The impact of land use on biodiversity in Xeric Succulent Thicket, South Africa

Christo Fabricius

Thesis presented for the degree of
DOCTOR OF PHILOSOPHY
in the Department of Zoology
UNIVERSITY OF CAPE TOWN

February 1997

higherarchy

the spin of the electrons 'round the atoms like the moon
molecules and puddles fill an ocean and soon
dna moulds microthings and every patch a
megaplace where magicthings
take place....to a
nevereven
tune

ACKNOWLEDGMENTS

The project would not have been possible without the support of my friends and colleagues. The following people deserve special acknowledgment:

Marius Burger, who was a pillar of support throughout the project and contributed to stimulating discussions, ably assisted with field work, and commented on and proofread earlier drafts; André Boshoff, the former Scientific Services manager of Eastern Cape Nature Conservation, who created opportunities, arranged adequate research funding, gave moral support and guidance and whose comments on earlier drafts were most useful; Phil Hockey, my academic supervisor, whose editorial comments greatly improved the quality of my writing; Graham Kerley of the Terrestrial Ecology Unit in the University of Port Elizabeth, who commented on the experimental design of the project and layout of the thesis; Jeremy Midgley of the Botany Dept., University of Cape Town, who commented on Chapter 4; Peter Norton, who commented on the project plan and arranged funds for satellite imagery and GIS work; and Roy Siegfried, former Director of the Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, who made extremely valuable inputs into the project plan. Tony Philips (Bucklands) and Ash Davenport (Hermanuskraal) permitted me to collect data on their properties. The Ndwayana community leaders gave us access to the communal area. Brad Fike made labour available for the construction of traps.

RESEARCH ASSISTANCE

This thesis represents my own unaided work, but the following people contributed to aspects of the research:

Field work: Marius Burger continuously and untiringly assisted with field data collection. Gerhard Gerber assisted with collecting and recording some of the arthropod and vegetation data, while L. Antony, C. Dubase, L. Gqamane, S. Hoyi, S. Loli and C. Tyatya assisted with collecting arthropod specimens.

Specialist assistance: Dr. Tony Palmer of the Range and Forage Institute, Agricultural Research Council, processed the SPOT satellite image data used in Chapter 3 and commented on earlier versions of that chapter. Dr. Nicky Allsopp of the Range and Forage Institute, Agricultural Research Council, analysed soil samples for mycorrhizal spores (Chapter 4), and commented on earlier drafts of Chapter 4;

Taxonomy: Marius Burger identified all herpetiles, and assisted with the curating and sorting of arthropod specimens into taxonomic units, supported by Dr. Martin Villet of the Dept. of Zoology and Entomology, Rhodes University. Drr. A. Dippenaar and R. Oberprieler of the Plant Protection Research Unit respectively identified spider and weevils (Appendixes 3 and 4).

CONTENT

The impact of land use on biodiversity in Xeric Succulent Thicket, South Africa

by Christo Fabricius

Ph.D. Thesis, University of Cape Town, February 1997

EXECUTIVE SUMMARY

Human-induced land management practices are key factors which influence the dynamics of landscapes, land elements and biotic communities in Xeric Succulent Thicket, a notoriously fragile and low resilience ecosystem in the Eastern Cape, South Africa. In its natural state this vegetation type is characterized by a continuous mosaic of clumps of diverse woody shrubs in a matrix of grass, hardy dwarf shrubs and bare ground. When indigenous herbivores are replaced by domestic livestock at unsustainable stocking rates, the ratio of clump to interclump areas decreases. This has impacts on biodiversity at the landscape level, and affects the composition and species richness of plant, arthropod and reptile communities and fungal symbionts.

The study has two main objectives: 1) to determine the local-level effects of different types of land use on biodiversity in Xeric Succulent Thicket; and 2) to better understand the factors which affect biodiversity in different taxonomic groups and at different spatial scales, so that the preservation function of protected areas could be enhanced. The key questions which are addressed in the thesis are

- *what does 'biodiversity' mean, and what are its different dimensions in Xeric Succulent Thicket;*
- *what roles do protected areas and other lands play in preserving biodiversity;*
- *how are different taxonomic groups affected by different types of land use; and*
- *how can biodiversity be monitored and measured?*

The regional 'conservation landscape' is seen as the protected area plus the land immediately adjoining it, and is viewed as an integrated mosaic of anthropogenic landscapes (land management units), land elements (patches within landscapes), producer communities (assemblages of interacting plant species), consumer communities (assemblages of interacting herbivores and predators) and soil micro-organisms. From a process point of view, the research relates the intensity of disturbance, mainly as a result of herbivory, to landscape complexity, the structure of land elements, and the species richness of producers and consumers within land elements. The patterns which emerge are interpreted in the context of ecosystem functioning, from the point of view of a practicing conservation biologist.

To achieve this, land management units across a gradient of land degradation, consisting of a nature reserve, a heavily stocked commercial ranch, a conservatively stocked commercial ranch and a communal area (CGA) were identified. Cross-boundary comparisons were made of the respective hierarchical levels of biodiversity mentioned above. At the regional and landscape level, the reflectance values in satellite images was used as an index of landscape complexity. At the same georeferenced localities the ratios of bushclumps to bare ground was measured, the abundance of plant species in bushclumps were recorded, arthropods and terrestrial reptiles were caught in pitfall traps, and the abundance of mycorrhizal spores were counted in soil samples. In addition to the cross-boundary comparisons, the relationship between the different levels of biodiversity was also calculated.

Landscapes: The nature reserve displayed significantly higher satellite-derived pixel CVs than the communal grazing area, and significantly higher ground-based diversity indexes than the commercial farms and possibly the communal grazing area. The means of the satellite-based and ground-based indexes were significantly and positively correlated. It is postulated that continuous intensive grazing in the absence of wild herbivores, such as in the CGA and some commercial farms, leads to a decrease in landscape patchiness, and that the presence of megaherbivores, coupled with naturally low stocking rates (as in the nature reserve), leads to an increase in landscape patchiness. The satellite-based technique is useful to identify potential sites of high biodiversity for more intensive sampling at a finer scale. It could also be used to monitor landscape degradation at a regional level.

Vegetation: The number of species in clumps was significantly correlated with bushclump area and the relationship was exponential. The nature reserve had significantly larger bushclumps than adjacent unconserved land and significantly more species per clump than both the commercial and communal rangeland. The proportions of sampling lines in the nature reserve which were intercepted by bushclumps, relative to the total length of the line, were significantly larger than that of unprotected land. The percentage cover of *Portulacaria afra* in bushclumps was significantly higher in the nature reserve than on unconserved land and confirmed the anticipated degradation gradient, while the cover of *Grewia robusta* was significantly higher in the nature reserve than in the communal area, but not significantly higher than on the commercial farm. Large clumps were characterized by bird-dispersed plant species, while the species which were not bird dispersed showed no significant association with any type of clump. Microsites in areas outside bushclumps contained significantly fewer mycorrhizal spores and less organic material, and very high aluminium concentrations compared to sites inside clumps. Microsites outside clumps seemed to be unsuitable for the establishment of seedlings. The underlying cause of degradation is postulated to be a reduction in bushclump size through overgrazing and human use, which leads to a decrease in nurse sites for seedlings of bird-dispersed plants and a gradual extinction of bird-dispersed trees and shrubs, together with other species associated with clump interiors. The environmental heterogeneity inside small clumps is also reduced, which results in an increase in the intensity of interspecies competition. Xeric Succulent Thicket has an extremely low sustainable stocking rate, whether in a pristine or degraded state. The profit-making phase is the transient period between a well-conserved and degraded condition: there is no evidence that the vegetation reverts to its former state after this shift has taken place. For conservation purposes, the size of bushclumps in Xeric Succulent Thicket should be monitored to record the proportion of bushclumps which exceed 5 m². This was the inflection point below which species richness in bushclumps decreased rapidly. To maintain Xeric Succulent Thicket outside protected areas, farm incomes should be supplemented by land uses other than commercial livestock production. These include nature tourism, stud farming or low-intensity commodity farming, e.g. feedlots and medicinal plants.

Terrestrial snakes and lizards: - Snakes and lizards were almost twice as abundant in the communal grazing area and had almost double the Hierarchical Richness Index (HRI) of any of the other localities, which had similar numbers of specimens and HRI values. In an ordination of localities and the eight most abundant species, the communal grazing area was associated with xeric-adapted species which distribution ranges are centred in the arid and semi-arid Western part of South Africa, whereas the other localities were mostly associated with species whose primary ranges lie in the less arid Northern and Eastern parts of the country. The relatively high abundance of reptiles in the communal grazing area is ascribed to the combined effect of improved conditions for thermoregulation and improved reptile hunting success in the open terrain, while reduced predation might have played a role. Xeric-adapted reptiles seem to be adequately conserved outside protected areas in the Xeric Succulent Thicket of the Eastern Cape. Species which are dependent on vegetation, e.g. those which lay their eggs in litter or are arboreal such as chameleons and tree snakes, are most sensitive to land degradation and require dense Xeric Succulent Thicket for their survival. Vegetation with this structure is rarely found outside protected areas, which play an important role in conserving arboreal reptiles.

Arthropods: - The nature reserve contained more Recognizable Taxonomic Units (RTUs) and a greater HRI than adjacent land for most arthropod taxonomic groups, and also contained the largest number of unique RTUs which were not collected on unconserved land. The communal grazing area differed most from the nature reserve in terms of richness and community similarity, followed by the conservatively stocked commercial farm. The historically overgrazed commercial farm was most similar to the nature reserve in terms of richness and community similarity. These differences and similarities between localities might be explained by the intermediate disturbance hypothesis. In an ordination, arthropods which were obligate herbivores were associated with well-vegetated localities while predatory arthropods were associated with the localities with poor vegetation cover.

The integrated picture: - Current understanding of biodiversity and ecosystem functioning in Xeric Succulent Thicket postulates that these ecosystems degrade according to an integrated process of reduction in patch productivity and within-patch heterogeneity. This leads to a decrease in within-patch species richness, and an increase in nutrient and energy flow from resource patches into the surrounding matrix. In smaller patches, palatable plants are exposed to herbivory, and good light competitors are outcompeted by good colonizers. This further reduces diversity. At the landscape level, landscape complexity is reduced through a decrease in the variety of patch types across the landscape and a reduction in species turnover between patches. Landscapes dominated by small patches are subject to perpetual 'drought' conditions. Arthropod species richness and abundance decrease because of the harsher and more simplified environment, which lead to more severe species interactions and the simplification of trophic and other ecosystem webs. Regression analysis of plant species richness on land element diversity, and arthropod species richness on plant species richness corroborates this paradigm: increasing levels of herbivory leads to a successive loss of species. As the spatial heterogeneity in the environment decreases, all species become rarer and recruitment eventually ceases. The abundance and species richness of weevils are especially well correlated with the diversity of other ecosystem elements higher up the hierarchy. Terrestrial snakes and lizards respond to different resources because of their unique physiology - their resource patches are the warm interclump areas where hunting success is high. They flourish in the degraded areas, especially since avian and mammalian predators are largely absent from such landscapes.

The key to the preservation of biodiversity in Xeric Succulent Thicket is the maintenance of high-quality (large) bushclumps through intermediate levels of herbivory by a variety of wild herbivores, and the preservation of different types of disturbance agents to create a diversity of disturbance patches across the landscape. At a regional level, the highest levels of biodiversity are attained when a variety of land use practices and, conversely, a diversity of land ownership, is promoted by land policy makers.

1. Introduction

Conservation biologists and plant ecologists believe that protected areas preserve more biodiversity than subsistence and commercial rangelands in Xeric Succulent Thicket (La Cock, Palmer & Everard 1990; Kerley, Knight & De Kock 1995; Moolman & Cowling 1994), but the data and models to substantiate this are largely unavailable. This study has two main objectives: 1) to determine the local-level effects of different types of land use on biodiversity in a notoriously fragile and low resilience ecosystem: the Xeric Succulent Thicket of the Eastern Cape, South Africa; and 2) to improve our understanding of the factors which affect biodiversity in different taxonomic groups and at different spatial scales, so that the biodiversity preservation function of protected areas could be enhanced if necessary.

The project was initiated by Eastern Cape Nature Conservation (now the Ministry of Economic Affairs, Environment and Tourism, Eastern Cape), following an extensive process of literature reviews, strategic planning and consultation with protected area managers and conservation scientists. The central questions which emerged during this issue-defining process were

- *what does 'biodiversity' mean, and what are its different dimensions in Xeric Succulent Thicket*;
- *how are different taxonomic groups affected by different types of land use;*
- *what role do protected areas and other forms of land use play in preserving biodiversity*;
- *how can biodiversity be monitored and measured?*

The rapid decline of biodiversity in most ecosystems, which is often a result of land use which is incompatible with conservation, necessitates urgent studies of the impact of land management on biodiversity (Schulze & Mooney 1994). Xeric Succulent Thicket is a particularly good laboratory to study the impacts of land use on fragile ecosystems (Nilssen & Grelsson 1995), as this vegetation type it is notorious for its slowness to recover after disturbance and degradation (Palmer 1981, 1990; La Cock, Palmer & Everard 1990; Midgley & Cowling 1993; Stuart-Hill & Aucamp 1993; Ainslie, Fox & Fabricius 1994; Kerley et al. 1995; see also Chapter 2). The sustainability [in terms of the definition of Chapin, Torn & Tateno (1996)[1]] of livestock farming and subsistence land use in this vegetation type is seriously questioned (Kerley et al. 1995; Kerley, Haschick, Fabricius & La Cock 1996).

Protected areas cannot be viewed in isolation, as if they are islands in a matrix with zero conservation value. Land adjacent to protected areas might contain unique species and processes which are absent from the protected area, and in some instances contain as much or more wild resources than the protected area itself (Western 1989; Schonewald-Cox et al. 1992). Besides, more than 90% of land in Xeric Succulent Thicket is situated outside protected areas, and most protected areas are much too small to preserve regional-level processes and species with large home ranges (Urban, O'Neill & Shugart 1987; La Cock, Palmer &

---

[1] "A sustainable ecosystem is one that, over a normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity, soil fertility, and rates of biogeochemical cycling" (Chapin, Torn & Tateno 1996).

Everard 1990; Franklin 1993). Land use policies need to take into account the impact of land use on biodiversity, not only because of the intrinsic value of species but also because of increasing evidence that diverse ecosystems can be utilized more sustainably and productively than less diverse ones (see next section for a more detailed analysis of these).

This type of integrated, holistic conservation approach requires research into the causes and effects of degradation at a variety of spatial scales and hierarchical ecosystem levels (Noss 1990; Turner & O'Neill 1995). Such an approach does not only improve our understanding of the processes which accompany land degradation, but also increases the ability of land managers to restore low-resilience ecosystems (Tilman 1994; Lawton & Brown 1994).

RESEARCH APPROACH

Land management practices are key factors which influence the dynamics of the landscapes, land elements and biotic communities of Xeric Succulent Thicket (La Cock, Palmer & Everard 1990). The regional 'conservation landscape' is seen as the nature reserve or protected area plus the land immediately adjoining it (Schonewald-Cox, Buechner, Sauvajot & Wilcox 1992), and is viewed as an integrated mosaic of anthropogenic landscapes (land management units), land elements (patches within landscapes), producer communities (assemblages of interacting plant species), consumer communities (assemblages of interacting herbivores and predators) and soil micro-organisms (Urban, O'Neill & Shugart 1987).

