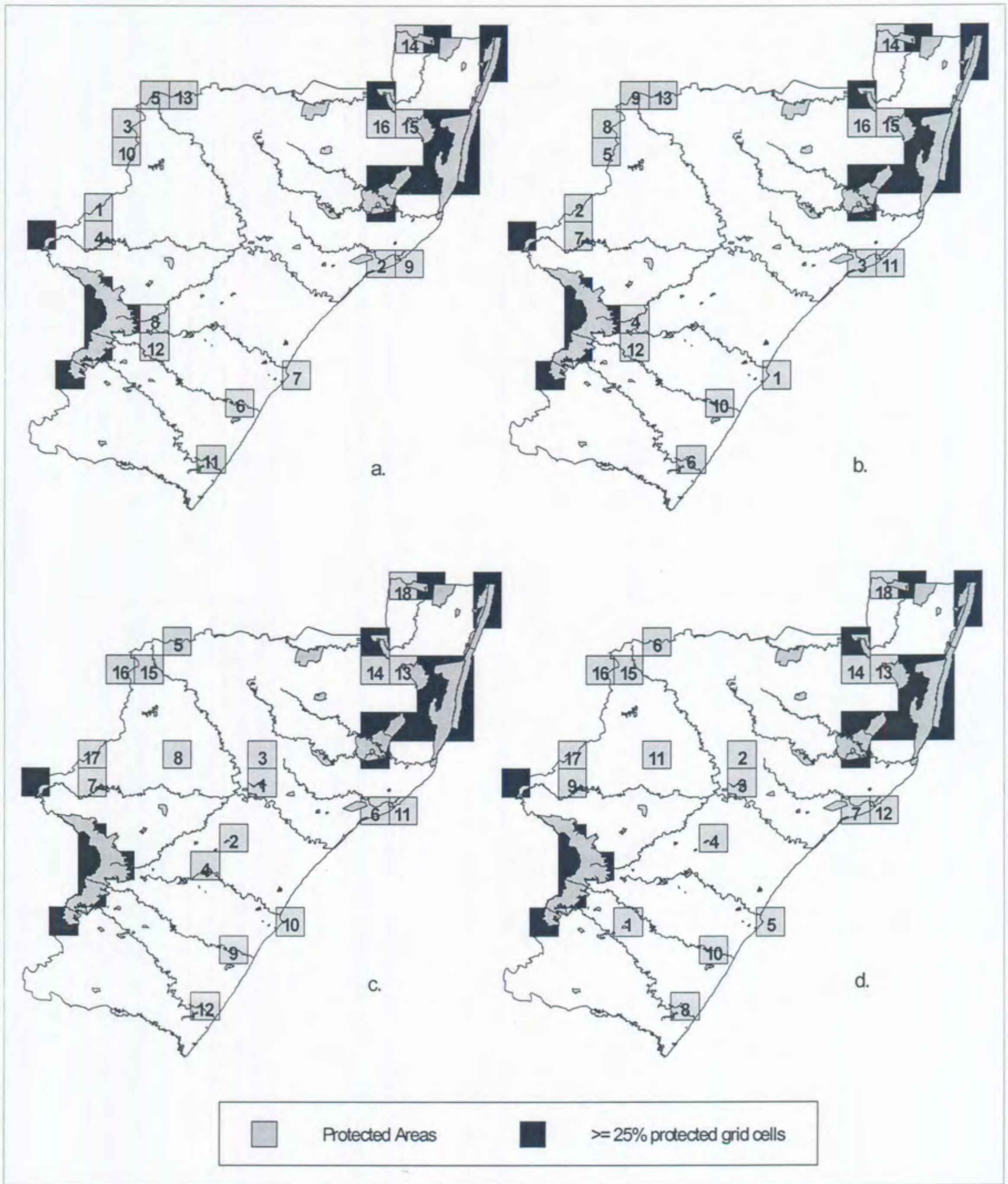

Figure 3.8: Selection order results for potential reserve networks based on either rarity or richness procedures for birds. (a) and (b) Results are based on a hierarchical mask of ranked landscape values based on four quadrants derived from 50% cutoff points in Figure 3.8; and (c) and (d) results are based on a hierarchical mask of ranked priority vegetation types based on current versus potential transformation (see Appendix B).

factors as the landscape attributes.

While chosen data layers and analytical methods are relatively objective, there are a number of decisions that require some *a priori* understanding of the landscapes under study. There are also data processing questions, such as determining, a statistically appropriate number of classification levels, selecting important variables or generalizing boundaries that require subjective, yet defendable decisions. It is unrealistic to expect that the process of landscape classification can be accomplished entirely by spatial and numeric analysis; human understanding is also an important component (Host et al., 1996). However, by defining a computationally repeatable methodology the knowledge of experts may be captured for future refinements within a data driven model.

3.3.1 Landscape Scale and Structure

Terrain analysis is the quantitative analysis of topographic surfaces with the aim of studying surface and near-surface processes. In short, terrain analysis provides the basis for a wide range of landscape-scale environmental models, which are used to address both research and management issues and objectives. It is widely recognised that landscape pattern analysis is sensitive to the resolution (spatial scale) of the source data (Turner et al., 1989). As the distance between neighbouring elevation samples increases, fine-scale features are lost and the surface becomes more generalised. However, when identifying landscapes there is a tendency to focus on specific finer detailed terrain or ecosystem elements *within a landscape* rather than the broad scale structures that truly define a landscape. For this study, a landscape was not defined traditionally as a mosaic where the mix of local ecosystems is repeated in similar pattern over a kilometers-wide area (Forman, 1995), but rather where the physical systems integrate together to define identifiable patterns over a kilometers-wide area. Therefore, the database of environmental layers defined at a resolution of $1km^2$ was considered appropriate for striking a balance between regional and local ecosystem heterogeneity.

3.5.2 Landscapes as an Element of Biodiversity for Use in Prioritisation Procedures

This study has shown that it is possible to produce an ecologically inclusive inventory of regional landscapes, notwithstanding the extensive areas they occupy and their inherent spatial complexity. Noss (1990) described landscapes as the upper level in a hierarchical framework that extends upwards from genes-species-ecosystems to describe the range of biological diversity. The analytical framework presented here is an appropriate model for elucidating the landscape level biodiversity dilemmas faced by conservation practitioners. By proposing a top-down, constraint based modelling and conservation assessment an approximation of the main processes and structure maintaining long-term biodiversity pattern can be used in more specific species protection and recovery plans. Biophysically defined landscapes containing elements of vegetation types with edaphic drivers determine and drive co-evolution with other species of mammal, reptile, bird and insect. The products of interacting organisms in a hierarchically defined landscape environment are ecosystems.

The majority of the work on preserving biodiversity and selecting priority areas for conservation has concentrated on the lower level of the biodiversity hierarchy: species (Pressey and Nicholls, 1989; Rebelo and Siegfried, 1990; Lombard, 1995; Pressey et al., 1996), populations (Lamberson et al., 1992; Breininger et al., 1995; Doak, 1995), and community (especially vegetation assemblages; Scott et al., 1993; Strittholt and Boerner, 1995; Barbult, 1995) patterns. Recently, criticism has been levelled at especially the species based approaches to identifying priority conservation areas (Noss, 1983; Franklin, 1993; Scott et al., 1993; Barbault, 1995; Maddock and du Plessis, 1999; Maddock and Benn, 2000). However, due to the hierarchical nature of biodiversity any approach, which only concentrates on one of the levels, is flawed. There has been virtually no research on designing reserve systems intended for long-term persistence of biodiversity in the face of global change. Such a strategy must embody the representation and retention of both biodiversity patterns as well as the processes that maintain and generate these patterns. Thus, more comprehensive and inclusive biodiversity protection can be obtained by focussing on as many levels as possible. Landscape areas representing high irreplaceability and vulnerability are focus areas for follow-up species and ecosystem representation analysis, and identification of key processes that are responsible for the maintenance and genesis of biodiversity. If the information is available, important constituent ecosystems within these priority landscapes can be identified using the classification procedure developed here. The dominance of mixed woodland and upland grassland vegetation functional types within the priority landscapes identified in the preliminary analysis suggests the ecosystems needing consideration, and gives significant insight into what conservation actions are needed on the ground.

Hierarchy theory (O'Neill et al., 1986) suggests that constraints operate downward in complex hierarchies such as ecosystems (i.e., from the more aggregated levels to the less aggregated levels). In recognising this, it has been suggested that using higher levels of biodiversity alone to select priority areas for conservation is preferable, especially in areas with inadequate region-wide biological data (Margules and Redhead, 1995). This is based on the assumption that diversity and spatial heterogeneity are intrinsically linked (Diamond, 1988;

Hunter et al., 1988; Samways, 1990; Forman, 1995). If for instance landscapes were to be used in this manner, it assumes that a predictable relationship (surrogacy) between diversity at the landscape level and lower levels exist. Unfortunately, little research has tested these assumptions, but some do suggest (see Harner and Harper, 1976; Burnett et al., 1998; Nichols et al., 1998) that the upper levels of biodiversity (e.g., Noss, 1990) may act as effective surrogates for biodiversity as a whole. However, this will vary between ecosystems and depend on levels of disturbance. Until such relationships are adequately explained, the best practice for selecting priority areas and preserving biodiversity will involve multiple levels of biodiversity (i.e., broader classification such as landscapes, vegetation, geology in conjunction with species data and human development induced threats) guided by the principles of retention of pattern and process.

A final issue that must be addressed is the robustness of the derived landscape classification system over time and space. The landscape classification system developed was based on both structural and climatic components. The structural data layers are expected to be robust over time and space due to their slow geological evolution, but climate may present resiliency problems for the current classification. Under a predicted climate change scenario for precipitation in southern Africa (Joubert and Hewitson, 1997) the growth days index can be expected to change over space and in magnitude. Re-defining the classification when newer climatic data sets become available can therefore retain the relevance of the landscape classification system. This is not in conflict with the objective of providing a classification system for a *functional landscape*, which is also expected to undergo evolutionary change over time. However, there is a trade-off between too much data resolution versus the expected resilience of the classification system, which can be tested through sensitivity analysis.

3.4 Summary

The use of regional ecological classification systems is increasing (Bailey, 1996; Host et al., 1996; Pressey, 1997). This is a result of efforts by resource and nature conservation managers to replace political boundaries with ecologically based management units that better reflect the spatial distributions of natural features. This is particularly true in water resource and nature conservation planning sectors, where landscape and regional ecology can be used to spatially combine natural processes and human activities to promote sustainable land management (Davis and Stoms, 1996). Developing a landscape classification allows for this often ignored level of biodiversity to be inventoried and considered in conjunction with species-based conservation prioritisation exercises.

The classification methodology proposed here is not totally objective in that data themes were chosen, and requires some *a priori* knowledge of the focus region's landscapes. However, the method is systematic and extensible to other areas. Furthermore, the method provides approaches for quantitatively classifying data, allows for quantitative understanding of the data heterogeneity among the themes, and can be updated as better data becomes available or environmental changes are documented.

By developing data layers for all the levels of biodiversity we can then provide a protocol for developing a reserve system that will enable biodiversity to persist into the next millennium. Rather than maximizing conservation of contemporary biodiversity patterns, a system should conserve ecological and evolutionary processes essential for sustaining biodiversity. The use of the landscapes-species hierarchy and the identification and role of processes in maintaining biodiversity patterns will help conservation planners to formulate clear representation goals in balance with human induced threat.

4. Species and Environment Representation: Selecting Reserves for the Retention of Avian Diversity

Considerable progress has been made in developing and testing practical protocols for designing representative conservation area systems (for review see Margules and Pressey, 2000). Historically, opportunistic methods have been used for assigning land with low potential for economic and political conflict; or high potential for recreation and tourism to biodiversity conservation, which has resulted in an inefficient and ultimately more costly means of conservation area allocation (see Pressey, 1994; Rodrigues et al., 1999). This has lead to the 'minimum set' approach to conservation planning to identify whole systems of complementary areas that collectively achieve some overall conservation goal in a more efficient manner (Pressey et al., 1993). Its prevailing conservation focus is to identify potential conservation areas that represent the greatest number of features (e.g., species, vegetation types) at least once. However, the extent to which conservation areas fulfill the role of securing a region's biodiversity depends only partly on the goal of sampling biodiversity pattern. The long-term retention of biodiversity also requires the representation of the processes that contribute to shaping and maintaining biodiversity patterns.

Several authors have emphasized that current biodiversity representation within conservation areas is not equivalent to the ultimate goal of maintaining biodiversity over the long-term (Cowling et al., 1999; Fairbanks and Benn, 2000; Margules and Pressey, 2000; Rodrigues et al., 2000). The representativeness concept implies that a reserve, or system of reserves, should contain biota that ideally represents the entire range of biological and environmental variation within a given geographical area (Margules and Usher, 1981; Kirkpatrick, 1983; Austin and Margules, 1986; Mckenzie et al., 1989). Fairbanks and Benn (2000), along with Margules and Pressey (2000), agree, but also emphasize the maintenance of natural processes as an important component of conservation area selection. Rodrigues et al. (2000) argue that as species distribution patterns change over time, the selection of conservation areas that are robust to turnover in species or environmental diversity is a critical component of conservation area selection for ensuring the long-term maintenance of biodiversity. Thus, in selecting nature reserves, one should attempt to identify the major gradients of biotic and environmental variation within habitat types of interest in the study area and, if possible, the environmental variables that most closely correlate with the distribution and abundance patterns of relevant taxa (DeVelice et al., 1988).

Emphasis should not only be placed on the identification and conservation of biodiversity pattern, but also the natural processes that control and maintain that pattern within the biodiversity hierarchy (Noss, 1990; Balmford et al., 1998). Conservation of ecosystem processes that sustain ecosystem structure and function (Fairbanks and Benn, 2000), and evolutionary processes that sustain lineages and generate diversity (Cowling et al., 1999), are essential for achieving the long-term maintenance of biodiversity in conservation areas (Nicholls, 1998). However, as Margules and Pressey (2000) point out, because conservation area selection is often a spatial exercise, protection of these natural processes is often based on their spatial surrogates rather then on the processes themselves. Nevertheless, by ensuring that conservation areas are large or span substantial environmental gradients it should be possible to accommodate, at least partially, many of these natural processes (Noss, 1996).

Ordination analyses have illustrated tremendous potential for identifying important environmental gradients responsible for biodiversity pattern (DeVelice et al., 1988; Faith and Norris, 1989; Saetersdal and Birks, 1993; Taggart, 1994). This analytical approach is used for integrating multiple environmental effects across a landscape (Bray and Curtis, 1957; Gauch, 1982; Jongman et al., 1995). Ordination, whether direct or indirect, is particularly useful when studying the relationships between species composition and environment (Jongman et al., 1995).

Beta diversity is concerned with species spatial turnover along habitat gradients (Whittaker 1977). Beta diversity is important in determining regional species richness patterns, yet little attention has been paid to this component of diversity in selecting conservation areas. If conservation areas are selected only to represent numbers of species, they may not necessarily continue to serve this purpose over a period of years (Margules et al., 1994; Virolainen et al., 1999; Rodrigues et al., 2000).

The present study addresses the issues of conserving natural processes and spatial turnover of species diversity in an investigation conducted to assist the KwaZulu-Natal Nature Conservation Service (South Africa). The goal was to identify additional potential avian conservation areas in KwaZulu-Natal Province, as an added component to their strategic plan (Armstrong et al., 2000) for the long-term maintenance of regional biodiversity. To date, no study has been carried out on the complete bird fauna of the province to assess its representativeness or relationships with environmental processes and features.

4.1 Methods

4.1.1 Ordination

The primary analytical tool used was canonical correspondence analysis (CCA; ter Braak and Prentice, 1988), a widely used direct gradient analysis method (Palmer, 1993), and detrended correspondence analysis (DCA), an indirect gradient analysis method (Gauch, 1982). The program CANOCO, version 4.0 (ter Braak and Smilauer, 1998), was used to conduct all gradient analyses. DCA and a hierarchical classifier were used to determine the avian species communities within KwaZulu-Natal (Legendre and Legendre, 1998). Environmental data (e.g., the 13 environmental parameters found under topography and climate in Table 1.1) were entered with the species data using stepwise CCA to investigate which environmental variables explained the patterns in observed avian diversity (ter Braak and Smilauer, 1998). Variables are added to the model in the order of greatest additional contribution to total variation explained, but only if they were significant ($P \leq 0.01$), where significance was determined by a Monte Carlo permutation test, and if adding the variable did not cause any variance inflation factors to exceed 20. Variables with large inflation factors are strongly multicolinear with other variables and contribute little unique information to the model (ter Braak and Smilauer, 1998). In order to combine this information on species patterns and the related environmental gradients responsible for those patterns into practical conservation planning techniques, I propose the use of spatial autocorrelation analyses.

4.1.2 Spatial Autocorrelation Analysis: Local Indicators of Spatial Association

In the analysis of spatial association among many spatial observations, the tendency is to assess spatial autocorrelation based on global statistics such as Moran's *I* or Geary's *c* (Cliff and Ord, 1981). A focus on local patterns of association (local spatial clusters) prompted the development of local indicators of spatial association (Anselin, 1995). This form of analysis was used to identify areas with high levels of species and associated environmental gradient turnover. The software packages Spacestat (Anselin, 1999) and S-plus with the spatial statistics component (Mathsoft, 1999) were used to conduct this part of the analysis.