At the landscape level, the approach strives to obtain knowledge of patch *content* (communities and populations inside patches) as well as patch *context* (the relation between the patch, the matrix and surrounding patches) in order to better understand the determinants of regional-level biodiversity (Watts 1996). By following a landscape approach, the importance of environmental heterogeneity, disturbance and large-scale land use in influencing and maintaining biodiversity is taken into account (Schluter & Ricklefs 1993; Chen, Franklin & Lowe 1996). After all, landscapes and ecosystems are the basic structural components where animals and plants live, and plant communities are merely 'phytometers' which reflect landscape change (Lapin & Barnes 1995). Land transformation primarily manifests itself at the landscape scale, and an incorporation of this scale is essential to detect large-scale changes in ecosystems (Friedman & Zube 1992). A landscape approach to conservation has the advantage of facilitating the protection, often by chance, of a variety of organisms which are either undescribed or undetected (Franklin 1993).

A landscape approach alone is however not adequate to explain changes in diversity within patches. At the community level, communities and populations are influenced by changes in the environment as well as by each other through co-evolved interactions. These processes have been shown to have a profound influence on the number of species in an area (Ricklefs & Schluter 1993; Tilman & Pacala 1993; Ehrlich 1994).

From a process point of view, the holistic approach attempts to relate the intensity of disturbance, mainly as a result of herbivory, to landscape complexity, the structure of land elements, and the species richness of producers and consumers within land elements. Thus a structural, process-oriented approach, which characterizes the domain of study of 'ecosystem ecologists' (Grimm 1995), is combined with a ecological community approach, which looks at the interactions between organisms which share the same space (Ricklefs & Schluter 1993; Diamond & Case 1986). The patterns which emerge are interpreted in the context of ecosystem functioning (Schulze & Mooney 1994), from the point of view of practising conservation biologists. The practical conservation implications of the research are discussed where applicable.

In this study, land management units across a gradient of land degradation were identified, using historical information from the literature, anecdotal evidence of stocking rates through interviews with agricultural extension officers and land managers, and biological evidence i.e. the relative abundance of indicator species. A nature reserve (the Great Fish River Reserve) was used as a reference point against which cross-boundary comparisons of biodiversity were made in adjoining sites with different management histories.

Most ecosystems are dynamic, and their true functioning cannot be revealed without long-term studies which investigate their change over time (Picket, Parker & Fiedler 1992). Because of practical constraints, it was not possible to use a long-term approach in this study. The study should therefore be seen as a 'snapshot' in time, where spatial variation in the form of different levels of land degradation was used as a substitute for temporal variation. The different land management treatments which occur in the study area can be regarded as a once-off uncontrolled experiment.

THE IMPORTANCE OF BIODIVERSITY

From a purely biocentric point of view, species are important for their intrinsic value (Norton 1986; Reid & Miller 1989; McNeely, Miller, Reid & Mittermeier 1990). From a more anthropocentric point of view, the cultural value of biodiversity is important for medicinal, spiritual and practical purposes such as firewood and construction materials (Fabricius & Burger 1997). Culture and biodiversity are closely linked (McNeely 1989, 1991; Norton 1992; Gadgill, Berkes & Folke 1993); human value systems have an impact on biodiversity, and indigenous knowledge can contribute much to biodiversity preservation (Pimbert & Pretty 1995). A diversity of cultural values leads to mosaic of land use types, because of differences in land management styles which different types of people have (Fabricius & Burger 1994). A more detailed discussion falls beyond the scope of this study, although the topic will be mentioned again later in the conclusions (Chapter 8).

The economic value of biodiversity has been extensively dealt with elsewhere (McNeely 1988; Ehrenfeld 1990; Swanson 1992; Pearce & Moran 1994). It is difficult to measure, and relies to a large extent on the non-tangible values of biological resources, such as existence value and bequeath values (Bishop & Welsh 1992). It is known that biodiversity has an economic value for tourism (Sherman &

Dixon 1991; Maille & Mendelsohn 1993), forestry (Pearce & Moran 1994) formal agriculture (West 1993; Tainton, Zacharias & Hardy 1989), informal agriculture (Splash & Simpson 1993) and biomedicines (Bennett 1992; Cunningham 1992, 1994).

The importance of biodiversity in ecosystem functioning

The thesis deals mainly with the relation between land management and biodiversity in the context of ecosystem functions, and therefore a more extensive discussion of this role than other roles of biodiversity is warranted.

At the landscape level, landscape complexity leads to a diversity of habitat types and niches for different organisms, which leads to a wide range of limiting resources which affect speciation across the landscape. A larger number of species are thus able to coexist in complex landscapes than in landscapes where spatial heterogeneity is low (Tilman 1982). A high landscape diversity causes a high turnover of species between patches (Schluter & Ricklefs 1993), ameliorates the intensity of interactions between organisms (Tilman & Pacala 1993; Tilman 1994a), and leads to a variety of pathways of energy flow in the system (Lawton & Jones 1995). Variable landscapes not only have spatial diversity in the horizontal plane, but vertical diversity also varies from one patch to another, i.e. different types of patches are dominated by plants of different heights (Briand 1983), creating additional niches for birds, arthropods and reptiles.

At the plant community level, diverse ecosystems are more buffered against catastrophes than species-poor systems (McNaughton 1994). Insects are protected from enemies and from competition through refuges created by diverse plant species, and each plant is recognized as a 'microlandscape' (Polis & Strong 1996). Many of the paradigms of the function of species-richness in ecosystems have been developed for grasslands, but may be equally applicable to other ecosystems (Tilman 1994b). Species-rich grasslands are more resistant to grazing than species-poor grasslands, but only when subjected to grazing by four or fewer species of grazers (McNaughton 1977). Plant productivity in particular is positively correlated with community diversity in model ecosystems, while a loss of diversity alters biogeochemical processes such as CO_2 fixation (Naeem et al. 1994, 1995). [Some ecologists are however highly sceptical of the relevance of artificial ecosystems such as micro- and 'mesocosms', and for good reason: the 'noise' which microcosms remove might be the very factors which drive real ecosystems (Carpenter 1996)]. Diverse grassland communities are more drought-resistant, and recover faster after major droughts than species-poor communities (Tilman & Downing 1994). Furthermore, the relationship between species richness and drought resistance is non-linear, i.e. the system's resistance to drought becomes disproportionately reduced as species-richness decreases (McNaughton 1994).

The relation between energy flow and diversity in ecosystems was conceptualized by McArthur (1955) who proposed that the more diverse the pathways of energy flow in the system were, the more likely the system would be to remain stable if one of the pathways was removed through an environmental perturbation or an extinction. Food webs containing a variety of species are larger and probably more stable than those with few species: species-poor systems in microcosms behave more chaotically than species-rich ones (Woodward 1994). In high-diversity systems consumer species are able to switch between prey species when the environment fluctuates, thereby maintaining the number of linkages in the food web (Lawton & Brown 1994). Extinctions at one hierarchical level in the food web lead to a cascade effect which affects other levels in the web (Yodzis 1993; Cohen & Newman 1985). Numerous authors found that the removal of lizards lead to a 2 - 3 fold increase in the abundance of ground-and canopy dwelling spiders, but to a decrease in the abundance of some insects which are the prey of spiders (reviewed by Dial & Roughgarden 1995). Other ecosystem webs such as 'mutualism webs' and 'ecosystem engineering webs' are equally interconnected, and are as sensitive to the cascade effect as food webs are (Martinez 1995).

Redundancy. Whether every species in the ecosystem has an important and unique role to play [Ehrlich & Ehrlich's' (1992) 'rivet' analogy; see also Gitay, Wilson & Lee 1996), or whether there is a high degree of redundancy in the system (Walker 1992) depends on the type of system. Lawton & Brown (1994) suggest that systems where biomass is readily restored after local extinction (i.e. where density compensation readily takes place), have a high degree of functional redundancy. At the taxonomic level, taxonomic groups with large numbers of lower taxonomic categories (e.g. genera or species) might also have a large degree of ecological redundancy because of the fine taxonomic subdivisions. It is known that density compensation in plants in Xeric Succulent Thicket (see Study Area chapter) is virtually non-existent (Palmer 1981; La Cock 1992; Kerley et al. 1995). It is therefore probable that the ecological redundancy of plant species in Xeric Succulent Thicket is low.

FACTORS AFFECTING BIODIVERSITY

Biodiversity is affected by a variety of biotic and abiotic factors which are extensively reviewed in Ricklefs & Schluter (1993) and Schulze & Mooney (1994). In Xeric Succulent Thicket, three related factors primarily affect biodiversity: environmental heterogeneity, disturbance, and resource availability.

Environmental heterogeneity

The level of environmental complexity, as reflected by landscape and land element diversity, is probably the most important determinant of biodiversity in most ecosystems (Scheiner 1992; Franklin 1993; Ricklefs & Schluter 1993; Tilman 1994a; DeAngelis 1995; James, Landsberg & Morton 1995). Variable landscapes are caused by diversity in abiotic resources (soils, geomorphological features and geology), but also by a diversity of biogenic disturbances. Heterogeneous environments allow different suites of species to coexist in the different habitat fragments (Tilman 1994b), while spatial and temporal environmental variability influences the length of food chains, which tend to be shorter in variable environments (Yodzis 1993). The spatial subdivision of ecosystems might explain why so many species are able to coexist, despite the finite number of limiting resources in the environment (Tilman 1994b).

The importance of bushclumps. For the purpose of this study, a bushclump is defined as a group of three or more woody species of which the branches or leaves touch one another less than 1 m above ground. Most vegetation types in arid areas have a clumped distribution (Milton, Dean, du Plessis & Siegfried 1994; Suzan, Nabhan & Patten 1996) and Xeric Succulent Thicket is no exception. The clumps are well-defined and vary in size between <1 - 25 m in diameter, with an average area of about 10 m^2 in well-preserved landscapes. Small clumps have a higher ratio of edge to interior, and the 'leakage' of energy and nutrients from the interior of the clump into the matrix is accelerated (James et al.1995). The clumps can be regarded as resource patches with higher concentrations of nutrients (P, N and organic matter) than areas outside clumps (La Cock 1992) and a higher moisture content than interclump areas (Palmer 1981). The clumps differ so much in species composition and structure from the interclump areas that it is tempting to agree with Palmer's (1981) hypothesis that Xeric Succulent Thicket is a remnant of vegetation which was established during a moist paleoclimatic regime, and that the bushclumps are remnants which remained on anomalous soils, where they maintained their own microclimate.

Productive environments are normally more species-rich than unproductive ones, although the relationship is unimodal i.e. extremely productive environments are characterized by a decrease in species richness (Rosenzweig & Abramsky 1993). The main reason for the unimodal curve might be the competitive exclusion of species in both highly productive and unproductive environments (Lawton & Brown 1994), although some researchers believe the unimodal curve is a sampling artefact (Oksanen 1996). At the plant community level, large patches lead to a greater degree of spatial variation in limiting resources inside patches, and a lower intensity of community interactions such as competition or predation (McLaughlin & Roughgarden 1993; Lawton & Brown 1994).

Disturbance

Disturbance influences biodiversity primarily at the community level (Connell 1978; Levin & Paine 1974; White & Picket 1985) although large-scale perturbations and disturbance are a major source of landscape change too (Romme & Knight 1982).

At the community level it is now widely accepted that intermediate levels of disturbance lead to the highest levels of species richness (Connell 1978; White & Picket 1985; Lawton 1994; Hobbie, Jensen & Chapin 1994). The mechanism for this is reasonably clear: in frequently disturbed ecosystems, two factors operate simultaneously (Rosenzweig & Abramsky 1993). First, a number of species are physically removed from the system during the disturbance event. Second, competitive exclusion takes place and rapid colonizers are favoured over good light and moisture competitors (Hobbie et al.1994). The entire system becomes early-successional and the community is simplified. In communities where disturbance events are far apart, the full range of successional habitats are present (Tilman & Pacala 1993). Additional species which are lesser competitors are able to migrate into the community before another disturbance event takes place, thereby increasing the diversity. When the time between disturbance events is very long, competitive dominance sets in and competitively inferior species are excluded from the community. The community becomes dominated either by good nutrient competitors (in low-productivity systems) or good light competitors in high-productivity systems (Hobbie et al. 1994).

A diversity of wildlife can influence landscape heterogeneity (Huntly 1995; Hulme 1996). Large herbivores cause structural 'damage' to the vegetation through physical breakage of branches and stems (Huntly 1995), and ecosystem engineers (Bond 1994) such as aardvark, which dig holes that other organisms subsequently use as shelter, may alter the environment substantially. Porcupines cause changes in the physiognomy of savannas by gnawing the bark of large trees which makes them susceptible to fire damage (Yeaton 1988), and zebra and warthog cause soil depressions though wallowing in mud which again causes small-scale patches in the landscape which collect water during rains and act as habitat for amphibians and other aquatic vertebrates and invertebrates.

Megaherbivores are particularly important ecosystem engineers (Owen-Smith 1988; Lawton & Brown 1994) and can significantly change the structure of ecosystems, especially in conjunction with other disturbance agents such as fire (Pellew 1983). Different-sized organisms deposit different types and sizes of dung, which provides habitat and food for a diversity of invertebrates. Even the variety of depressions created by the hoofprints of animals of different hoof and body sizes create different types of micro-landscapes for small organisms (Wiens 1989).

At the community level, herbivory might be as or more important than competition in determining the composition and diversity of terrestrial plant communities (Hulme 1996a). Apart from acting as defoliating agents, herbivores also influence competitive interactions between plants, thereby affecting biodiversity, through competitive release or exclusion (Tilman & Pacala 1993). Herbivores affect different plant species differently, and allow grazing or browsing-resistant plant species to outcompete species which are sensitive to grazing or browsing. The most important influence of herbivores, especially in woody plant communities, is not on adult plants but on seedlings (Hulme 1996b). This might explain the dominance (in biomass) of vegetatively reproducing plants in Xeric Succulent Ticket (Midgley & Cowling 1993) . Seed predation by herbivores in the immediate vicinity of the parent plant may, however, increase diversity under certain conditions by promoting the establishment of species which would have otherwise been outcompeted (Janzen 1970).

The effect of domestic livestock. On commercial farms, large herbivores (except the most cryptic or mobile species) are replaced by domestic livestock, because of the former's incompatibility with farming. This has three effects: herbivory intensifies because of the short-term economic viability of unsustainable stocking rates (Kerley et al. 1995); the relaxation of herbivory, which accompanies characteristic natural population fluctuations, does not take place or is less prolonged because livestock are fed during droughts; and the diversity of biogenic disturbance agents and feeding strategies in the system is reduced (Huntly 1995). Intensive herbivory, especially by domestic goats, reduces the size of the bushclumps from the edge inward (Stuart-Hill 1992). This puts seedlings, which need the microclimate and protection of bushclumps to establish, at risk (La Cock 1992). Intensive continuous herbivory also reduces the biomass of palatable woody plants (Stuart-Hill, Aucamp, Le Roux & Teague 1986), and the species richness of rare succulents which grow in the shelter of large clumps (Moolman & Cowling 1994). Plant communities do not benefit from prolonged rest periods which are essential for seedling establishment and the maintenance of biomass (Stuart-Hill et al. 1994; Huntly 1995). This leads to a simplification of landscape diversity at a range of spatial scales, from the scale of a bushclump down to the microlandscape level. The diversity in size and texture of individual plants is reduced, the size and consistency of dung middens are simplified, depressions created by hoofprints and the width of animal paths vary little, and the size distribution of litter particles become more homogenous. The process of landscape degradation is set in motion, which is eventually reflected in a reduction in community diversity, energy flow pathways, productivity and below-ground diversity. Domestic livestock may, however, also increase environmental heterogeneity by the piospheres they create around water and feeding points (James & Friedel 1995).