Using Moran's *I* analysis, based on the information gained from the previous CCAs, local spatial clusters of integrated species compositions and their associated environmental gradients were identified. A grid cell with a high positive Moran's *I* value is highly autocorrelated or is similar to neighbouring grid cells in terms of avian species contained and environmental parameters. A grid cell with a negative to low positive Moran's *I* value shows low levels of autocorrelation and is thus very different from surrounding grid cells in terms of species assemblage and the associated environmental variables. Thus, those grid cells with low levels of spatial autocorrelation are indicative of areas with high turnover in species composition as well as strong environmental gradients.

4.1.3 Conservation Area Selection

An algorithm based on species rarity or richness (Rebelo and Siegfried, 1992; Howard et al., 1998; Reyers et al., 2000) for selecting a set of complementary reserves was initially run on the birds species distribution data. However, such selection procedures do not successfully select areas for the representation of natural processes responsible for generating biodiversity patterns. Furthermore, they do not target areas of high beta diversity, i.e. areas with a high turnover in feature diversity. I attempted to include steps in these algorithms that selected areas high in beta species diversity and with associated environmental gradients by ranking the grid cells from lowest spatial autocorrelation to highest and iteratively incorporating the required species for representation using either species rarity and richness approaches. Moran's I values were used as indicators of the importance of grid cells in terms of species and environmental turnover. This then made it possible to represent not only alpha diversity patterns (numbers of species within a community), but also beta diversity patterns and sample the underlying environmental gradients during the reserve selection procedure.

First, a grid cell was considered protected if $\geq 25\%$ of its area fell within protected areas. The species found within these grid cells were removed from the analysis. Second, Moran's I values of each grid cell were categorized and ranked into four groups: negative autocorrelation, weak positive autocorrelation, moderate positive autocorrelation, and strong positive autocorrelation. Third, two analyses were completed, one based on complementary rarity and the other on complementary richness. The algorithm starts by selecting grid cells from the first category of spatial autocorrelation (i.e. grid cells in the negative autocorrelation category) and scans them for un-represented species not removed in the first step. The algorithm then proceeded in a stepwise fashion through all spatial autocorrelation categories until all species were represented at least once. In this way two real-world reserve system outputs were developed for comparison, based either on species rarity or richness, but also incorporating areas with dissimilar species compositions and different environmental characteristics from neighbouring and previously selected grid cells (high beta diversity). This beta diversity (BD) algorithm, therefore, selects a network that not only represents all species in the area, but also bases its selection on the spatial structure of the species assemblages and environmental gradients, i.e. it samples both biodiversity pattern and process in a representative manner.

4.2 Results

4.2.1 Ordination Analysis

Geographic patterns of hierarchically classified DCA scores are indicated in Figure 4.1 illustrating the five avian communities identified within the province. The Maputaland community in the northeast, the East Coast, the Drakensberg Escarpment, Central Zululand forming a transition between the Drakensberg and Maputaland communities and the Central-southern Midlands community at the southern end of the province, each contain unique combinations of species. The most important bird species in each community, based on indicator species analysis (Dufrene and Legendre, 1997) is provided in Table 4.1. Eigenvalues and gradient lengths were moderately higher for DCA than for CCA for the first two axes (Table 4.2). This fact together with the strong and significant correlations between the DCA for axis 1 and axis 2 with the explanatory variables (Table 4.3) suggested that much of the variation in avian diversity distribution is related to the measured environmental variables. The stepwise CCA reduced the number of significant variables required to explain the variation in species turnover (Table 4.4). Most (81%) of the variation in bird species assemblages in KwaZulu-Natal was accounted for by the explanatory environmental variables of elevation heterogeneity, mean growth days, mean growth temperature, mean annual evapotranspiration, and seasonality of precipitation.

The CCA results are graphed as a biplot, in which arrow length and direction indicate the correlation between the explanatory variable and the CCA axes, and smaller angles between arrows indicate stronger correlations between variables (Figure 4.2). The dominant compositional gradient (axis 1) reflected an altitudinal gradient, which was represented by the mean growth temperature and the seasonality of precipitation, from the sub-tropical climate of the coast to the temperate-afromontane climate of the Drakensberg Escarpment. Grid cells towards the higher lying areas experienced higher seasonal variability in temperature and precipitation, whereas low lying coastal regions experienced lower seasonal variability in temperature, higher temperatures, and lower variability in precipitation. The seasonality of precipitation and elevation heterogeneity are moderately correlated with each other, but reflected low inflation factors in the CCA analysis therefore each was able to provide explanation for the turnover in species composition. This altitudinal gradient runs roughly east-west from the Maputaland coastal plain to the Drakensberg Escarpment, reflecting the strong climatic influence of the Indian Ocean and the generally north-south orientation of the Drakensberg Escarpment.

The second CCA axis was a gradient in growing season moisture stress, from the areas of warm, dry growing seasons around Maputaland and the Lebombo Mountains, which are characterized by arid woodlands to areas of warm, wet growing seasons along the southern East

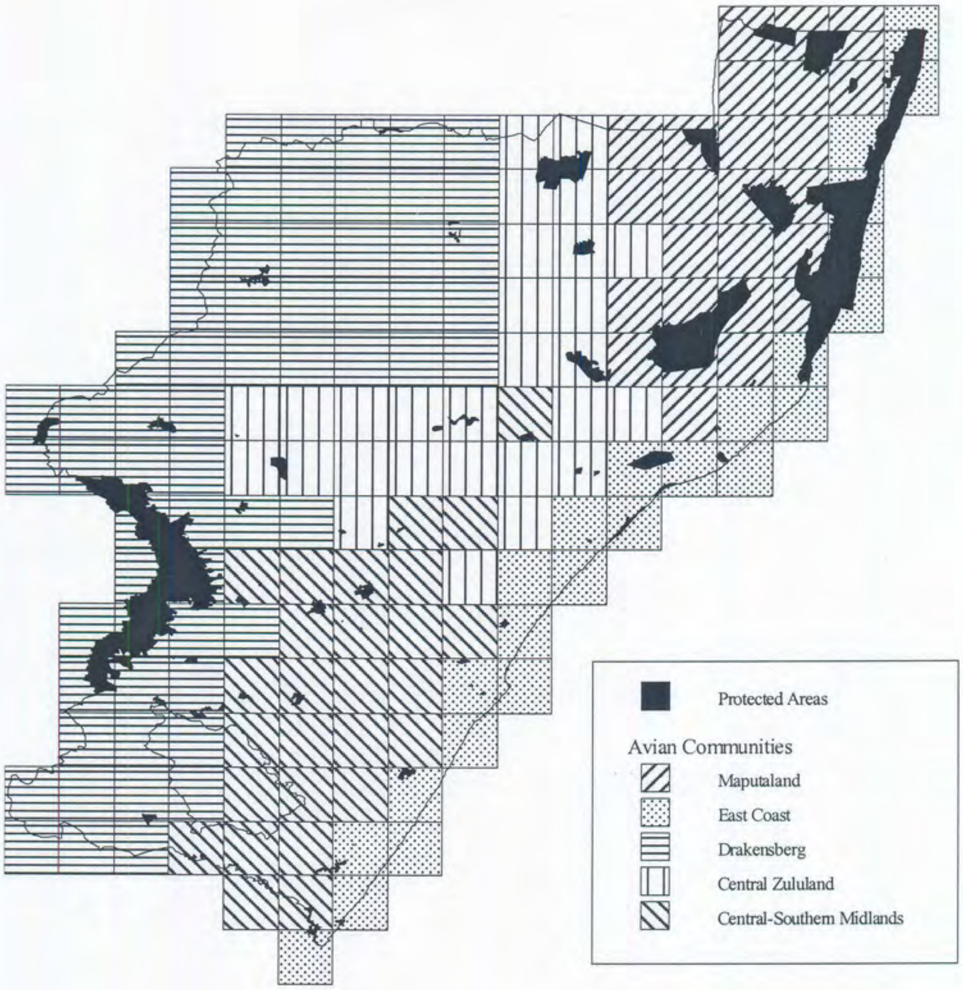

Figure 4.1: Identified avian diversity assemblages derived from hierarchical classification of first two axes of the detrended correspondence analysis results.

Coast (Figure 4.2). Areas of low summer precipitation and high annual evapotranspiration included the interior valleys to the west of the Lebombo Mountains, especially northern Zululand, and the White Mfolozi and Tugela River basins. The Central-southern Midlands represents areas of higher summer precipitation with variable elevation owing to lower annual evapotranspiration being able to support montane forests and upland grassland.

An analysis of the available vegetation habitat and human impact on the bird communities of KwaZulu-Natal illustrates the conservation conflicts and habitats to be managed. In Table 4.5 potential functional vegetation types (Fairbanks and Benn, 2000) that would have occurred today, were it not for all the major human-made transformations, were combined with currently mapped major land-use types (Fairbanks et al., 2000). The proportion of vegetation types for each avian community (Figure 1.3) provides a general description of the habitat requirements. The land-use

Table 4.1: Avian bioindicators in order of importance based on Dufrene and Legendre (1997) indicator species value measure for each identified avian community assemblage.

Community		Community	
Maputaland		**Central Zululand**	
Trigonoceps occipitalis	whiteheaded vulture	*Aquila rapax*	tawny eagle
Eupodotis ruficrista	redcrested korhaan	*Cossypha humeralis*	African whitethroated robin
Torgos tracheliotus	lappetfaced vulture	*Cisticola chiniana*	rattling cisticola
Coracias naevia	purple roller	*Merops pusillus*	little bee-eater
Eremomela usticollis	burntnecked eremomela	*Hieraaetus spilogaster*	African hawk eagle
Nectarinia neergaardi	Neergaard's sunbird	*Vidua paradisaea*	paradise whydah
Tockus erythrorhynchus	redbilled hornbill	*Aquila wahlbergi*	Wahlberg's eagle
Terathopius ecaudatus	bateleur	*Tricholaema leucomelas*	pied barbet
Cossypha heuglini	Heuglin's robin	*Turtur chalcospilos*	greenspotted dove
Eremomela icteropygialis	yellowbellied eremomela	Sylvietta rufescens	longbilled crombec
East Coast		**Central-Southern Midlands**	
Morus capensis	cape gannet	*Hirundo atrocaerulea*	blue swallow
Sterna hirundo	common tern	*Zoothera gurneyi*	orange ground thrush
Sterna bengalensis	lesser crested tern	*Serinus scotops*	forest canary
Calidris alba	sanderling	*Poicephalus robustus*	cape parrot
Sterna sandvicensis	sandwich tern	*Tauraco corythaix*	Knysna lourie
Charadrius leschenaultii	sand plover	*Ploceus bicolor*	forest weaver
Sterna albifrons	little tern	*Anthus lineiventris*	striped pipit
Sterna paradisaea	Arctic tern	*Seicercus ruficapillus*	yellowthroated warbler
Sterna bergi	swift tern	*Nectarinia chalybea*	lesser doublecollared sunbird
Larus dominicanus	kelp gull	*Anthreptes collaris*	collared sunbird
Drakensberg Escarpment			
Eupodotis caerulescens	blue korhaan		
Hirundo spilodera	SA cliff swallow		
Chaetops aurantius	orangebreasted rockjumper		
Francolinus africanus	greywing francolin		
Euplectes afer	golden bishop		
Spreo bicolor	pied starling		
Gypaetus barbatus	bearded vulture		
Chersomanes albofasciata	spikeheeled lark		
Myrmecocichla formicivora	southern anteating chat		
Amadina erythrocephala	redheaded finch		

Table 4.2: Eigenvalues and gradient lengths (1 Standard Deviation) for the first two axes from DCA and DCCA of all bird species for KwaZulu-Natal.

	Axis 1		**Axis 2**	
	DCA	DCCA	DCA	DCCA
Eigenvalue	0.21	0.19	0.09	0.08
Gradient length	1.96	2.45	1.51	1.23

Table 4.3: Spearman's rank correlation of explanatory factors with axis scores from DCA and intraset correlation coefficients from CCA that included all explanatory variables. †

	Axis 1		Axis 2	
	DCA	CCA	DCA	CCA
DEMMEAN	0.93	0.93	-0.05	-0.05
DEMSTD	0.59	0.59	-0.5	-0.023
GDMEAN	0.05	0.04	0.83	0.84
MAP	-0.03	-0.86	0.73	-0.21
GTMEAN	-0.88	-0.92	-0.21	-0.11
NGTMEAN	-0.91	-0.91	-0.11	-0.10
MAT	-0.91	-0.03	-0.09	0.74
HOTMNTHMN	-0.89	-0.89	-0.16	-0.17
MINMNTHMN	-0.93	-0.93	0.02	0.01
EVANNMN	-0.42	-0.42	-0.66	-0.69
PSEAS_MN	0.85	0.86	0.06	0.04
TSEAS_MN	0.53	0.54	-0.49	-0.52
MXSEAS_MN	0.57	0.57	-0.40	-0.42

† Sign reflects arbitrary selection of gradient direction by CANOCO.

Table 4.4: Summary of results from stepwise CCA. †

	Axis 1	Axis 2
DEMSTD	0.61	-0.001
GDMEAN	0.05	0.86
GTMEAN	-0.88	-0.21
EVANNMN	-0.44	-0.72
PSEAS_MN	0.87	0.04

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

information provides an indication of the current transformation processes taking place within the avian community assemblages. The heterogeneous nature of the Central Zululand and Central-southern Midlands vegetation structures and avian assemblages is apparent. The environmental heterogeneity found within the Central-southern Midlands community has also provided ample development opportunities for humans, with 43% of the landscape having been transformed, and most of the existing protected areas here are small. The small sizes of these protected areas, their scattered locations, their progressive isolation through the loss of connecting habitats are cause for concern.

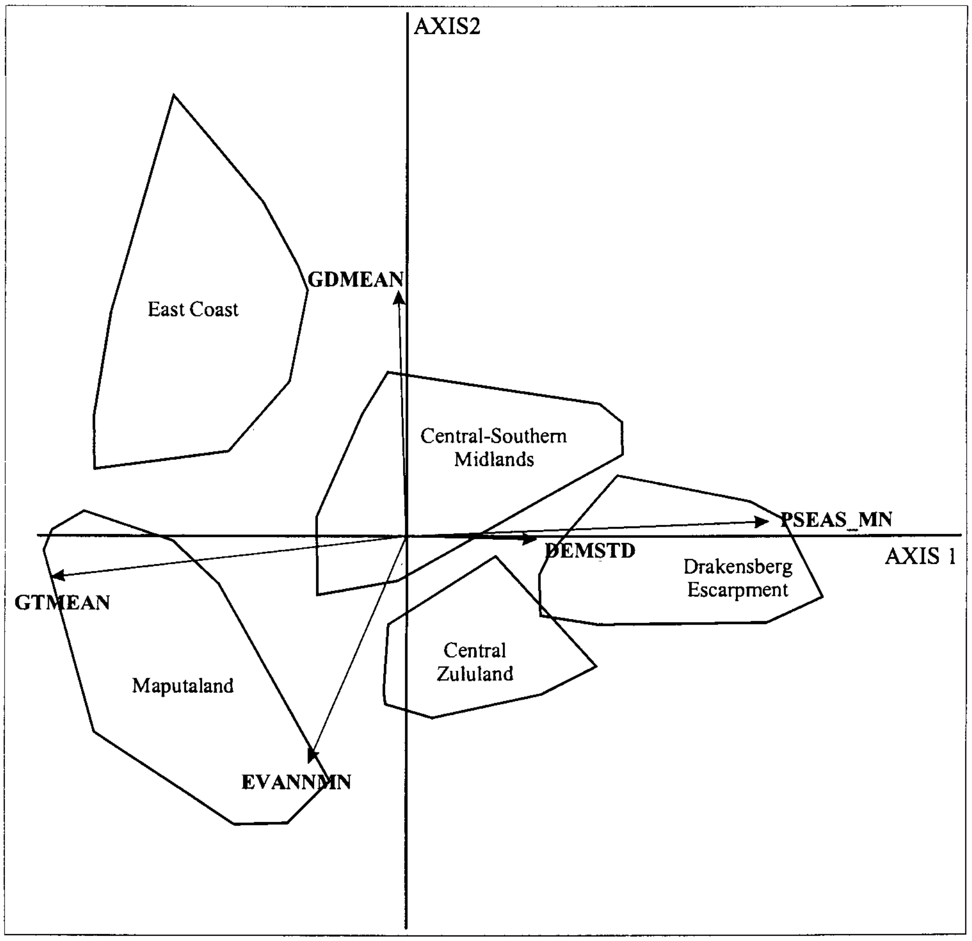

Figure 4.2: Species-environment gradients identified from stepwise canonical correspondence analysis with convex hulls of avian community biogeographic zones. GTMEAN - Annual mean of the monthly mean temperature (°C) weighted by the monthly growth days; PSEAS_MN - Precipitation seasonality from the difference between the January and July means; DEMSTD - Elevation heterogeneity; GDMEAN - Number of days per annum on which sufficient water is available for plant growth; and EVANNMN - Total annual pan evapotranspiration (mm).