Resource availability

In broad terms, one of the main factors affecting species diversity is the number of limiting resources in the environment (Tilman 1994). The number of species which are able to coexist in a given homogenous environment should theoretically be equal to the number of limiting resources in that environment. The rationale for this is that each species has one or more unique evolutionary adaptations, which allows it to survive and outcompete other species without that particular adaptation, *provided that the environmental limitations towards which that adaptation is aimed, are present*. This is what gives different species different competitive advantages. The more limiting factors there are, the more evolutionary adaptations are possible and the greater the degree of speciation (Tilman 1994).

The composition of plant communities might be shaped by the relationship between resource availability, light availability and thus the productivity of the habitat (Hobbie et al. 1994; Tilman & Pacala 1993). In habitats with a gradient of productivity, there is a variety of 'domains' in the two-dimensional light - nutrient plane. In a high-nutrient, productive environment, light is the limiting factor and the community is dominated by good light competitors, whereas in a low-nutrient environment the community is dominated by good colonizers which are mostly poor competitors for light. In highly productive environments, light becomes the main limiting resource and species richness declines as colonizers are excluded. In low productivity, nutrient-poor environments the opposite is true: good colonizers outcompete good light competitors. This results in a unimodal ('hump-shaped') relationship between diversity and productivity, reviewed by Rosenzweig & Abramsky (1993). The unimodal relationship might however be an artefact of sampling: when plots of fixed size are used, as is often the case in comparative studies, communities with a high biomass, at the high-productivity end of the curve, normally consist of fewer but larger individuals, and *de facto* have a lower diversity (Oksanen 1996). The reality of the unimodal distribution has been challenged because of the lack of evidence that competition is responsible for the shape of the curve, and because many productivity-diversity relationships have been shown to be monotonic (Abrams 1995).

Historical factors are important determinants of biodiversity, and are extremely difficult to identify or control. In Xeric Succulent Thicket, with its slow recovery rate after disturbance, historical influences on biodiversity are more severe than in more resilient ecosystems. The history of every locality was carefully researched before and during the course of the project, and in one instance where the site history could not be satisfactorily determined, the site was excluded from further study.

INFLUENCE OF SCALE AND REGIONAL PROCESSES ON LOCAL BIODIVERSITY

Biodiversity can be measured at different spatial scales. Gamma diversity is the number of species contained in the full mosaic of landscapes at a regional scale. This can be subdivided into alpha diversity (the number of species in a single habitat, patch, land element or plot) and beta diversity, which is the turnover of species between habitats [the inverse of Sorenson's (1948) community similarity]. Gamma diversity is thus a product of alpha and beta diversity (Whittaker 1972), and is dependent on the cumulative effect of local diversity and the mosaic of landscapes and land elements present in a region. Local diversity is however strongly influenced by regional diversity - migration of species from rich landscapes in the region can elevate the diversity of impoverished landscapes. It is however difficult to assess whether regional diversity primarily influences local diversity, or *vice versa* (Ricklefs & Schluter 1993; Holt 1993). It is therefore essential for researchers to sample the ecosystem at a variety of scales which reflect these different levels of diversity (Ricklefs 1987).

Different organisms experience resource patches differently, depending mainly on their size and mobility (Wiens 1989). Studies of the interaction between different members of ecological communities, such as food web studies (Hengeveld 1987) are particularly sensitive to the scale used. The amount of environmental heterogeneity measured in a system also depends entirely on the scale used, and its relevance depends on how it relates to the scales at which the various organisms in the system respond to the environment. Different taxa have different patterns of movement across microlandscapes, as reflected by the fractal dimensions of these movements; ants, for example, seem to perceive a finer-grained environment than beetles (Wiens, Crist, With & Milne 1995). Measurements at a variety of spatial scales are essential for studies of environmental heterogeneity and its impact on diversity in various taxonomic groups (Wiens 1989). It might be true that coarse-scale patterns in the landscape are perpetuated as fractals to finer and finer scales (Wiens & Milne1989). Large herbivores, on the other hand, might perceive the habitat at the individual plant or clump level when foraging, but their selection of shelter is influenced by coarser-scale landscape features (Senft, Coughenour, Bailey, Rittenhouse, Sala & Swift 1987).

INDICATORS OF BIODIVERSITY

Conservationists need to determine which indicators best reflect changes in biodiversity at an appropriate scale, to be able to identify protected areas and to set up monitoring programmes (Franklin 1993). This will result in an improvement in conservation efficiency, budget savings and improved long-term planning (James at al. 1995).

Although African savannas are to some extent driven by large mammals (Owen-Smith 1989; Stuart-Hill 1992; Bond 1994) these animals might be unsuitable indicators of biodiversity change, mainly because their distribution in Xeric Succulent Thicket is influenced by human-induced extinctions and relocations. With the exception of the most mobile mammals which easily move across standard fences (e.g. kudu, leopards and caracal), or the most solitary, cryptic and secretive herbivores (e.g. bushbuck and blue duiker)[2], the distributions of most large mammals on private land and in the recently-established protected areas in South Africa are the result of artificial re-establishment by humans (Benson 1991).

An appropriate suite of indicators to study the impact of land management of biodiversity should be:

- functional at a variety of spatial scales;
- compatible with the technical abilities of the research team, i.e. relatively easy to collect and identify;
- sensitive to the measuring instrument used;
- present in all the land management treatments and replicates in the study area;
- sufficiently abundant to yield enough data, but rare enough to be habitat specialists;
- undeterred by fences which separate the respective land management units; and
- relatively immobile (Samways 1994; Rivers-Moore & Samways 1996).

At the regional and landscape level, reflectance values in satellite images are sensitive to differences and variation in light reflectance in the 0.30 - 0.69 µm light spectra (Lillesand & Kiefer 1987; Forman & Godron 1986). Satellite imagery is available at a relatively affordable cost in South Africa, and the software, hardware and human resources to manage and interpret it at the required scale are available. Plant species are easy to collect and identify, and local herbaria contain representative collections.

Arthropods are the most diverse group of described organisms, and have an important influence on ecosystem functioning as pollinators, decomposers and pest controllers (Kim 1993). Arthropods are more difficult to identify at the species level than plants, but if rapid assessment methods are used (cf. Chapter 6 and Beattie, Majer & Oliver 1993) in conjunction with the specialist advice of taxonomists, the data yield is high compared to that of other taxonomic groups (Samways 1994). They are sensitive to anthropogenic stress, and are therefore good indicators of ecosystem change (Milton & Dean 1992; Kim 1993; Samways 1994). Arthropods have short generation times, and reflect changes in the environment more rapidly than do larger organisms with longer generation times do. This contributes to their usefulness as ecosystem indicators (Hafernik 1992).

Reptiles are not known as good indicators, and often thrive on disturbed land (Germano & Hungerford 1981), but provisional surveys indicated that reptiles were abundant in the study area and that their inclusion might yield a large amount of

---

[2] Appendix 1 contains a complete list of scientific names of mammals mentioned in this document

data per unit effort. At the soil micro-organism level, mycorrhizae are sensitive to change in soil chemistry and structure, and play an important mutualistic role in nutrient uptake and seedling establishment (Read 1994).

LAYOUT OF THE THESIS

Over the following seven chapters, this hierarchical relationship between land use and biodiversity is further explored. In Chapter 2, the study area is described and a model is put forward for the influence of biological and non-biological factors on biodiversity in Xeric Succulent Thicket. Chapter 3 investigates differences in landscape diversity, at the land element level, between the different land management treatments. In Chapter 4, the impact of different types of land use on vegetation structure, plant species richness and mycorrhizal abundance is investigated. Chapter 5 assesses the species richness and abundance of terrestrial snakes and lizards in the various land management treatments. Chapter 6 compares the same impacts on terrestrial arthropods, and explores the arthropod species traits associated with different intensities of herbivory. In Chapter 7 the relationships between the different hierarchical levels of biodiversity are analyzed, and the general conclusions are summarized in Chapter 8.

2. Study area

GENERAL DESCRIPTION

The Great Fish River Nature Reserve and neighbouring land is situated in the mid-Fish River Valley, about 30 km north of Grahamstown in the Eastern Cape Province, South Africa. The study area is bisected by the Great Fish (Nxuba) River, which is the historic boundary between the former Ciskei to the east, and the former Cape Province to the west (Figure 1). The two administrative areas have since 1994 amalgamated into a single administrative region, the Eastern Cape Province.

Vegetation and physical environment

The vegetation is an unusual type of arid savanna (Rutherford & Westfall 1986) with a high species diversity compared to other savannas, and an extremely low resilience[1] (La Cock, Palmer & Everard 1990; Stuart-Hill & Aucamp 1993; Midgley & Cowling 1993). It was originally classified as Valley Bushveld (Acocks 1988) and is nowadays called Xeric Succulent Thicket, a suborder of Subtropical Transitional Thicket (Everard 1987; La Cock, Palmer & Everard 1990).

The vegetation has three main components: i) a woody tree and tall shrub component, structurally classified as tall dense shrubland; ii) a grass component and iii) an unpalatable dwarf shrub component. It is regarded as a transition between subtropical forest, fynbos, Karoo and grassland, and these different origins are recognizable in the diversity of life forms which grow under different soil and moisture regimes, often within the same land form (Cowling & Holmes 1991).

The first impression is that the vegetation is a continuous thicket (Figure 2), but closer inspection reveals that it actually consists of bushclumps of varying sizes, interspersed by bare areas (Figure 3). In some instances the bushclumps are densely packed and barely recognizable, while in other instances (mostly degraded conditions) they are scattered and well-defined (Figures 4 and 5)[2]. The many conspicuous fence-line contrasts which can be observed throughout this vegetation type indicate that the differences in vegetation density are a result of agricultural management practices (Figure 6; see also Kerley, Knight & de Kock 1995).

Landscapes in Xeric Succulent Thicket thus consist of two different, interwoven ecosystems: bushclumps, which consist of a core of woody bird-dispersed forest trees and shrubs and a fringe of vegetatively reproducing succulents; and interclump areas, which consist of a mixture of grass and dwarf shrubs. The vegetation of the bushclumps has a high seasonal drought-resistance but a low resilience, while the interclump areas have a weak seasonal resistance to drought but a high resilience (provided that the soil remains).

Most of the long-lived woody trees and shrubs are palatable and evergreen, and are adapted to moderate levels of browsing. There are two main mechanisms of dispersal of woody plants, reflected in the reproductive strategies of the different

---

[1] Defined here as the system's ability to recover to a natural state after a disturbance event.

[2] These clumps should not be confused with Palmer's (1981) Bushclump Savanna, which consists of sparse bushclumps, containing mainly forest elements which grow on termite mounds in a matrix of high-elevation grassland.

growth forms: vegetative dispersal by ramets characterises the succulent component (Midgley & Cowling 1993), and zoochory, mainly by birds, characterises the subtropical and montane forest component (Cowling 1983). The evergreen woody and succulent component is particularly fragile, as most of these species are either highly palatable and nutritious, or require 'nurse sites' inside bushclumps to establish (La Cock 1992). The vegetation could be a relict from higher rainfall regimes approximately 10 000 years ago (Palmer 1990), which explains its fragility and anomalous physiognomy in relation to the present low rainfall. The structure and species composition of the vegetation can be accurately predicted from elevation alone, so that sites at similar elevations should contain similar plant communities if the effect of management is excluded (Palmer & Avis 1994).

The Great Fish River Valley is characterised by large variations in topography, with elevations ranging from 300 m to 820 m above sea level. The many drainage lines and tributaries of the Great Fish River contribute to the landscape complexity. The geology consists entirely of shales of the Ecca variety, which range in colour from yellowish-brown to black, in areas close to intrusions of igneous rock. The soils which feed the bushclumps have a higher rain-use efficiency, Ca and Mg content, organic material content and moisture-holding capacity than the inter-patch areas (Palmer 1981). These are elevated relative to the interclump areas, and are often aerated, possibly as a result of the activities of termites and earthworms, and their high organic content (pers. obs.). All soils have a high clay content of about 22% (La Cock 1992). In the interclump areas the soils are shallow, to the point where the shales are often exposed, and they contain very high levels of aluminium (La Cock 1992). While winters are mild and mainly frost-free, maximum temperatures in excess of 35 ° C are recorded on most December and January days. The mean annual rainfall ranges from 550 mm in the grassy, high-lying areas to 350 mm in low-lying areas and falls mainly in summer.

For the purpose of this study, three main land use types are distinguished in the study area: i) nature conservation on government-controlled land; ii) commercial ranching on private land; and iii) below-subsistence natural resource use by rural villagers on communally-owned land.

Land use types

Nature Conservation. The Great Fish River Nature Reserve was, at the time of writing, managed by two different agencies (Eastern Cape Nature Conservation and Contour) with slightly different management philosophies and missions. The sections which were previously called the Andries Vosloo Kudu Reserve and Sam Knott Nature Reserves are managed by Eastern Cape Nature Conservation, which focuses mainly on preserving biodiversity, while the Double Drift nature reserve is managed by the Conservation and Tourism Corporation (Contour), which focuses more strongly than the Government department on deriving revenue from conservation.

The Andries Vosloo Kudu Reserve (where my sampling localities in the Nature Reserve were located) was established when the farms Kentucky, Double Drift and Grasslands were bought from commercial farmers in 1973. In 1976 the farm Lowestof was added, and the reserve increased in size to about 6500 ha. In

1988 the late Mr. Sam Knott bequeathed several farms to the Southern African Nature Foundation (now WWF-SA), with an agreement that the Cape Provincial Administration would manage the area. This increased the size of the new reserve to 23000 ha. Since then, five chalets and an entrance gate have been built, internal fences and windmills have been removed, a new perimeter fence has been erected and various large mammal species were introduced.

On the former Ciskei side of the Great Fish River, the L.L. Sebe Game Reserve was established in 1982 after 10 farms had been bought by the South African Development Trust to consolidate the Ciskei. In 1990, after Mr. Sebe was toppled by Brig. Gqozo, the name changed to the Double Drift Game Reserve. Between 1987 and 1990 more than 400 labourers of the previous white farmers were relocated with compensation, and in 1990 a game-proof fence was erected and large herbivores were introduced.

In 1993 a joint management committee was initiated, and the process to manage the three reserves as a single unit commenced. By 1995 a single management plan had been drawn up (Eastern Cape Nature Conservation and Contour 1996), but by March 1996 the area was still managed by two authorities with different mandates and jurisdictions. The size of the combined area is approximately 45 000 ha, and the human population density in the reserve is about 1.2 people / km^2, consisting of staff and their families. The goals of the new reserve are to

- conserve ecological systems and processes which characterize the Fish River Valley, and which are vanishing on unconserved land;
- conserve and utilize the cultural and natural heritage of the Reserve;
- provide appropriate opportunities for recreation, education and research;
- manage the area in an economically viable manner; and
- contribute to the quality of life of neighbouring communities

(verbatim from Eastern Cape Nature Conservation and Contour, 1996).