4.2.2 Spatial Autocorrelation Analysis

The analysis was performed on axis 1 and 2 of the CCA results (Figure 4.3a, b). The resultant Moran's I axis values were then derived for each grid cell for the analysis of the species-environment spatial structure in the reserve selection procedure. On axis 1 strong positive autocorrelated clusters of similar species-environment compositions were located along the northern coast, Maputaland coastal plain, and Drakensberg Escarpment. Negative autocorrelated clusters were identified in the interior associated with the Central Zululand and Central-southern

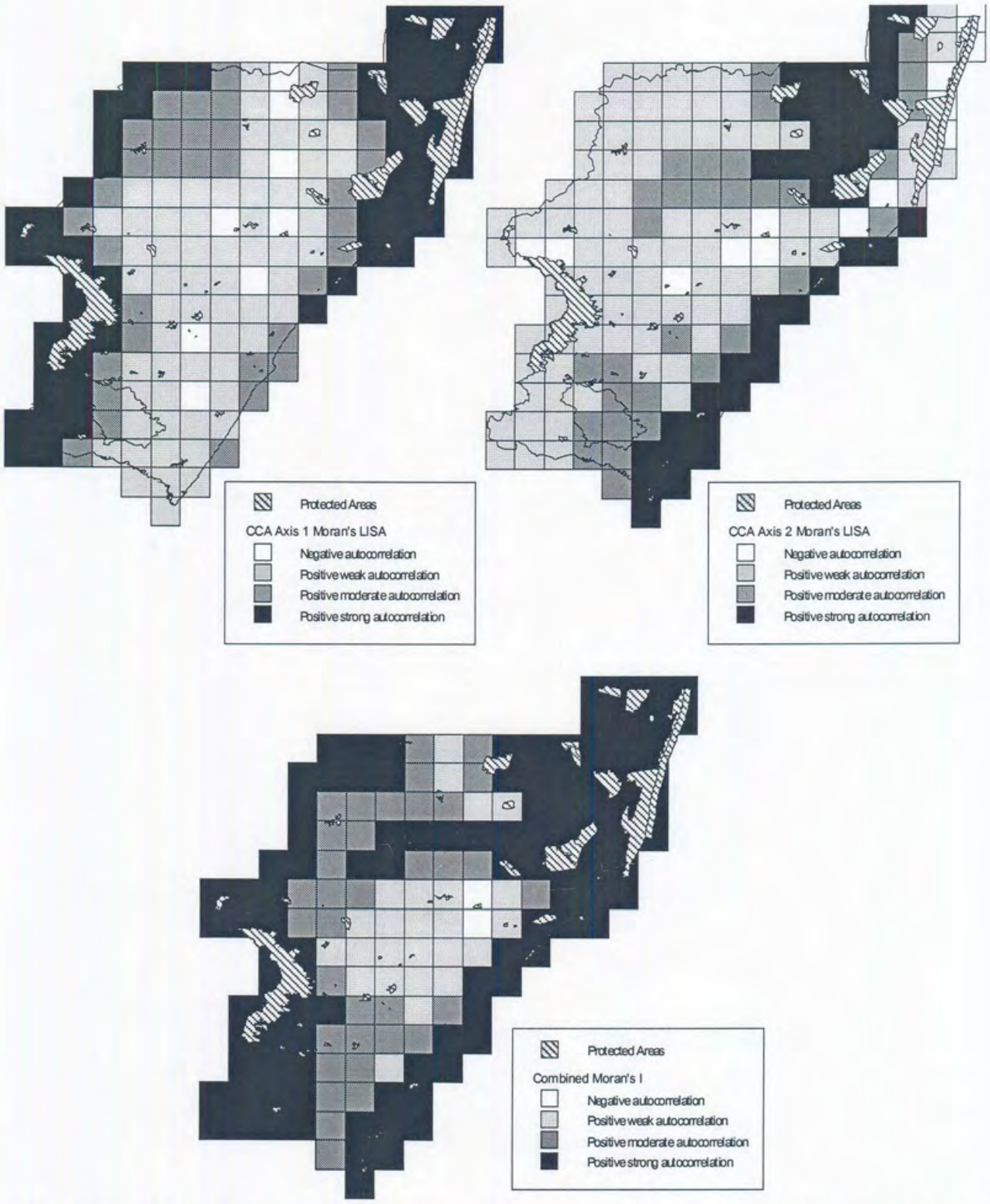

Figure 4.3: Moran's *I* spatial autocorrelation results: (a) CCA axis 1; (b) CCA axis 2; and (c) combined Moran's *I* axes 1 and 2.

Midlands avian communities. These grid cells represent dissimilar species-environment compositions from their immediate neighbours and therefore represent areas of high species turnover along the identified environmental gradients.

Moran's *I* analysis of the second axis identified strong positive autocorrelated clusters in the arid woodland region of northern Zululand, Maputaland and the Lebombo Mountains and along the southern East Coast. Negative clusters were found in the Tugela and Mhlatuze river basins, central Drakensberg Escarpment and northern East Coast.

Table 4.5: Percentage of functional vegetation and land-cover/land-use types per identified avian community assemblage.

	Maputaland[†]	East Coast[†]	Drakensberg	Central Zululand	Central-Southern Midlands
Coastal Forest	0.6	1.8	0.0	0.0	0.0
Afromontane Forest	0.1	0.7	0.7	0.5	1.2
Arid Woodland	46.6	0.1	0.7	9.8	0.0
Moist Woodland	9.6	25.2	0.0	0.0	2.0
Mixed Woodland	7.6	4.9	18.0	31.9	13.3
Thicket	0.0	3.9	0.3	16.3	9.6
Upland Grassland	0.0	2.9	19.2	4.5	20.6
Highland Grassland	0.4	0.0	36.7	6.4	3.3
Wetlands	4.4	6.2	1.0	0.1	0.5
Bare	0.1	0.5	0.5	0.5	0.0
Degraded	11.8	7.5	5.6	9.6	10.0
Exotic plantation	1.8	8.8	3.4	5.8	16.1
Agriculture Dryland	16.5	22.1	10.5	13.7	19.5
Agriculture Irrigated	0.4	0.1	2.0	0.5	2.0
Urban	0.1	7.4	1.3	0.4	2.0

[†] Missing area measurements from coast and Mozambique border.

Spearman's rank correlation analysis of the individual Moran's *I* axis values and combined values revealed relationships between the Moran's *I* values and definitions of land type heterogeneity (Table 4.6). A combined model of landscape types (Figure 3.2) and functional vegetation types (Figure 1.3) had the highest correlations with Moran's *I* values for axis 1 and combined Moran's *I* values. There was no meaningful relationship for the axis 2 Moran's *I* results. This relationship depicts decreasing Moran's *I* values as the variety of landscape-functional vegetation types increases, i.e. with increasing environmental heterogeneity (Figure 4.4). This implies that local bird diversity turnover is more strongly linked to landscape and vegetation structure (e.g., MacArthur, 1964; Wiens, 1989a) within the Central Zululand and Central-southern Midlands, than to broad climate. These areas appear to represent important transitionary regions for birds, between the richer and more homogenous high grassland areas of the Drakensberg Escarpment, the Maputaland arid woodlands and East Coast moist woodlands. These heterogeneous areas may also be of significance as zoogeographical barriers to avian distributions because of deeply incised river valley conditions (Figure 1.2a - also see Benson et al., 1962; Clancey, 1994). Microclimates, diverse habitat assemblages, and geomorphology all seem to play important roles in maintaining and driving the unique bird assemblages and rapid species turnovers across the province's interior regions (Figure 4.3c).

Table 4.6: Spearman's rank correlation coefficients of the Moran's *I* analysis and the diversity of landscape definition types (see Table 1.1).

	Axis 1	Axis 2	Combined
LAND	-0.52	-0.16	-0.49
LANDVEG	-0.62	-0.07	-0.54
LANDVEGF	-0.70	-0.04	-0.59
VEG	-0.37	0.11	-0.23
VEGF	-0.51	0.14	-0.32
LCLUTYPES	0.01	0.09	0.00
LCLULAND	-0.57	-0.05	-0.49

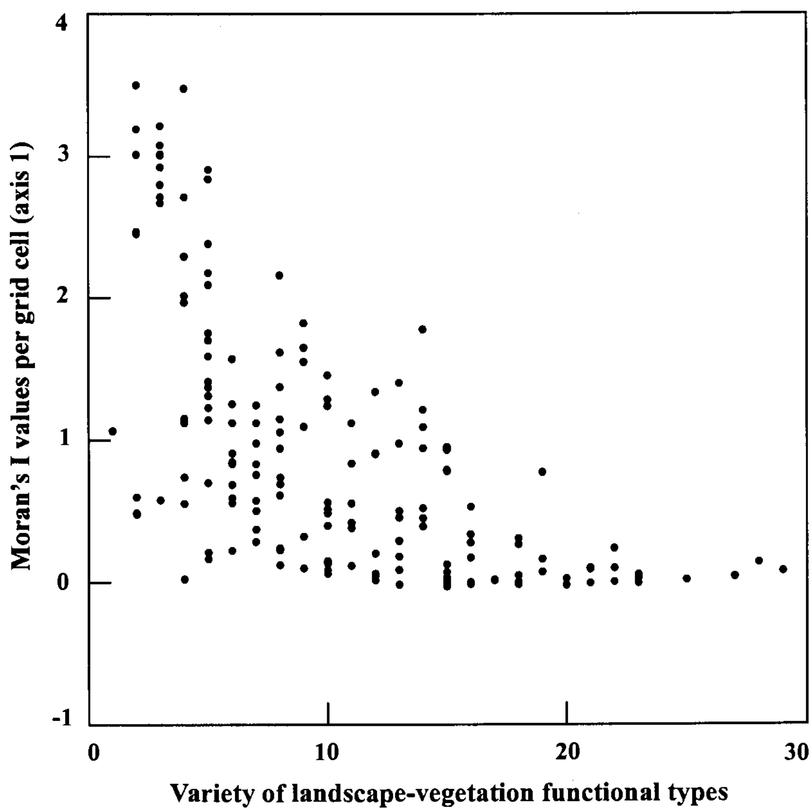

Figure 4.4: Graph of CCA axis 1 Moran's *I* values relationship to the variety of landscape-vegetation functional types found within each grid cell.

4.2.3 Priority Conservation Areas

The study area of 165 grid cells included 19 (11.4%) grid cells that were considered protected, i.e. ≥ 25% protected. These grid cells are located almost entirely within the central Drakensberg Escarpment and Maputaland areas, and represented 529 (93%) of the 566 recorded bird species. This illustrates that these larger existing reserves do contribute significantly towards the goal of conserving all avian species. The rarity and richness-based complementary algorithms selected 15 (10%) and 14 (9%) of the remaining 147 grid cells respectively to represent the remaining 37 species at least once (Figure 4.5a,c). To achieve the goal of adequately sampling all species while also representing the identified environmental gradients, the BD (beta diversity) algorithm for both the rarity and richness-based analyses needed 18 (12%) grid cells (Figure 4.5b,d).

Figure 4.6 illustrates the rates of species accumulation for the four algorithms. The richness-based algorithm rapidly represented most species (> 90%) within 7% of the remaining land area, with the rarity-based algorithm requiring only slightly more land (9%). The rarity-based algorithm also illustrates the break levels its search rules creates by looking for pockets of rare species while constrained by proximity rules to pick grid cells that are closer to the previously selected grid cells. The richness-based BD algorithm initially selected species at a slow rate but increased after the first 3.5% of the grid cells were selected and the rarity-based BD algorithm shows the same breaks but chose more land area earlier.

The results outlined above assume that the protected areas that are already proclaimed are adequate, and that the procedure used can only produce results that add to defining an all inclusive representative reserve network. Once the environmental gradients that are associated with birds species turnover are identified it may be more appropriate to ask what would an "ideal" network for total bird protection look like if the current protected areas were not assumed adequate. Figure 4.7 provides such a result, which might provide a more resilient and thus viable option for long-term retention of the provinces bird diversity. For either algorithm, the contrasts with the status quo of using straight species-based complimentary procedures versus incorporating associated environmental gradients are strikingly apparent.

The original rarity and richness-based algorithms were the most efficient representing all species in the least amount of land area possible. These algorithms obviously concentrated on the areas of high species richness and rarity. The algorithm rules for either approach (rarity or richness) select grid cells in a locally optimal manner, based on the species database and grid cell proximity, rather than selecting based on regional optima. The grid cells picked for either the rarity or richness-based algorithms are similar, except for the selection order, with most areas

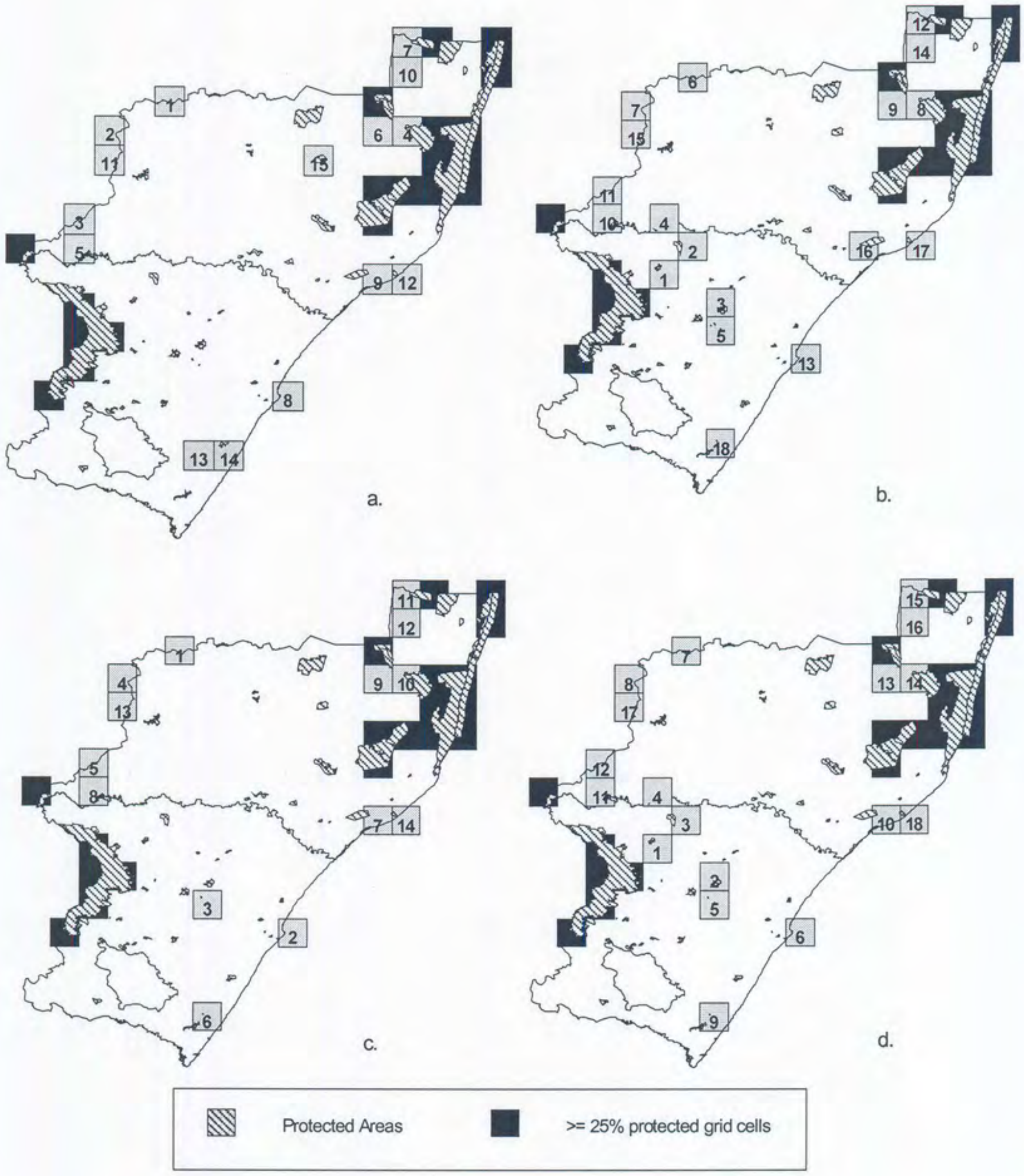

Figure 4.5: Comparison of algorithm results: (a) species rarity-based algorithm; (b) species rarity and beta diversity algorithm; (c) species richness-based algorithm; and (d) species richness and beta diversity algorithm.

selected in the Maputaland, Drakensberg Escarpment and East Coast regions. The BD algorithm attempts to provide the algorithm rules with important environmental information about the entire region using the ranked spatial autocorrelation classes. Although similar grid cells are selected for both the rarity and richness-based BD algorithms, the masking action of the ranked spatial autocorrelation categories forces the algorithms in this region to search the interior of the province (Figure 4.3c) first to locate grid cells containing the required species. Four to five grid cells are chosen from the southern areas of Central Zululand and northern areas of the Central-southern Midlands depending on the algorithm emphasis (Figure 4.5b,d). The other significant differences