The fence surrounding the nature reserve keeps most large herbivores inside, but it is not high enough to confine kudu, which regularly move between the reserve and neighbouring commercial farms, while warthog sometimes burrow through to adjacent land despite the lower strands of the fence being electrified. The grazing intensity is relatively low at about 17 ha / LAU (Large Animal Unit) of continuous grazing, calculated in June 1995. The nature reserve contains a variety of large herbivores which occur neither on private farms nor in the communal areas. Of special relevance are the megaherbivores buffalo (about 150), eland (65), black rhinoceros (22) and small herd of hippopotamus (5). Kudu occur at densities of 6 - 12 / km^2 on the nature reserve (East Cape Nature Conservation and Contour 1996), which is possibly higher than on adjacent commercial rangeland, and reputed to be the highest in the country. Amongst the small mammalian herbivores, the warthog population fluctuates between 600 and 1700 depending on rainfall, and there are about 120 red hartebeest, 20 springbok and 20 - 30 ostriches. Numerous cryptic small antelope such as bushbuck, grey and blue duiker and steenbok also occur on the Reserve.

Commercial ranching. This type of agriculture is practiced mainly by European farmers, assisted by their Xhosa-speaking labourers. On most commercial farms the human population density is about 3 people / km². The land is managed for commercial livestock production, with some alfalfa fields on alluvial soils next to the river. Large wild mammals on commercial farms are limited to the most cryptic and mobile species, i.e. kudu, warthog, bushbuck, grey and blue duiker and carnivores - leopard, black-backed jackal and caracal.

The livestock density (mainly Angora goats) varies between 8 and 13 ha / Large Animal Unit or LAU, depending on the level of degradation of the vegetation and the annual rainfall (ARDRI 1994). The minimum size of a viable commercial farm is between 2000 and 2500 ha (R. Dempsey, Dept. of Agriculture, Grahamstown, pers. comm.).

The commercial farming community is well-organized through local-level Farmers' Associations which are affiliated to the South African Agricultural Union, and they have free access to the advice of highly qualified government-employed agricultural extension officers. Until recently their marketing was done through agricultural control boards such as the Mohair Control Board and the Meat Board, and farmers with financial problems, often due to overgrazing, received government subsidies. These subsidies were later replaced by stock reduction schemes, whereby farmers were compensated for a reduction in livestock numbers. By 1996 the subsidies were phased out.

Commercial Farm 1 or CF1 (the farm Hermanuskraal) has a history of overgrazing. During the previous century (between about 1820 and 1880) it formed part of a military outpost when the Eastern Cape was under British rule (Coetzee 1994) and was subject to prolonged intensive grazing by cattle and horses. After the military activities ceased towards the end of the century, it became commercial farmland and was incorporated into the farm Resolution. Up until 1960 the farm was heavily stocked with sheep and goats. This was consistent with the conventional dogma of that era that dense vegetation harboured ticks and had to be cleared, and that the "open" form of Xeric Succulent Thicket was more productive than the dense form. In this instance the impact was particularly severe because of the small size of the property (about 200 ha) and the fact that it does not have internal fences. By 1960 the impact of heavy grazing necessitated a lighter stocking rate, but even then the farm was subject to periods of up to four times the recommended stocking rate, until 1993, when the property's only stock was 100 head of cattle for 2 months of the year for the following three years (A. Davenport, Resolution, P.O. Grahamstown, 6140, *in litt.*).

CF2 (the farm Bucklands) has a history of successful commercial farming since 1970 and is conservatively stocked and intensively managed for commercial livestock production. Livestock are rotated according to a fixed pattern, following a short-duration grazing system. The system consists of many camps arranged in the shape of wagon-wheel (the Savory method, Tainton 1981), which allows long rest periods interrupted by short bouts of intensive grazing. Camps are grazed by mohair goats (about 70% of stock) and cattle (about 30% of stock) for 12 - 38 days per year and rested for the rest of the year, and the condition of the vegetation is continuously monitored. Stocking rates average about 8.5 ha / LAU, but vary with rainfall (A. Phillips, Bucklands, P.O. Grahamstown 6140 *in litt.*). The property is referred to by the Dept. of Agriculture as a benchmark for vegetation condition assessment in the region (R. Dempsey, Dept. Agriculture, Grahamstown 6140 pers. comm.).

Communal land use. Land on the eastern side of the Great Fish River is inhabited and collectively managed by Xhosa-speaking people, but owned by the State. The human population density is extremely high at 70 people / km². The maximum sustainable population density of an area with a slightly higher mean annual rainfall (475 mm / year) in the South Sahel is estimated to be 13 people / km², while it is estimated that South Sudan, with a mean annual rainfall of more than 1050 mm, can sustain 51 people / km² (Kessler 1994).

Up until 1994 the communal area formed part of the former Ciskei. About 6 million people from places throughout South Africa, but mainly from the Eastern Cape, were forcibly moved to the Ciskei between 1970 and 1982 to enforce the apartheid policies of the time. In 1994 the Ciskei became part of Eastern Cape Province of the 'New South Africa', but until present this has had little effect on the quality of life of the people in the area. More than 65% of the people in the communal areas are unemployed, and the area is inhabited by mainly retired people, and children of school-going age (Ainslie, Fox & Fabricius 1994).

In this communal grazing area (CGA), land is managed under communal and tribal ownership, and the main land use is subsistence livestock "farming" and cultivation. Cultivation is limited because of unsuitable soils and aridity, and takes place around homesteads and in government-run irrigation schemes (ARDRI 1994).

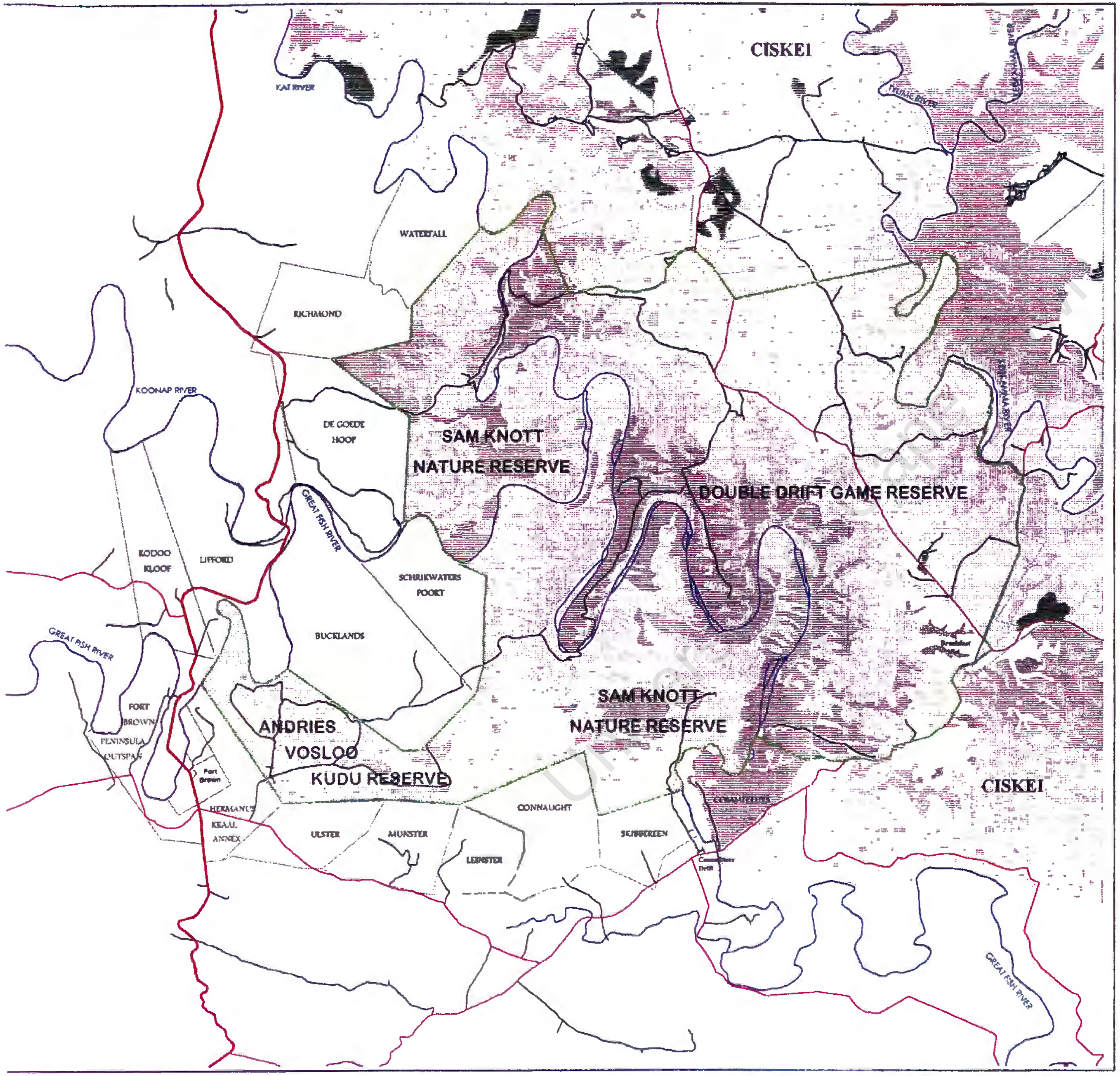
Institutional structures such as local authorities or municipalities hardly exist because of political strife and the historical unwillingness of the previous "homeland" government to give up central power before 1994. Basic infrastructure is limited to gravel roads which are in a poor condition. Electricity, telephones or other forms of electronic communication, sewerage and piped water are all but absent.

Infrastructure is weak and poorly maintained. Although public electricity is available in some areas, the local people still rely on dung and wood for heating and cooking because of the low household incomes (Ainslie et al. 1994). The environmental cost of wood and dung collection has been high. All animals larger than rabbits are absent from the CGA as a result of habitat transformation, direct persecution for meat and general disturbance as a result of the high human population density. The livestock density (mainly cattle and to a lesser extent goats) is estimated at 4 - 6 ha per LAU, which is 3 to 4 times the recommended rate for sustainable farming. Severe livestock die-offs occur during droughts. There are no organized agricultural associations, and agricultural extension officers do not regard the communal areas as a priority (Ainslie et al. 1994).

These three land use types were selected to represent a crude degradation gradient, from Commercial Farm 2 at the low degradation end, through Commercial Farm 1, with the Communal Grazing Area at the high degradation end.

Figure 1. Map of the Great Fish River Nature Reserve

GREAT FISH RIVER RESERVE COMPLEX AND SURROUNDING LAND



Reserve Boundary

Major Road (Tarred)
Other Roads
Regional Road (Gravel)
Secondary Road
Rivers
Farm Boundaries

Vegetation
- ■ Acacia Communities
- ▨ Euphorbias and Evergreen Thicket
- ▨ Grasslands and Shrublands
- ▨ Portulacaria
- □ Valley Bushveld and Bushclumps

Composite Map Derived and Digitized from data on:

1:50 000 Sheets:
3226DC FORT BEAUFORT
3226DD ALICE
3326BA FORT BROWN
3326BB BREAKFAST VLEI

Vegetation Map Series:
FISH/KAT RIVER BASINS
- Loxton Hunting & Associates
KEISKAMMA RIVER BASIN
- Hill Kaplan Scott & Partners
ANDRIES VOSLOO KUDU and SAM KNOTT NATURE RESERVES
- A.R. Palmer and G.D. La Cock

Produced By:
EASTERN CAPE NATURE CONSERVATION
GIS LAB
SCIENTIFIC SERVICES
PRIVATE BAG X1126
PORT ELIZABETH, 6000
potgies@cncpe.ecape.gov.za

MAP REFERENCE CODE: KUDU.APR MARIUS (Feb 1995)

Figure 2. Pristine Xeric Succulent Thicket on the valley escarpment in the Great Fish River Nature Reserve.

Figure 3. Well-defined bushclumps in the Great Fish River Nature Reserve, near locality NR3.

Figure 4. Difference between bushclumps on Commercial Farm 1, close to locality CF1, on the left side of the fence, and clumps in the nature reserve, close to locality NR1, on the right. Bare areas on the left are masked by the high grass cover after rain.

Figure 5. Extremely degraded Xeric Succulent Thicket in the communal area, near locality CGA.

Figure 6. An extreme example of a fence-line contrast due to prolonged intensive herbivory, near a human settlement outside the study area, in Xeric Succulent Thicket.

3. Landscape Patchiness and the Management of Xeric Succulent Thicket: Satellite Imagery is on the SPOT

ABSTRACT

Nature reserves in Xeric Succulent Thicket are subject to a wider variety of disturbance types, in the form of herbivores of different body sizes and different feeding strategies, than are communal and commercial rangeland where wild herbivores are either reduced or are absent. This might result in nature reserves having a greater structural diversity at the micro-landscape or land-element level, here defined as features distinguishable at a scale finer than 1:10 000. Such features could substantially influence the reflectance captured in a single 20 x 20 m pixel in a SPOT image, e.g. a bushclump, termitarium, bare patch or animal wallow. Reflectance diversity in a SPOT satellite image and land element diversity in plots on the ground were used to compare land element diversity in a nature reserve with that on two commercial farms and a communal grazing area. This was done as part of a bigger study to evaluate the contribution of the nature reserve to the preservation of biodiversity in the Xeric Succulent Thicket of the Eastern Cape, South Africa. A second objective was to develop and test broad-scale techniques to evaluate rapidly the conservation significance of protected and unprotected areas. As a first step, the Coefficients of Variation (CVs) of groups of 12 picture element (pixel) values of a SPOT satellite image were calculated for two commercial farms CF1 and CF2 and the communal area (CGA) as well as for corresponding paired localities in the nature reserve. The next step was to record the variety of 20 m x 20 m plots on the ground, also in groups of 12 plots, at the same geographical coordinates as the satellite-based measurement. For logistic reasons the communal grazing area could not be included in this part of the study. The nature reserve displayed significantly higher satellite-derived pixel CVs than the communal grazing area, and significantly higher ground-based diversity indexes than the commercial farms and possibly the communal grazing area. The means of the satellite-based and ground-based indexes were significantly and positively correlated. It is postulated that continuous intensive grazing in the absence of wild herbivores, such as in the CGA and some commercial farms, leads to a decrease in landscape patchiness, and that the presence of megaherbivores, coupled with naturally low stocking rates (as in the nature reserve), leads to an increase in landscape patchiness. The satellite-based technique is useful to identify potential sites of high biodiversity for more intensive sampling at a finer scale. It could also be used to monitor landscape degradation at a regional level.

INTRODUCTION

The purpose of this chapter is two-fold: to compare the landscape diversity on a nature reserve in semi-arid Xeric Succulent Thicket savanna to that of neighbouring commercial and communal rangeland, and to develop and test broad-scale techniques to assess rapidly the potential of areas to preserve biodiversity.