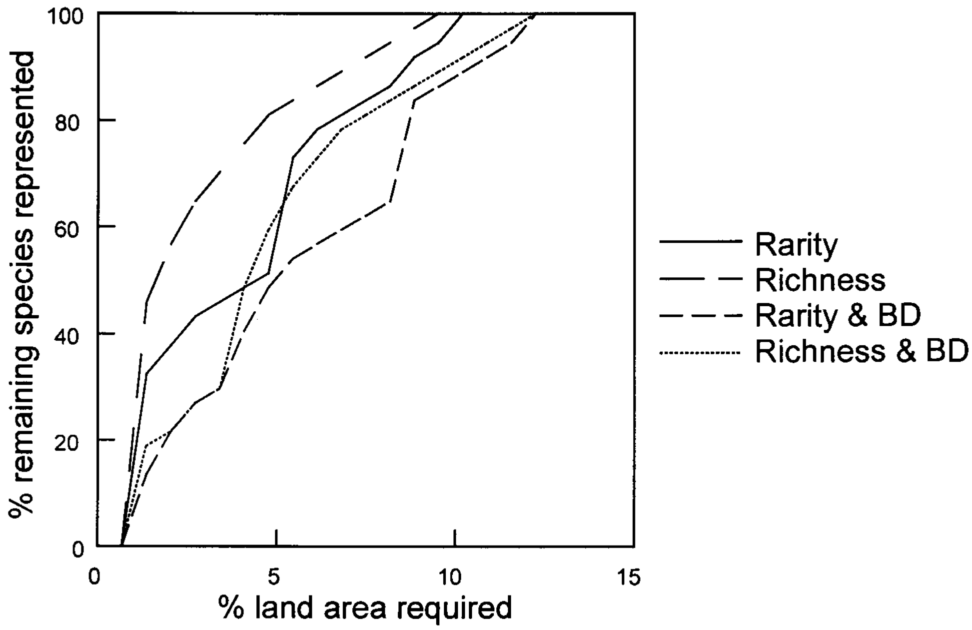

Figure 4.6: Graph of algorithm efficiencies detailing species representation versus percent land area required. (BD = beta diversity).

among algorithm outputs are the selection orders. In this case, the rarity-based BD algorithm results are the most useful for conservation as it ranks the rarest birds, landscapes and natural processes most important for immediate conservation action (Table 4.7).

4.3 Discussion

Like most other systematic conservation procedures (see review Margules and Pressey, 2000), this proposed procedure is useful for identifying conservation-worthy areas because it is flexible and multivariate. The framework of complementarity analysis can contribute to assessing the efficient selection of un-represented species for conservation. The long-term retention of those species should also be improved by extending this methodology to select by spatial changes in environmental gradients and associated species.

4.3.1 Evaluation of the Techniques

Existing protected areas within the province are concentrated mostly within the Maputaland region and the central Drakensberg Escarpment along the Lesotho border. This leaves the other avian communities identified largely un-represented or under-represented with small (< 1000 ha) ineffective reserves. The traditional complementarity-based algorithms emphasizing rarity or richness do little to correct this representation bias as they select additional grid cells in the already sufficiently conserved areas, leaving Central Zululand and the Central-

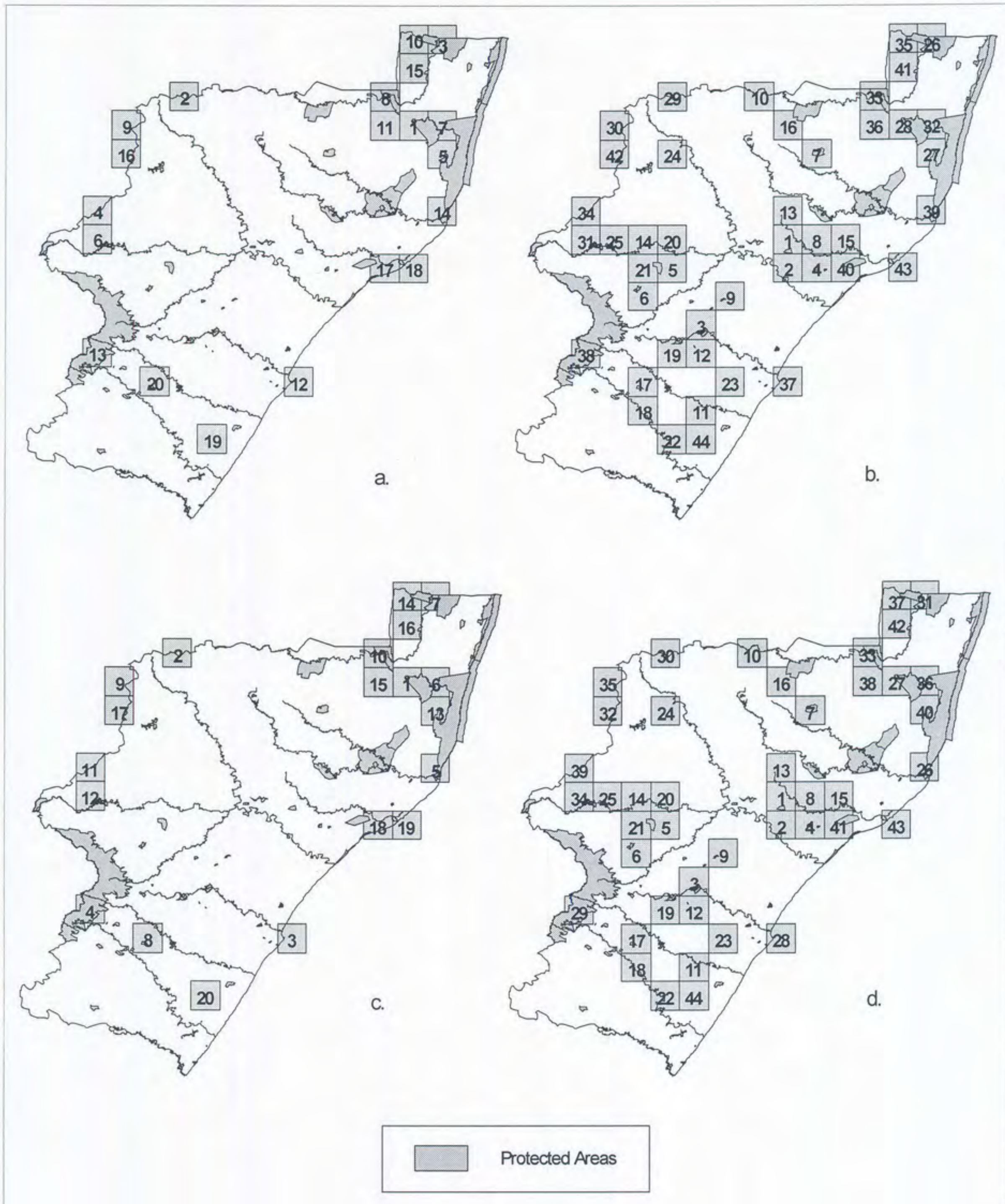

Figure 4.7: Comparison of algorithm results based on an ideal network, i.e., not taking into account current protected areas: (a) species rarity-based algorithm; (b) species rarity and beta diversity algorithm; (c) species richness-based algorithm; and (d) species richness and beta diversity algorithm.

southern Midlands avian communities largely unnoticed and under protected. This is due mostly to the fact that the Maputaland, East Coast and Drakensberg Escarpment regions are highly species rich, containing >90% of the avian species recorded for the province. Thus, once these

Table 4.7: Species conservation status and representation selection order based on algorithm type.

Species name	Common name	Conservation status	Species rarity	Species rarity and BD	Species richness	Species richness and BD
Accipiter ovampensis	Ovambo sparrowhawk	rare	10	14	12	16
Botaurus stellaris	bittern	critically endangered	12	17	14	18
Bubalornis niger	redbilled buffalo weaver	common resident	6	9	9	13
Campethera notata	Knysna woodpecker	globally near threatened	13	18	6	9
Chersomanes albofasciata	spikeheeled lark	near endemic, common	1	1	1	1
Ciconia abdimii	Abdim's stork	migrant visitor	11	15	13	17
Circus macrourus	pallid harrier	globally near threatened	5	10	8	11
Crex egregia	African crake	locally common	8	4	2	4
Cryptolybia woodwardi	Woodward's barbet	local endemic, vulnerable	9	16	7	10
Cursorius rufus	Burchell's courser	vulnerable, southern Africa	2	7	4	8
Daption capense	pintado petrel	common visitor	8	13	2	6
Diomedea melanophris	blackbrowed albatross	common visitor	8	13	2	6
Eupodotis afraoides	northern black korhaan	common resident	2	7	4	8
Falco rupicoloides	greater kestrel	common	1	1	1	1
Falco vespertinus	western redfooted kestrel	common migrant	1	1	1	1
Gallinula angulata	lesser moorhen	common	9	5	3	5
Glareola nordmanni	blackwinged pratincole	globally near threatened	3	11	5	12
Glaucidium capense	barred owl	rare	4	8	10	14
Hirundo atrocaerulea	blue swallow	rare, threatened	15	3	3	2
Larus fuscus	lesser blackbacked gull	uncommon	8	13	2	6
Macronectes giganteus	southern giant petrel	common visitor	8	13	2	6
Mirafra apiata	clapper lark	near endemic	2	7	4	8
Mirafra cheniana	melodious lark	endemic, threatened	3	2	5	3
Mirafra ruddi	Rudd's lark	local endemic, critically endangered	1	6	1	7
Numenius arquata	curlew	common, vulnerable	8	13	2	6
Oceanites oceanicus	Wilson's storm petrel	common	8	13	2	6
Pachycoccyx audeberti	thickbilled cuckoo	rare	7	12	11	15
Pinarocorys nigricans	dusky lark	uncommon	4	8	7	10
Podiceps nigricollis	blacknecked grebe	common	1	6	1	7
Poicephalus robustus	cape parrot	endemic, endangered	13	3	3	2
Prinia flavicans	blackchested prinia	near endemic, common	1	6	1	7
Procellaria aequinoctia	whitechinned petrel	common	8	13	2	6
Serinus atrogularis	blackthroated canary	common	1	1	1	1
Spermestes fringilloide	pied mannikin	rare, indeterminate conservation	14	18	6	9
Spizocorys conirostris	pinkbilled lark	near endemic, local nomad	1	4	1	4
Spizocorys fringillaris	Botha's lark	local endemic, endangered	1	6	1	7
Zoothera gurneyi	orange thrush	vulnerable, southern Africa	15	3	3	2

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

This makes the investigation and identification of the species community structure, as well as, the environmental gradients associated with that structure an essential component of conservation area selection procedures. By attempting to protect not only the biodiversity pattern but also the processes responsible for that pattern, conservation design may come closer to guaranteeing the representation, as well as the long-term retention of regional biodiversity. The grid cells selected by the BD algorithm, although similar to those selected by the traditional algorithm, differ in that some grid cells fall within the under-represented avian communities, particularly the highly heterogeneous areas in the Central Zululand and northern Central-southern Midlands communities. Both variants of the BD algorithm are able to begin selection in the

Central-southern Midlands and southern Central Zululand then move progressively to the higher richness areas of the East Coast, Maputaland and northern Drakensberg Escarpment.

In addition to the under-representation of the avian communities in the province's interior by the traditional reserve-selection procedures, it is obvious from the CCA analyses that these procedures succeed in representing the extremes of the CCA species-environment gradients. By focussing on species representation alone, the low lying, moist, hot Maputaland region and high, wet, cool Drakensberg Escarpment are well represented, but the climatically variable interior mid-altitude areas with their unique species assemblages are excluded.

Spatial autocorrelation analysis proved to be a valuable tool in the identification of areas of high beta diversity, as opposed to employing simple measures of alpha diversity traditionally used by reserve-selection techniques. Moran's I values for both the identified altitudinal-temperature environment gradient of axis 1 and the water balance environment gradient of axis 2 from the CCA analysis (Figure 4.2) enabled the identification of areas high in beta diversity. These areas highlighted by low Moran's I values contained very different species assemblages from their neighboring grid cells, as well as different environmental variables associated with these assemblages. By focussing on grid cells with low levels of spatial autocorrelation, the BD algorithm identified areas with highly dissimilar species, and environmental compositions from neighboring grid cells in the southern Zululand and northern Central Midlands. The Tugela River basin and Central-southern Midlands are the transition zones for flora and fauna from the Drakensberg Escarpment and coastal plains (Poynton, 1961) and these dominant river valleys may represent barriers to avian dispersal (Benson et al., 1962; Clancey, 1994). They also represent areas of high species turnover along the identified environmental gradients.

The contrasting selection orders (Figure 4.5) of the algorithms illustrate the highly dissimilar approaches and values assigned to each selected grid cell by the four procedures. The richness method favours areas of high species richness (Drakensberg Escarpment, East Coast and then Maputaland regions) and the rarity method favours the Drakensberg, Escarpment, Maputaland and then East Coast regions. The BD method using richness places emphasis on the interior regions, as it should, but must pick up the remainder of the required species from the Drakensberg Escarpment, East Coast and Maputaland regions. The BD and rarity method chooses a similar selection order for the interior but re-assigns selection order importance to grid cells in the Drakensberg Escarpment and Maputaland region. The spatial autocorrelation method employed here allows for the incorporation of measures of beta diversity into what are traditionally alpha diversity based reserve selection techniques. The results of the present study illustrate the value of the inclusion of areas with high levels of alpha and beta diversity. This investigation also highlights that the avian communities of high protection (Drakensberg

Escarpment and East Coast) are also skewed in their representation along north-south geographic gradients. The central Drakensberg Escarpment is adequately protected in the south and the East Coast protected areas lie in the north. Both the rarity and richness algorithms for all scenarios place emphasis on adequately protecting the full length of the Drakensberg Escarpment and strategic locations along the coastline.

However, as with any species-based reserve selection algorithm, problems emanating from error or particular areas in the available databases are immediately evident. The grid cell covering the city of Durban and its harbor contains eight species of Palaearctic seabirds only found there because of the fishing trawlers that they follow for food sources (Harrison et al., 1997) and the tidal mudflats. Several of these birds are near globally threatened and will require the conservation authorities to develop appropriate management plans at Durban harbor, which will not necessarily lead to the declaration of extra coastal reserves, but will require the extensive restoration of the mudflats and mangroves (Allan et al., 1999).

4.3.2 Practical Area Selection for Improved Conservation

Biological representativeness should be used as the first objective in selecting conservation worthy areas (Margules, 1986). To date complementary approaches to conservation have focussed primarily on maximising the conservation of contemporary alpha diversity patterns using measures of species, habitat richness or rarity (Margules and Pressey, 2000). The present study shows that the use of principles such as complementarity on species data alone does not always produce adequate biologically meaningful results. Although they represent the required species efficiently, they do little to address the long-term retention of species diversity through the conservation of underlying natural processes and turnover patterns that support this diversity pattern (Balmford et al., 1998; Cowling et al., 1999; Fairbanks and Benn, 2000; Rodrigues et al., 2000).

Climatic variables are generally important at coarser scales, whereas disturbance variables (e.g., management or successional stages), geology, or biotic factors tend to be important at finer scales. Of course, decisions on which environmental variables to include in direct gradient analysis will largely depend on the scale of the study (Wiens, 1989b). Nevertheless, by applying techniques such as CCA it is possible to find what the important environmental variables are, if no *a priori* knowledge exists about the possible predictor variables. In this study, the landscapes and physiographic basins contain climatic patterns, which interact to limit the species pool. By applying methods like CCA and spatial autocorrelation analysis, it is possible to consider all these environmental variables and their spatial arrangement in an integrated manner. Future studies will however, need to incorporate landscape connectivity (Forman, 1995; Wessels et al., 2000) and biological community structure (Soulé and Simberloff, 1986).

Fairbanks et al. (1996) presented evidence from Californian floral communities that the end points of species-environment gradients, where the climate is overly cold, hot, or dry, were more strongly affected by climate change and therefore more liable to species composition change. A South African climate change study conducted on invertebrate and vertebrate taxa estimated that 66% of all species found within the Kruger National Park would have a < 50% chance of being found there after a doubling of CO_2 levels (van Jaarsveld et al., 2000). It is important to raise the problem of how to preserve communities in a continually changing environment (White and Bratton, 1980), although fluctuations in natural communities over a variety of temporal scales are generally accepted (Wiens, 1984). How climate change impacts on current conservation, is an issue often discussed but rarely applied in conservation planning (Peters and Darling, 1985; Balmford et al., 1998; Huntley, 1998). Climatic change will certainly affect bird populations, though its precise effects are difficult to predict (Botkin et al., 1991; Furness and Greenwood, 1993). Therefore, although the BD algorithm is less land-use-efficient it manages to spatially represent the under-represented species, avian communities, and the identified environmental gradients in the two proposed conservation area networks. It could therefore be a surrogate for representing potential changes in temporal species assemblages (e.g., Rodriguez et al., 2000).

4.4 Summary

African conservation agencies are charged with the task of incorporating broader levels of biodiversity in an integrated manner to maintain systems and services (Maddock and du Plessis, 1999). However, the budgets of public conservation organizations fall far short of being able to fund the acquisition of all the new reserves the province will require to be truly representative of the avian biodiversity pattern identified in this study. Therefore, the development of a biologically sound logic and methods for identifying conservation areas must not be limited to identifying a reserve network. This study identified only broad conservation-worthy linkages among existing protected areas. This is the first of several steps in demarcating areas that could contribute to longer-term retention of avian diversity outside the formally protected areas (Armstrong et al., 2000). Implementation will need to ensure that landowners are amenable to conservation and that identified areas remain untransformed. In the short-term emphasis should be placed on identifying critical conservation areas for all the major taxonomic groups, which can then be included in a comprehensive regional conservation plan, integrating formal reserves and priority areas in the human-managed matrix.