Landscapes can be classified in various ways depending on the level of resolution required by the study. The hierarchical classification approach advocated by Bell & McShane (1984) was adopted in this study. At scales which are relevant to herbivore and human use, three landscape classes are distinguishable: land units, land facets and land elements. A *land unit* is an area consisting of a single catenary sequence, which can be distinguished on the basis of geomorphology, petrology, soil type, and drainage pattern. It is suitable for mapping at about a 1:50 000 scale. A *land facet* is a single component within a catenary sequence, e.g. a ridge top, slope with a particular aspect or a valley floor, which can be mapped at a scale between 1:50 000 and 1: 10 000, while a *land element* is an individual feature within a land facet, e.g. a sand bank, rock outcrop, bushclump or bare area which requires a finer resolution than 1:10 000 to be detectable on a map or image. This study investigates diversity at the land element level.

The diversity of land elements in a landscape may provide a potentially useful index of biological diversity, because a diversity of land elements provides a diversity of habitats for plants and animals (Forman & Godron 1986). Such an index could be used for identifying sites of conservation significance for future protected areas, evaluating environmental impacts, determining conservation priorities and monitoring vegetation change.

Satellite-based radiometers can measure the reflectance of sunlight in various wavelengths from landscape features such as vegetation, soils, water and rock outcrops. In the case of SPOT HRV data, a single pixel recorded by the satellite-borne radiometer is an integration of the reflectance across a 20 m x 20 m plot on the ground. Structurally homogeneous landscapes, with a small variety of land elements, should contain a smaller variety of pixels than structurally diverse landscapes. This is evident from the greater color variation in complex landscapes when a satellite image is visually examined - a cultivated land is an extreme example of land element homogeneity, where the lack of colour variation is clearly visible on the satellite image.

In commercial and subsistence agriculture, domestic herbivores have been introduced with a simultaneous increase in stocking rate and grazing or browsing intensity. This results in a decrease in the variety of indigenous herbivores because of competition for resources by domestic livestock, and direct persecution by pastoralists. In this study the hypothesis was tested that the patch diversity within landscapes decreased under such conditions.

Landscape patchiness is relevant to conservation because landscapes with a high patch diversity provide habitat for a large variety of biota. This increases the Beta-turnover of species across landscapes, with a corresponding increase in species richness at the regional level. A technique which could cost-effectively and objectively measure landscape patch diversity would be useful to monitor coarse-scale changes in landscapes over time. Such a technique would also be useful to identify sites of conservation significance at an exploratory stage.

METHODS

In an effort to quantify landscape patch diversity, the reflectance diversity of groups of picture elements (pixels) in a SPOT satellite image was calculated to provide an index of the diversity of 20 m x 20 m squares in the landscape. These data were supplemented by a ground-based method, which was used to calculate an index of structural diversity related to disturbance, vegetation height and cover. Comparisons were restricted to paired localities inside and outside the nature reserve, because of differences in topography and elevation between localities positioned far apart.

Satellite-derived reflectance diversity

Band 1 (0.50 - 0.59 µm) of a recent SPOT image was rectified to a geographic projection, using the GRASS 4.1 software package (USACERL 1994). The reflectance values captured as picture elements (pixels) by the image were radiated from 20 x 20 m squares on the ground at known coordinates at Site I (CF1 and NR1), Site II (CF2 and NR2) and Site III (CF3 and the CGA). The remotely sensed reflectance values of 120 pixels, arranged in 10 groups (G) of 12 pixels (P) each were extracted from the digital image (Figure 1). Coordinates of pixels are in Appendix 5. This enabled the calculation of 10 coefficients of variation (CVs), one for each group G, for the two respective paired localities at a site. The "distance" between each group of pixels was the equivalent of 50 m on the ground, and the groups were selected to represent localities no closer than 50 m and no further than 100 m from the boundary of the nature reserve. Groups of pixel values were laid out in similar fashion at all localities (Figure 1).

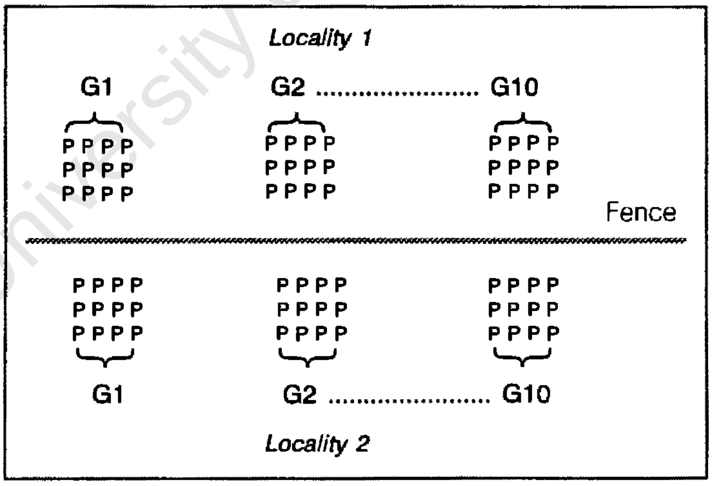


Figure 1. Diagrammatic presentation of a site, showing the lay-out of pixels and ground plots (P) and groups of pixels (G) which were used to collect data across fence-lines to compare paired locaties

For the 12 pixels in each group the CV of their reflectance values was calculated as a single measure of reflectance diversity within the group. The rationale was that a greater diversity of land elements (detectable at a scale of 20 x 20 m) in a group would result in a greater variety of reflectance values and a higher CV, compared to groups with a smaller diversity of landscape elements.

Land element diversity on the ground

The diversity of land elements on the ground was recorded at Sites I and II, but not at Site III because of logistic reasons. Ground surveys and the recording of the satellite image took place in the same season and year, in the winter of 1992.

A land element is defined here as a square plot of 20 x 20 m, while land element diversity is defined as the variety of such plots which make up the landscape. In this study area, these land elements were well defined bush clumps, disturbance patches or bare areas which ranged in size from 10 m to 30 m in diameter.

One hundred and twenty plots of 20 x 20 m on the ground were positioned at the same coordinates as the remotely sensed reflectance values as described above. Using GRASS, the coordinates of these ground-based plots were extracted from the digital satellite image to match the coordinates of the satellite-derived pixel values. A Global Positioning System without differential correction was then used to find the localities on the ground to the nearest 5 m. Thus a ground-based plot was located for every picture element on the satellite image. The lay-out of the ground-based plots followed the same configuration as the satellite-derived pixel values (cf. Fig. 1) in 10 groups of 12 plots each.

Within each 20 x 20 m plot the following data were recorded:

- geographic coordinates,
- average percentage canopy cover of the vegetation in five categories: 1-20%, 21-40%, 41-60%, 61-80%, >80%;
- average height of the vegetation in five height categories: < 0.5 m, 0.5-1 m, >1-1.5 m, >1.5 - 2 m, >2 m, and
- presence of disturbance features: erosion gullies, termitaria, other zoogenic mounds, animal wallows, animal paths, temporary lakes (pans), dams, lands, and roads and tracks.

For each of the groups of plots G1 to G10 on the ground a crude land element diversity index $D = n_c + n_h + n_d$ was then calculated where

- n_c = number of different cover classes present in the 12 plots constituting the group
- n_h = the number of different height classes in the 12 plots
- n_d = the number or variety of different disturbance features in the 12 plots.

It was thus possible to calculate 10 D values for each locality. Each D value matched a satellite-derived CV, both in size and geographical position.

The CVs and land element diversity indexes of the paired localities were graphically compared, using multiple "box and whisker" graphs (Tukey 1977). In such graphs, samples of the same population are presented as boxes, with a central horizontal line representing the sample median, and the vertical dimensions of the box representing the upper and lower quartiles, above and below the median.

For each site the hypothesis was tested that the satellite-derived CVs and ground-based D values of the NR were respectively higher than those of unconserved land, using a nonparametric Wilcoxon test with P = 0.05.

The correlation between the mean respective land element diversity values (D) at CF1, NR1, CF2 and NR2 and the mean satellite-derived pixel CV values at the same localities was also calculated.

RESULTS

Satellite-derived reflectance diversity

Different types of land use had an influence on the diversity of reflectance values radiated from 20 x 20 m plots. Significant differences between paired localities in the nature reserve and unconserved land could be detected in extreme treatments such as the contrast between the nature reserve NR3 and the CGA.

For paired localities, the median pixel CVs of the reflectance values at localities in the nature reserve (NR1-NR3) were consistently higher than those of corresponding pairs on unconserved land, i.e. CF1 and 2 and the CGA (Fig. 2). The lower quartile of NR3's CVs and the upper quartile of the CGA's CVs did not overlap, suggesting a substantial difference in the medians and distribution of their CVs.

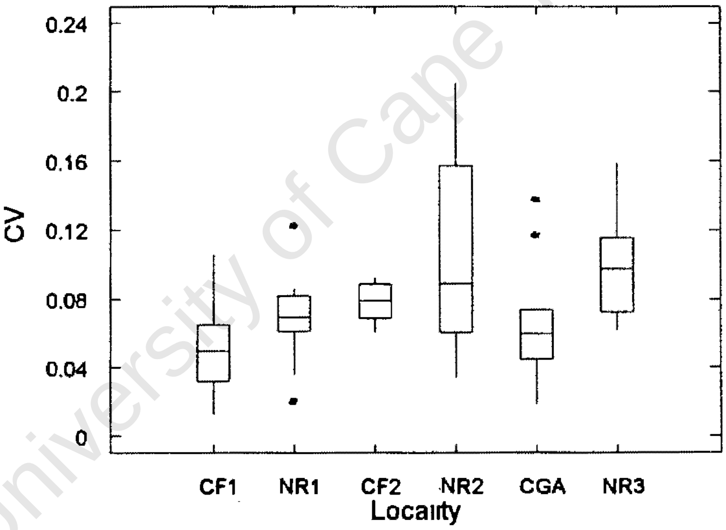


Figure 2. "Box and whisker" plot of the coefficients of variation (CV) at Great Fish River Nature Reserve (NR1-NR3), commercial farms (CF1 & 2) and the Communal Grazing Area (CGA). Paired localities for comparison are NR1 and CF1, NR2 and CF2 and NR3 and CGA. The central horizontal lines represent the medians, the central boxes represent the upper and lower quartile values and the central vertical lines represent the range. Outliers are indicated as points

In a pairwise Wilcoxon test (n=10), the CVs in the nature reserve at NR3 were significantly higher than those in the CGA in a one-tailed comparison, but the CVs at NR1 and NR2 were not significantly higher than those at CF1 and CF2 respectively (Table 1). In the comparison between NR1 and CF1, P was less than 0.10 but greater than 0.05.

Table 1. Comparison between the CVs of pixel values at a locality in the nature reserve and on unconserved land for each respective site. The hypothesis was tested that the CVs of localities in the nature reserve (NR) and that of localities on unconserved land (CF and CGA) were similar, using a Wilcoxon pairwise test. At each site n = 10 pairs. NS = P > 0.05

	Site I		**Site II**		**Site III**	
	NR1	**CF1**	**NR2**	**CF2**	**NR3**	**CGA**
Median	0.07	0.04	0.09	0.08	0.10	0.06
Z	1.5		0.5		2.2	
P	NS		NS		0.01	

Land element diversity on the ground

The diversity of 20 x 20 m plots on the ground reflected the same pattern as that displayed by the pixel CVs, although NR3 and the CGA were not included in this part of the study. When resepective pairs were compared, the nature reserve had a significantly higher land element diversity D on the ground than that of CF1 and CF2 respectively (Figure 3 and Table 2).

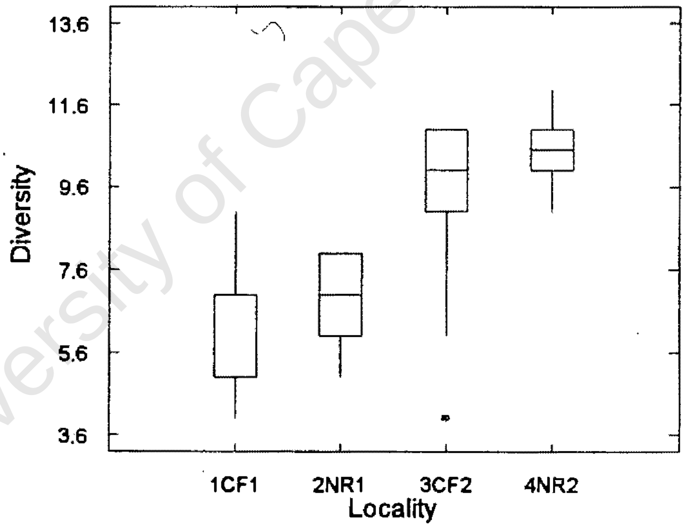


Figure 3. "Box and whisker" plot of ground-based land element diversity indexes D at Great Fish River Nature Reserve (NR1 and NR2) and commercial farms (CF1 and CF2). Paired localities for comparison are NR1 and CF1; NR2 and CF2. The central horizontal lines represent the medians, the central boxes represent the upper and lower quartile values and the central vertical lines represent the range. Outliers are indicated as points

Table 2. Comparison between the ground-based land element diversity indexes D in the nature reserve and on unconserved land at each respective site. The hypothesis was tested that the D's of localities in the nature reserve (NR1 and NR2) and that of localities on unconserved land (CF1 and CF2) were similar, using a Wilcoxon pairwise test. NR1 and CF1, and NR2 and CF2 were respectively compared. In each instance n = 10 pairs

	Site I		**Site II**	
	NR1	**CF1**	**NR2**	**CF2**
Median	7	5	11	10
Z	1.7		2.1	
P =	0.05		0.02	

Relation between pixel CVs and measured land element diversity

There was a strong relation between the satellite-base CVs and ground-based land element diversity indexes D. The means of the two indexes at the four localities were highly correlated ($r = 0.96$, df = 2, $P < 0.05$, Figure 4). Unknown D values could be predicted from satellite-derived CVs, as was done for CF3 and CGA (dotted lines, Figure 4). The interpolation indicated that the mean D value of the nature reserve at NR3 could have been about 1.4 times higher than that of the CGA.

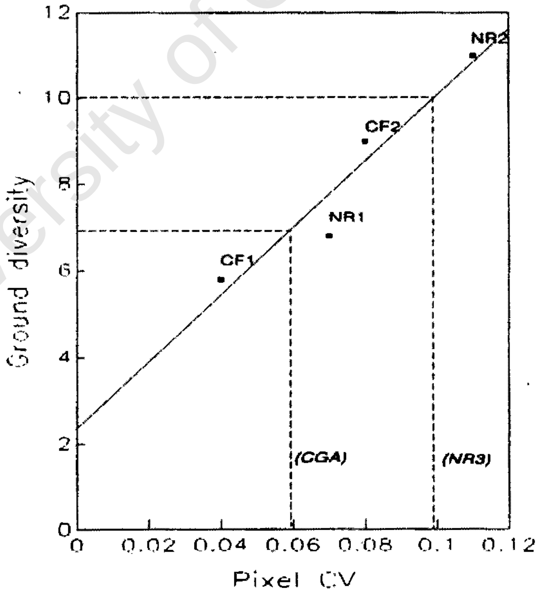


Figure 2. Regression of average land element diversity indexes D on average coefficients of variation (Pixel CV). Dotted lines, representing NR3 and CGA, are interpolated to obtain D values, as only CVs were recorded for those two localities[1]

---

[1] Although it is highly unlikely that ground-based diversity is dependent on pixel CV, the intention with the model is to estimate ground-based diversity when satellite data only are available.

DISCUSSION

This study indicates that, in a comparison between paired sites, localities in the nature reserve have a greater land element diversity, as indicated by a higher diversity of reflectance values, than corresponding paired localities in the communal grazing area. In the same pairwise comparison, the nature reserve also has a greater land element diversity than all adjacent unconserved localities. These differences apply to paired localities only: localities which are positioned far apart, such as CF2 and NR1 for example, cannot be compared in this way because of pobable between-site differences in abiotic factors such as topography, rainfall and substrate.

It is postulated that the low pixel diversity or land element diversity at unconserved localities is a result of continuous heavy grazing by domestic livestock on the vegetation of eutrophic clay-rich soils in a semi-arid area, coupled with intensive collection of firewood in the communal grazing area. This causes a decrease in the size of bushclumps until they disappear entirely or until they decrease to a size which can not be detected on the satellite image (cf. Chapter 4). The greater land element diversity in the nature reserve resulted in a greater diversity of habitats and is linked to a greater faunal species diversity, e.g. there is a positive correlation between foliage height diversity and bird species diversity at the regional level (Recher 1969). Rodent diversity is also linked to the complexity of structure in plant communities (cf. Whitford, Dick-Peddie, Walters & Ludwig 1978).

Savannas comprise a mosaic of patches, with a structure and distribution which is influenced by the types and levels of disturbance as well as abiotic factors. These factors take effect at various hierarchical scales (Urban et al. 1987). At the land unit level (Bell & McShane 1984), patchiness is influenced by gradients in elevation, rainfall and radiation, fire as well as the differential habitat utilization by large herbivores. Herds of large herbivores can alter the structure of landscapes at a coarse scale by removing trees over large areas (Owen-Smith 1988) and maintaining short grass (Novellie 1990). Humans influence landscape structure through livestock management (Friedel & James 1995), cultivation and deforestation (Forman & Godron 1986). At a finer resolution, e.g. the land element scale at which a termitarium or a 20 m x 20 m bush clump is detectable, the activities of vertebrates and invertebrates also influence landscape heterogeneity. This happens when indigenous megaherbivores such as buffalo, eland or rhinoceros remove or damage trees and shrubs (Owen-Smith 1989), and short grass grazers such as red hartebeest and springbok preferentially graze at nutrient-rich patches which they often denude of vegetation (Novellie 1990). Rodents such as porcupines influence landscape structure by gnawing the bark of trees and exposing them to fire (Yeaton 1988), while fossorial animals such as aardvark create burrows which are subsequently used as dens by warthog, jackal and porcupine (Hansell 1993). The areas around such burrows are noticeably different from their surroundings. This scale is relevant to the habitat selection of large herbivores, e.g. browsers which typically move from one vegetation patch to another instead of systematically foraging over an entire area (Fabricius 1994).

It is postulated that the variety of herbivores in the nature reserve, especially the megaherbivores black rhinoceros and buffalo, contribute to the landscape diversity by creating a variety of land element types through differential disturbance. Fossorial mammals such as aardvark and large rodents such as porcupine also play a role in creating a variety of disturbances. The absence of the megaherbivores from commercial farms and almost all wild animals from the CGA contributed to the lower land element diversity at the unconserved localities.

This study showed that it was possible to quantify land element diversity by calculating the diversity of reflectance values in radiometrically derived satellite imagery, but the satellite-based method was only statistically effective in extreme treatments, where differences were easily visible. The satellite-based method might however have been more effective, from a statistical point of view, if the sample size were increased, i.e. if more CVs were calculated. This was especially true for the comparison between NR2 and CF2.

Various methods have been used to quantify landscape diversity, most of which require GIS software and vectorized data which are measured as polygons. These include affinity analysis (Scheiner 1992), patch richness, dominance measured by the Shannon index (O'Neil et al. 1992), the Simpson index (Baker & Cai 1992), or fractal geometry (Mladenoff et al. 1993). As far as could be ascertained, the present study was the first which used coefficients of variation of values in a rasterized image as an index of patch diversity. The technique was simple to apply, given that the appropriate hardware, software and data were available, and made use of unsophisticated algorithms. In view of the low cost of the study once the hardware and satellite data had been purchased, the method was as effective as other, more sophisticated and expensive techniques in achieving the project objectives. Because the goals of the study could be reached by using this approach, no attempt was made to use any of the other indexes proposed by Baker & Cai (1992).

One of the shortcomings of the method is that topography influences pixel diversity, because topographically diverse areas contain a greater variation of pixel values than uniformly flat areas. It could be argued that topographically diverse areas inherently contain a greater variety of habitats. The method used here should however be applied with circumspection when two or more sites are compared for the purpose of making inferences about the impact of land management. In such instances it would be extremely important to ensure that the topographical variation of the sites being compared was similar. The paired sites which were compared in this study did not differ significantly in topography.

Another possible shortcoming was that "real" habitat patches on the ground did not always occur in the centre of a satellite pixel or a ground-based plot. In an extreme scenario, some patches could have occurred at the intersection of four pixels, which would have produced similar reflectance values for those pixels despite the greater patch diversity on the ground. This would have resulted in an underestimate of patch diversity.

Different levels of resolution are appropriate to different studies (Cullinan & Thomas 1992), and it is therefore important to select a meaningful scale of measurement. In this study the resolution of a 20 m x 20 m grid seemed appropriate from an ecological point of view, because 20 m x 20 m reflected the approximate size of real patches in the landscape. The main reason for choosing 20 x 20 m was that it was the best available scale in satellite imagery. The satellite-based technique might be appropriate in landscapes where patches occur at a coarser scale than 20 x 20 m, but probably not in landscapes where patches occur at finer scales.

CONCLUSIONS

The technique described here can be used to derive landscape diversity maps from SPOT satellite images. Based on the assumption that landscape diversity is related to faunal and floral species richness, such maps can be used to identify priority areas for more detailed sampling at the species or higher taxonomic level. The use of the method to monitor landscapes for early signs of land degradation should also be investigated. It has the potential to be used at a regional scale, provided that sufficient benchmark sites are available as a basis for comparison.

4. Impacts of Land Use on the Diversity of Xeric Succulent Thicket Vegetation: blame it on the bushclumps

ABSTRACT

This study assesses the influence of domestic herbivores and consumptive use by humans on the size, species richness and floristics of bushclumps in Xeric Succulent Thicket. The vegetation structure and diversity of a commercial farm and a communal area were compared to the vegetation of a nature reserve, using paired transects inside and outside the nature reserve. Pairs of transects were situated close together on opposite sides of the nature reserve boundary. The percentage cover of the most palatable shrub species, *Portulacaria afra* and *Grewia robusta*, was estimated in a sample of bushclumps at each respective locality as an index of range condition. An index of bushclump area was obtained by multiplying the longest axis of a clump by the widest part of the clump perpendicular to the first axis, i.e. each clump was placed in an imaginary rectangle. The line intercept method was used to determine the clump:interclump ratios in 10 transects of 500 m at each locality. The woody and herbaceous species in each clump were recorded, and the number of species was related to bushclump area.

- The number of species in clumps was significantly correlated with bushclump area and the relationship was exponential.
- In a comparison between paired localities, the nature reserve had significantly larger bushclumps than adjacent unconserved land.
- The nature reserve contained significantly more species per clump than both the commercial and communal rangeland.
- The proportions of sampling lines in the nature reserve which were intercepted by bushclumps, relative to the total length of the line, were significantly larger than that of unprotected land.
- The percentage cover of *P. afra* in bushclumps was significantly higher in the nature reserve than on unconserved land and confirmed the anticipated degradation gradient. The percentage cover of *G. robusta* was significantly higher in the nature reserve than in the communal area, but not significantly higher than on the commercial farm.
- Large clumps were characterized by bird-dispersed plant species, while the species which were not bird dispersed showed no significant association with any type of clump.
- Microsites in areas outside bushclumps contained significantly fewer mycorrhizal spores and less organic material.

Microsites outside clumps seemed to be unsuitable for the establishment of seedlings. The underlying cause of degradation is postulated to be a reduction in bushclump size through overgrazing and human use, which leads to a decrease in nurse sites for seedlings of bird-dispersed plants and a gradual extinction of bird-dispersed trees and shrubs, together with other species associated with clump

interiors. The environmental heterogeneity inside small clumps is also reduced, which could result in an increase in the intensity of interspecies competition. Xeric Succulent Thicket has an extremely low sustainable stocking rate, whether in a pristine or degraded state. The profit-making phase is the transient period between a well-conserved and degraded condition: there is no evidence that the vegetation reverts to its former state after this shift has taken place. For conservation purposes, the size of bushclumps in Xeric Succulent Thicket should be monitored to record the proportion of bushclumps which exceed 5 m². This was the inflection point below which species richness in bushclumps decreased rapidly. To maintain Xeric Succulent Thicket outside protected areas, farm incomes should be supplemented by land uses other than commercial livestock production. These include nature tourism, stud farming or low-intensity commodity farming, e.g. feedlots and medicinal plants.

INTRODUCTION

The influence of different land management types on ecosystem functioning is unclear. In particular, it is unknown which plant species and land elements are conserved in protected areas, i.e. nature reserves and national parks, that are not conserved on agricultural land. For some conservationists it is important to manage protected areas to maximize their contribution to biodiversity conservation. If this information can be linked to an understanding of the mechanism of the loss of vegetation diversity, it can provide guidelines for programmes to monitor the success of conservation efforts.

To evaluate the role of different land management types, especially protected areas, in preserving Xeric Succulent Thicket, the Nature Reserve's vegetation was compared to the vegetation of neigbouring land used for commercial and subsistence agriculture.

It is known that continuous heavy grazing and browsing decreases the productivity of this vegetation type, but only after the vegetation has been damaged beyond recovery (Aucamp & Tainton 1984). *Portulacaria afra*, a palatable evergreen succulent which is responsible for the bulk of vegetation production in Succulent Thicket, is the first species to decrease in abundance (Aucamp & Tainton 1984, Stuart-Hill & Aucamp 1993). Once this has taken place, the vegetation type takes a long time to recover. Heavy grazing by livestock and to a lesser extent by megaherbivores such as African elephant results in a decrease in species diversity, especially amongst succulent species (Moolman & Cowling 1994). Heavy grazing by goats causes bushclumps to shrink from ground level upward, as opposed to browsing by elephants which causes the fringes of bushclumps to expand at ground level (Stuart-Hill 1992). It has been postulated that the succulent component of Xeric Succulent Thicket does not regenerate through seedlings and that most if not all of the biomass production is through vegetative regeneration - the vegetation has been likened to a "hedge" (Stuart-Hill & Danckwerts 1988; Midgley & Cowling 1993), while the forest component reproduces sexually and the seeds are bird-dispersed (Cowling 1983). Although a large body of knowledge about the impact of grazing on Xeric Succulent Thicket exists and the symptoms are well researched

(Danckwerts & Teague 1989; Stuart-Hill & Aucamp 1993), there is no accepted model for the mechanism of degradation.

In this study the vegetation is characterized as clumps of woody vegetation dispersed in a matrix of grass or dwarf shrubs, depending on rainfall and local land management. The clumps are situated on slightly elevated, deeper than average soils. Under pristine conditions the individual clumps are barely recognizable and are separated only by animal paths or the occasional bare area. Increasing grazing intensity leads to an increase in the width of animal paths and bare areas, as herbivores fragment the large bushclumps from the perimeter inward, and the fragmented clumps become more conspicuous. The result is a decrease in the size of bushclumps and an increase in the interclump areas. The interiors of bushclumps become exposed and saplings and seedlings which normally find refuge there are subject to browsing. After prolonged continuous heavy browsing, the number of species in receding bushclumps decreases, as does production, and recruitment decreases or ceases altogether. In the most extreme cases the bushclumps no longer provide nurse sites for seedlings and saplings, and comprise only a few rounded and stunted woody shrubs. This leads to local extinctions of many plants and animals and a gradual impoverishment of the ecosystem to a point where recovery is no longer possible. This paradigm leads to a number of key questions and hypotheses. Specifically, this study addressed the following key questions.

- What is the relationship between bushclump area and plant species richness?
- What is the influence of vegetation management on plant species richness in bushclumps?
- What is the influence of herbivory on bushclump area?
- What is the influence of bushclumps on mycorrhizal activity?
- What is the role of bushclumps in the establishment of seedlings in Xeric Succulent Thicket?.
- Do soil conditions differ inside and outside bushclumps?
- What are the possible ecological mechanisms of a change in biodiversity?

METHODS

The vegetation of the nature reserve was compared to a commercial farm and a communal grazing area respectively. Site I and Site II contained two paired localities each, which were situated on opposite sides of the boundary between the reserve and unconserved land. Site I consisted of the commercial farm CF1 (Hermanuskraal) and a corresponding locality in the nature reserve (NR1). Site II consisted of a locality in the communal grazing area (CGA) near the village of Ndwayana, and a corresponding locality in that part of the nature reserve (NR3) known as Selbourne. Paired localities were as close together as possible and had the same elevations, slopes, geological substrata and aspects. Localities were selected to represent a crude gradient of grazing intensity, in the order (from heavy to light grazing): CGA, CF1, NR1, NR3. The choice of the gradient was based on interviews with land managers, reserve and farm records and literature surveys of the management history of the areas. (CF2 and NR2, which were situated at a substantially higher elevation than the other sites, was not sampled in this part of the study as its vegetation did not represent typical Xeric Succulent Thicket).

A bushclump was defined as a group of three or more woody species of which the branches or leaves touched one another less than 1 m above ground. To compare the size of bushclumps a 100 m transect was laid out inside and outside the reserve at each respective locality. Each bushclump intercepted by the transect was measured (maximum length x maximum width) and the area was calculated assuming a rectangular shape. Within each bushclump the woody and non-grass herbaceous species were recorded (numbers were assigned to unknown species).

To assess the impact of bushclump size on species composition, the non-grass species in a sample of large (> 7 m^2) and small (< 6 m^2) bushclumps were recorded. A chi-squared test was used to test the hypothesis that the observed frequency of each species in small and large bushclumps respectively was the same as the expected frequency. This was done for individual localities as well as for a pooled sample of bushclumps. Where either of the sample sizes was less than five, which invalidated that use of chi-square tests, binomial tests were used. [A small sample of clumps (10 at each of two localities) was first compared in this manner, and only those species which showed a "significant" ($P < 0.2$) preference for either large or small clumps were included in the larger sample.]

To determine whether changes in clump sizes were accompanied by reciprocal changes in interclump areas, the linear distances which were intercepted by bushclumps along 500 m long lines was measured. The ratio of transect length intercepted by bushclumps to total transect length was calculated for 10 such transects at each locality.

An index of vegetation condition at each survey locality was determined by estimating the percentage projected cover of *P. afra* and *Grewia robusta* in each bushclump. These species are the preferred browse plants for livestock in Xeric Succulent Thicket and *P. afra* is the first species to decrease under conditions of heavy grazing (Stuart-Hill & Aucamp 1993).

Mycorrhizal spores were counted in soil samples taken inside randomly located bushclumps and outside bushclumps. Cores of soil samples were collected to 10 cm depth. Spores were separated using wet sieving and decanting followed by centrifugation in 50% sucrose (Brundrett et al. 1994). Spores were counted under a stereomicroscope.

Pseudoreplication was avoided, following suggestions by Hurlbert (1984) by i) testing for differences between means rather than for that between individual samples, thereby reducing the number of degrees of freedom to an acceptable level (Crawley 1993); ii) using bushclumps as a unit of measurement, with the assumption that each bushclump represented an independent sample, having a separate microclimate which was uninfluenced by neighbouring clumps; iii) positioning replicated transects (at the same locality) at separate catenal sequences across the landscape (cf. Hurlbert 1984).

RESULTS

The average proportional cover of *P. afra* per bushclump decreased along the grazing intensity gradient (Figure 1 and Table 1) and also differed significantly between paired localities. The average percentage cover of *G. robusta* per bushclump did not differ significantly between NR1 and CF1, but differed significantly between NR3 and the CGA (Figure 2).

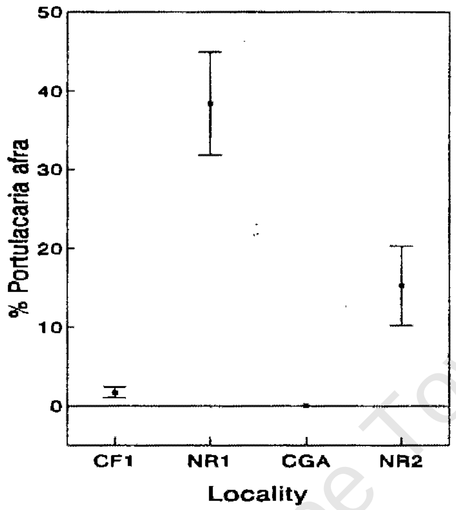


Figure 1. A comparison of the mean percentage cover (± S.E.) of *P. afra* per bushclump. NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. Paired sites are NR1, CF1 and NR3, CGA.

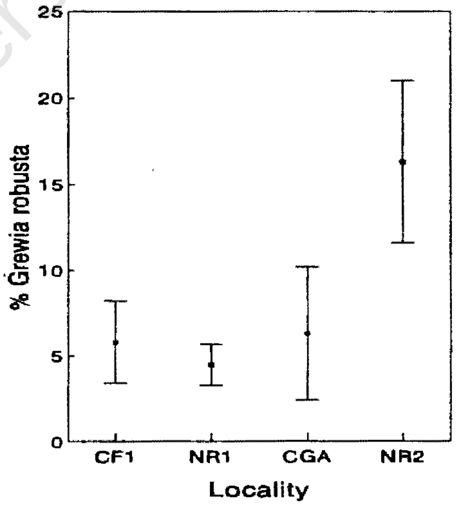


Figure 2. A comparison of the mean percentage cover (± S.E.) of *G. robusta* per bushclump. Localities are the same as in Fig. 1a.

This corroborated our choice of the sites along a postulated grazing continuum, based on anecdotal evidence of past and present stocking rates provided by local land managers. The large and significant differences between paired localities indicated that herbivory could have been responsible for this pattern, as these paired sites were positioned close together, the only difference between them being the type of land management, specifically the type and intensity of herbivory (Table 1).

Table 1. Comparison of percentage cover of *P. afra* in bushclumps. NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. The hypothesis was tested that the percentage cover of *P. afra* at paired localities did not differ, using a Wilcoxon test.

	Site I		**Site II**	
	NR1	**CF1**	**NR3**	**CGA**
Mean	38.4	1.7	15.3	0.0
S.E.	6.5	0.7	5.1	0.0
Z		9.9		9.9
P		<< 0.001		<< 0.001

The exponential regression of the number of species per clump on bushclump area (Figure 3) was highly significant ($P<<0.001$), and meant that small bushclumps had disproportionately fewer species than large bushclumps. The critical bushclump size, i.e. the inflection point of the curve below which species richness decreased rapidly, was about 10 m^2.

The main effect of an increase in herbivory was a decrease in the size of individual bushclumps. The clumps at the two localities on the nature reserve were the largest, those on the commercial farm were intermediate in size and the bushclumps in the communal grazing area were by far the smallest (Figure 4). Because the localities at a paired site were located in similar landscapes, the difference was most probably a result of differences in land management.

The clumps inside and outside the nature reserve at Site I were significantly different in size, while the clumps at Site II (paired localities NR3 and the CGA) differed even more significantly (Table 2). The decrease in clump size was accompanied by a significant increase in interclump areas. The ratio of transect length intercepted by clumps to total transect length for localities in the nature reserve was significantly larger than for unconserved land (Table 3).

Table 2. Comparison of bushclump sizes between localities. NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. The hypothesis was tested that the bushclumps sizes at paired localities did not differ, using a Wilcoxon test.

	Site I		**Site II**	
	NR1	**CF1**	**NR3**	**CGA**
Mean	8.5	5.2	10.4	1.7
S.E.	1.5	1.0	1.2	0.2
Z		-2.1		6.9
P		0.018		<<0.001

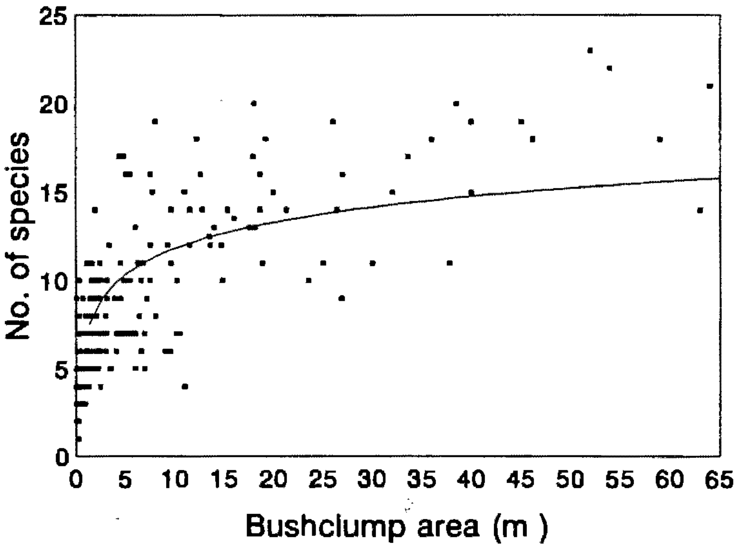


Figure 3. Regression of number of species per clump on bushclump size. Each point represents an individual clump. The apparent unusual shape of the curve is influenced by the many points with indistinguishable coordinates at the lower end of the y axis.

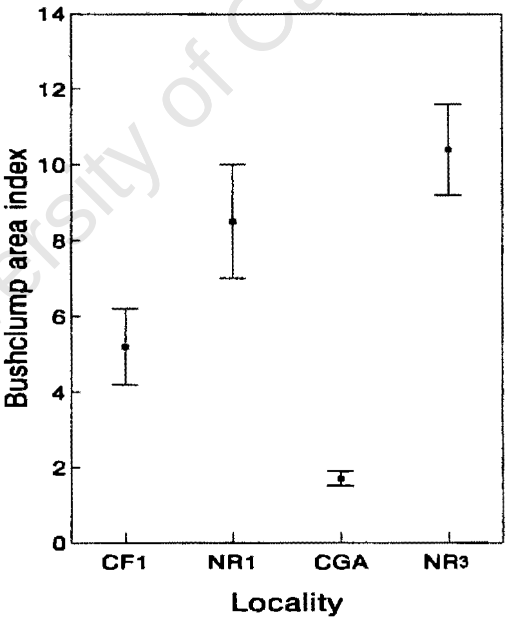


Figure 4. A comparison of mean bushclump sizes (± S.E.) at different localities. NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. Paired sites are NR1, CF1 and NR3, CGA .

Table 3. Clump:total transect ratios. The hypothesis was tested that the clump:transect ratios of a sample of 10 transects of 500 m did not differ between paired localities, using a T-test. (Abbreviations as for Table 2).

	Site I		Site II	
	NR1	CF1	NR3	CGA
Mean	0.618	0.453	0.499	0.116
S.E.	0.023	0.033	0.027	0.013
P		0.004		<<.001

The landscapes of the nature reserve consisted of a matrix of clumps, interspersed with a smaller proportion of interclump areas. This situation was reversed outside the nature reserve: the localities on unconserved land contained more interclump areas than clumps, i.e. the matrix consisted of interclump areas (Karroid shrubs and grass) while the patches consisted of bushclumps.

As a consequence of the reduction in bushclump size, the mean number of non-grass species per bushclump decreased markedly along the grazing gradient, following the same pattern as the decrease in bushclump size (Figure 5).

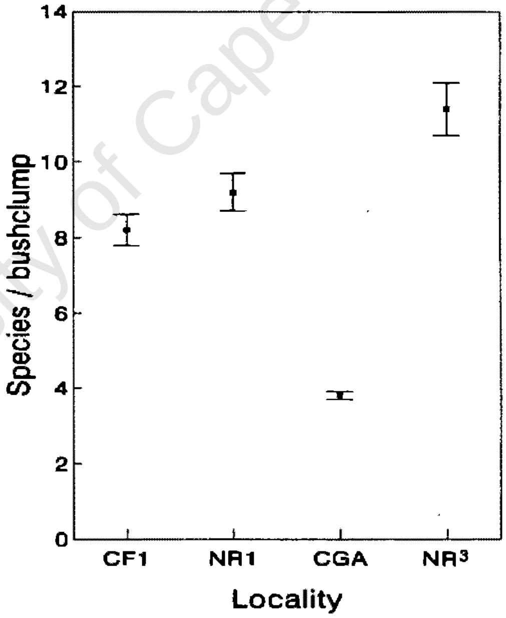


Figure 5. A comparison of the mean number of non-grass species (woody plants and herbs combined) per bushclump (± S.E.). NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. Paired sites are NR1, CF1 and NR3, CGA

The nature reserve had the most species, the commercial farm had fewer species and the communal grazing area the least. When paired sites across the boundary were compared, the nature reserve (NR1) had more species in total than the commercial farm (CF1). It also contained significantly more woody species per clump. In the comparison between the nature reserve (NR3) and the communal grazing area (CGA), NR3 had significantly more woody species as well as total species than the CGA (Tables 4 and 5).

Table 4. Comparison of the number of woody species per bushclump. NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. Paired sites are NR1, CF1 and NR3, CGA. A Wilcoxon test was used to test the hypothesis that the number of woody species in bushclumps at paired localities did not differ.

	Site I		Site II	
	NR1	CF1	NR3	CGA
Mean	6	4.6	8.1	3
S.E.	0.34	0.28	0.5	0.1
Z		-2.9		8.8
P		0.0018		0

Table 5. Comparison of total number of non-grass species per bushclump. NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. Paired sites are NR1, CF1 and NR3, CGA. A Wilcoxon test was used to test the hypothesis that the total number of species in bushclumps at paired localities did not differ.

	Site I		Site II	
	NR1	CF1	NR3	CGA
Mean	9.2	8.2	11.4	3.8
S.E.	0.5	0.4	0.7	0.1
Z		-1.4		9.9
P		0.075		0.000

Most of the species occurred more frequently in large bushclumps (> 7 m^2) than would be expected if these species were evenly distributed across both categories of clumps when the total number of clumps are included in the test (Table 6). The exceptions were *Euphorbia bothae*, *Sarcostemma viminale* and *Lycium* sp., the latter being the only species which occurred more frequently in small clumps than would be expected. These species are unpalatable, if not inedible (Stuart-Hill & Aucamp 1993), and are not animal-dispersed (Batten & Bokelmann 1966; Pooley 1993). The first two species are defended against herbivory by a poisonous milky latex, whereas *Lycium* sp. has very small leaves and spiny branches, and is recognized as an unpalatable invader of overgrazed areas in semi-arid systems (Milton & Hoffman 1994). The bias towards large bushclumps should be considered when the significance levels are interpreted: all species are less likely to occur in small bushclumps than in large clumps because of the effect of area.

Table 6. The most abundant species and their frequencies in large (> 7 m²) and small (< 6 m²) bushclumps at the respective localities. A Chi-squared test was used to test the hypothesis that the observed number of small and large clumps containing a species were the same as the expected number, if the species was represented in equal proportions in small and in large clumps. Where either sample had a frequency less than five, a binomial test was used. Small and large bushclumps in the CGA were not statistically compared because of the rarity of large clumps. NS: $P > 0.05$

	CGA		NR3					CF1					NR1					Total				
	Small clumps	Large clumps	Small clumps	Large clumps	Expected Small	Large	P	Small clumps	Large clumps	Expected Small	Large	P	Small clumps	Large clumps	Expected Small	Large	P	Observed Small	Large	Expected Small	Large	P
n	46	3	32	42				38	36				48	35				164	116			
Maytenus capitata	4	1	1	12	6	7	0.01	1	14	8	7	<.01	4	21	14	11	<.01	10	48	34	24	<.001
Grewia robusta	10	0	7	24	13	18	0.02	11	24	18	17	0.02	8	28	21	15	<.01	36	76	66	46	<.001
Rhoicissus tridentata	0	0	4	26	13	17	<.01	0	20	10	10	<.01	9	31	23	17	<.01	13	77	53	37	<.001
Protasparagus sp.	9	0	19	38	25	32	NS	9	26	18	17	<.01	8	29	21	16	<.01	45	93	81	57	<.001
Euclea undulata	0	0	2	5	3	4	NS	0	12	6	6	<.01	7	19	15	11	<.01	9	36	26	19	<.001
Jatropha capensis	13	1	24	34	25	33	NS	16	26	22	20	NS	18	30	28	20	<.01	71	91	95	67	<.001
Portulacaria afra	0	0	19	40	26	33	NS	9	19	14	14	<.05	31	35	38	28	NS	59	94	90	63	<.001
Ozoroa mucronata	0	0	0	8	3	5	0.01	0	3	2	1	NS	1	12	8	5	<.01	1	23	14	10	<.001
Grasslily	0	0	13	28	18	23	NS	13	13	13	13	NS	18	20	22	16	NS	44	61	62	44	<.001
Capparis sepiaria	2	0	2	3	2	3	NS	0	0	0	0	-	0	1	1	0	-	4	4	5	3	NS
Euphorbia bothae	5	0	2	6	3	5	NS	38	34	37	35	NS	37	33	40	30	NS	82	73	91	64	NS
Rhigozum obovatum	7	1	14	30	19	25	NS	18	23	21	20	NS	23	16	23	16	NS	62	70	77	55	<.01
Sarcostemma viminale	7	0	7	11	8	10	NS	9	19	14	14	<.05	11	6	10	7	NS	34	36	41	29	NS
Lycium sp.	13	1	1	0	0	1	NS	0	2	1	1	NS	0	0	0	0	-	14	3	10	7	<.05
Ptaeroxylon obliquum	11	0	2	14	7	9	0.01	3	12	8	7	0.01	5	8	8	5	NS	21	34	32	23	<.01

Mycorrhizal spores were more abundant inside bushclumps than outside bushclumps (Table 7). Although the concentration of spores inside bushclumps did not differ between properties, the overall mycorrhizal density decreased, due to the decrease in the size of bushclumps and an increase in interclump areas, as grazing intensity increased (Table 3).

Table 7. Comparison of mean mycorrhizal spore density inside and outside bushclumps. NR1, NR3 are sites in the nature reserve, CF1 = commercial farm, CGA = communal grazing area. Paired sites are NR1, CF1 and NR3, CGA. A Wilcoxon test was used to test the hypothesis that mean spore densities inside and outside clumps did not differ.

	Inside clumps	S.E.	Outside clumps	S.E.
NR1	24.1	4.8	5.9	2.1
CF1	15.7	3.9	3.2	0.7
NR3	12.5	2.1	7.4	0.9
CGA	12.6	0.9	6.7	1.2
Z				2.01
P				0.04

DISCUSSION

Main findings

The main mechanism of degradation in Xeric Succulent Thicket is through unsustainable levels of consumptive utilization by domestic livestock and humans, which leads to a reduction in the size of bushclumps. If most of the bushclumps in an area are reduced to less than 7 m², the number of species in that area will be reduced by approximately 20%. The proportion of the landscape consisting of bushclumps decreases with increasing herbivory, with the nature reserve characterized by a ratio of 0.5 - 0.6, degraded commercial farms by a ratio of about 0.45 and the highly degraded communal area by a ratio of 0.1

Decreasing bushclump size is paralleled by a decrease in forage biomass, the first species to decrease in abundance and volume being the nutritious *P. afra*. *Grewia robusta* is more persistent and decreases only at very high levels of herbivory as in the CGA. These two species are the dominant woody plants in Xeric Succulent Thicket, and theoretically a decrease in their abundance should increase biodiversity because of the competitive release of inferior competitors (Hulme 1996a). The reason why this does not take place is that these two species are also keystone elements in the maintenance of the benign microclimate which characterizes large bushclumps.

A further consequence of a reduction in bushclump size is that seedling establishment of bird-dispersed plants, but also of plants which are conventionally regarded as vegetatively reproducing, is adversely affected. La Cock (1992) found no seedlings of any species outside bushclumps, whereas up to eight *P. afra* seedlings / 100 m^2 germinated inside bushclumps. This finding was contrary to the conventional dogma that Valley Bushveld does not regenerate through seedlings (Danckwerts & Stuart-Hill 1988; Midgley & Cowling 1993).

The distribution of *Maytenus capitata*, *Rhoicissus tridentata* and *Grewia robusta* were strongly non-random. All were more abundant in large bushclumps, at all localities, than expected. These species have fleshy fruits and are bird dispersed; their ranges are centred toward the eastern coastal areas of South Africa (Pooley 1993). It is postulated that the intra-clump microclimate becomes more xeric when bushclumps are fragmented, and that species which are not xeric-adapted decrease in abundance under such conditions. It might also be that their dispersal agents avoid small bushclumps, and that these plants therefore regenerate only in large bushclumps.

The plants whose incidence was independent of clump size were mostly wind- or mechanically dispersed (*Euphorbia bothae, Sarcostemma viminale.*) but there was also one species with fleshy fruit in this category (*Lycium* sp.). These three species occur primarily in the western and central low-rainfall parts of South Africa (Palmer 1981) and are therefore adapted to aridity. They are also avoided by livestock (Danckwerts & Teague 1989) and are possibly defended against herbivory by having poisonous latex (*E. bothae* and *S. viminale*) and spines. *Lycium* is widely recognized as an indicator of degraded range conditions (Milton & Hoffman 1994) and was also the only species which was significantly more frequent in small bushclumps than in large clumps, mainly because of its abundance in the CGA.

All species were more likely to occur in large bushclumps than in small clumps, because of the effect of the larger area covered by large clumps. The counter-argument is that the effective area covered by small clumps plus bare patches in degraded Xeric Succulent Thicket is the same as that covered by large clumps in well-conserved vegetation (cf. Table 3). It would thus not be valid to compensate for the area effect by, for example, reducing the frequencies of species in large clumps by an arbitrary factor. The bias was borne in mind when the significance levels in Table 6 were interpreted, by focusing on the species which were associated with small clumps, using conservative significance levels and searching for consistent trends across all localities.

Mechanisms

It is postulated that there are three main causes for this loss of species along the degradation gradient. Firstly there is a decrease in environmental heterogeneity inside clumps as clumps become smaller, because of the simplified light, temperature, moisture and nutrient gradient from the centre of clumps to the perimeter. Species which are good light competitors, i.e. the bird-dispersed forest elements which normally grow in the centre of large clumps, are replaced by good nutrient and moisture competitors, i.e. succulents and small-leaved shrubs (Hobbie Jensen & Chapin 1994). Secondly, small clumps offer less protection against the elements and herbivory than large clumps (Jaksic & Fuentes 1980). Plant species which are sensitive to herbivory, and especially their seedlings or ramets, are particularly vulnerable (Hulme 1996) and are excluded by unpalatable, spiny or poisonous species. Thirdly the ratio of patch edge to patch interior is greater in small clumps than in large ones, and this possibly leads to the leakage of nutrients and energy from the patch into the matrix, and a reduction in the production potential of a clump (Friedel & James 1995).

Substantial differences in the microclimate, as well as plant and animal species between the interior and edge of patches, have been documented by Forman & Godron (1986), Gutiérrez & Carey (1985), Maehr & Cox (1995) and Suzan, Nabhan & Patten (1996). The nursing effect of large clumps is compounded by favourable soil conditions inside clumps, e.g. a major decrease in aluminium and a sharp increase in organic material inside bushclumps (La Cock 1992). The abundance of mycorrhizal spores inside clumps possibly played an important role in further improving conditions for growth and germination inside bushclumps (Harley 1989; Read 1994).

The occurrence of high quality resource patches in an unproductive matrix is not restricted to Xeric Succulent Thicket. Suzan, Nabhan & Patten (1996) found that nurse sites under large ironwood (*Olneya tesota*) shrubs in the Sonoran desert were about 15° C cooler than exposed areas in summer, and 4° C warmer in winter. This resulted in species-rich plant communities or 'islands of diversity', including a disporportionate number of bird-dispersed species, developing in the benign environment created by the nurse plants. The structural diversity in their nurse sites was also higher than that of the surrounding matrix.

At the landscape level, the environmental heterogeneity decreases when clumps become smaller. In natural landscapes the ratio of resource patches (bushclumps) to matrix is between 0.5 and 0.6, i.e. good light competitors and good moisture competitors have equal opportunities for growth and establishment. Degraded landscapes are dominated by the matrix of bare ground, which discriminates against good light competitors and favors the good moisture competitors. This reduces diversity (Hobbie et al. 1994).

Management implications

It is clear that the nature reserve contributes to preserving the structure and plant species diversity of Xeric Succulent Thicket by, *inter alia,* maintaining large bushclumps. This in turn provides shelter for interior species which results in a higher arthropod diversity, and possibly bird diversity, inside the nature reserves compared to unconserved land (Chapter 6). The maintenance of large bushclumps in the nature reserve is possible only because the state can afford light stocking rates, and possibly because the type of utilization by large indigenous herbivores favours large bushclumps, compared to, for example, utilization by goats (cf. Stuart-Hill 1992).

In other vegetation types with a similar structure, e.g. the Chilean matorral, it has been shown that interior species are affected by herbivory, with microclimate playing a lesser role (Jaksic & Fuentes 1980). Older shrubs seem to play an important role as nurse plants in various vegetation types (e.g. La Cock 1992; Fuentes et al. 1986).

The results reported here supplement Stuart-Hill's (1992) model of goat damage, and help to explain why Xeric Succulent Thicket recovers so slowly after degradation. Although it is accepted that most of the regeneration takes place through vegetative growth, as stated by Stuart-Hill & Danckwerts (1988), regeneration through seedlings is important if the full diversity of annual and perennial species which characterize Xeric Succulent Thicket is to be preserved.

Farmers in Xeric Succulent Thicket face a dilemma if their objective is to maximize animal production. Large bushclumps with large inaccessible interiors have a low forage availability because most of the browse is hidden inside clumps. The only way to make the browse more accessible is to fragment the clumps. This results in an increase in the proportion of exposed edge and a concomitant loss of core species and their replacement by xeric-adapted species. This shift to a xeric state applies to snakes, lizards and arthropods as well (cf. Chapters 5 and 6). Consequently Xeric Succulent Thicket has a very low sustainable stocking rate, whether the system is well-conserved or overutilized. Once Xeric Succulent Thicket is over-utilized, the change is irreversible. The profit-making stage for the land manager is the relatively short period of high intensity grazing between a well-conserved state and a degraded one. In terms of biodiversity preservation, it is therefore imperative to maintain those forms of land use which do not rely on solely on livestock production to generate income.

The economic implications of the degradation of Xeric Succulent Thicket go beyond commercial livestock production. When indigenous traditional healers participated in a survey of medicinal and other useful plants in the nature reserve and at the communal grazing area, they found the abundance of these species to be 30% lower at the communal area than in the nature reserve at CF3. The nature reserve also contained 25 useful plant species which were not found in the communal grazing area (Appendix 2).

Procedural constraints

The main shortcoming in the methodology used here was that the assumed grazing intensity gradient could not be verified *a priori*. The assumed degradation gradient was equated with the crude range condition index, linked to a decrease in the incidence of *P. afra*. The decrease of this species along the gradient of increased herbivory, coupled with anecdotal and historical information, provided circumstantial evidence that the assumption was valid. It was impossible to rule out the role of historical management, and differences in the type of utilization by indigenous herbivores, cattle and goats respectively on the structure and composition of the vegetation is poorly understood. There was also the danger of pseudoreplication when working across fence-lines, but it is argued that each respective bushclump represented an independent sample. The risk of pseudoreplication was further reduced by positioning transects sufficiently far apart across catenas to be considered true replicates, and by averaging soil samples and comparing the averages.

Species-area curves (Werger 1972; Cowling, Gibbs Russel, Hoffman & Hilton-Taylor 1989; Hart & Horwitz 1991) were not used because they did not adequately reflect the impact of land use on plant species richness in Xeric

Succulent Thicket (C. Fabricius, unpublished data). Although the curves for NR3 and the CGA were noticeably different, the curves for NR1 and CF1 had similar shapes and asymptotes. This is because herbivory causes the extinction of a species in a significant number of bushclumps, but not its total extinction over an entire land management unit. This means that even those species which are reduced to very low densities are eventually recorded in nested plots, because species-area curves make use of the cumulative *frequencies* of species. At the lower end of the species-area curve, the impact of herbivory on species richness is also not evident, because the reduction in bird-dispersed and palatable species is compensated for by the increase in xeric-adapted, Karroid species in the interclump areas of degraded sites. Species-area curves are not suitable to compare sympatric vegetation communities in open ("non-insularized") systems.

The preservation of Xeric Succulent Thicket outside protected areas depends entirely on a realization by successive generations of farmers that the optimal stocking rate of this vegetation type is low, and that the average farm income needs to be supported by practices other than commercial livestock production. Wildlife tourism and trophy hunting are potential alternatives which could make farming units commercially viable at low stocking rates.

5. Do Protected Areas Promote Lizard Diversity in Xeric Succulent Thicket?

ABSTRACT

An understanding of the effect of different forms of land use on ectothermic vertebrates such as reptiles is a prerequisite for the formulation of cost-effective conservation management strategies for these animals. As a step towards this, the species richness, species composition and abundance of terrestrial lizard and snake assemblages in a nature reserve and on two commercial farms and a communal grazing area were determined. Pitfall traps were positioned at paired sites across the boundary fence, inside the nature reserve and on the respective unconserved localities. Over a period of 864 trap-days 164 specimens belonging to 15 species were captured. The six localities had similar numbers of species, but each individual locality contained less than 55% of the total number of species captured over the study period. Snakes and lizards were almost twice as abundant in the communal grazing area and had almost double the Hierarchical Richness Index (HRI) of any of the other localities, which had similar numbers of specimens and HRI values. In an ordination of localities and the eight most abundant species, the communal grazing area was associated with xeric-adapted species which distribution ranges are centred in the arid and semi-arid Western part of South Africa, whereas the other localities were mostly associated with species whose primary ranges lie in the less arid Northern and Eastern parts of the country. The relatively high abundance of reptiles in the communal grazing area is ascribed to the combined effect of improved conditions for thermoregulation and improved reptile hunting success in the open terrain, while reduced predation might have played a role. Xeric-adapted reptiles seem to be adequately conserved outside protected areas in the Xeric Succulent Thicket of the Eastern Cape. Species which are dependent on vegetation, e.g. those which lay their eggs in litter or are arboreal such as chameleons and tree snakes, are most sensitive to land degradation and require dense Xeric Succulent Thicket for their survival. Vegetation with this structure is rarely found outside protected areas, which play an important role in conserving arboreal reptiles.

INTRODUCTION

In this chapter the relation between the abundance, species composition and diversity of terrestrial snake and lizard species and different types of land use is investigated. Conservationists need to understand how protected areas and unconserved land respectively contribute to the preservation of species and processes so that they can formulate sound management strategies for the protection of reptiles. From a cost-benefit point of view, it will also be important to determine whether nature reserves are essential for the preservation of reptiles. The contribution of different types of land use to biodiversity preservation at the regional level is poorly understood, and the conventional dogma that overgrazing and other forms of overutilization of resources have a severe negative impact on biodiversity relies to a large extent on anecdotal information and intuition.

While it is clear that overutilization and either too much or too little disturbance has a negative impact on the biodiversity of terrestrial arthropods (Chapter 6; Dean & Milton 1995) and plants (Chapter 4; Moolman & Cowling 1994), the impact of the overuse of vegetation on reptiles might not follow the trends observed for plants and arthropods. Reptiles are ectothermic and may be disadvantaged by shade. Additionally they are usually not directly dependent on plants for their survival. For example, a higher diversity of lizards occurs in deserts and semi-deserts than in high-rainfall areas (Pianka 1989); this trend is in direct contrast to diversity trends of plants, birds and arthropods (Rozenzweig & Abramsky 1993). The causes of high reptile diversity in deserts are not clear (Morton 1994); it might stem from differences in prey abundance and diversity (Pianka 1989), or the negative effect of shading on egg hatchability and adult thermoregulation (Mushinsky 1992). If land degradation through unsustainable utilisation by humans and livestock is the functional analogue desertification, as suggested by Grainger (1982), then degraded sites might be expected to harbour more species and higher numbers of reptiles than sites where the vegetation and soils are well-preserved.

To understand the evolutionary causes of extinction, it is necessary to look beyond conventional taxonomy. Instead of concentrating on species or other taxonomic categories when attempting to understand the impact of land use on biodiversity, it might be more informative to concentrate on biological characteristics, e.g. life history strategies and other evolutionary adaptations (Bond 1989). An advantage of this approach is that it might guide scientists towards understanding the underlying causes of a decrease of some species and an increase in others. It will also be cost-effective to focus conservation efforts on those types of organisms which are associated with rare types of land use, such as protected areas, while being less concerned about those types which thrive on the most common forms of land use.

A nature reserve was compared to neighbouring unconserved land in terms of snake and lizard species richness and numbers of individuals captured. Another objective was to ascertain which trap localities (land use types) and reptile species were associated with one another, and to relate this to the life-history traits which the species assemblages had in common.

The key questions were:

1) how do different types of land use (nature conservation, commercial farming and communal grazing) affect the species richness and abundance of terrestrial lizards and snakes in Xeric Succulent Thicket;
2) which species are associated with the respective land use types;
3) do the species associated with the respective land use types have common characteristics; and
4) how can this information be used to formulate conservation strategies for reptiles?

METHODS

Three areas, viz. a heavily grazed commercial farm CF1 (Hermanuskraal), a conservatively grazed commercial farm CF2 (Bucklands) and a communal grazing area CGA (the Ndwayana location in the former Ciskei) were compared to the nature reserve (NR1-NR3, the Andries Vosloo section of the Great Fish River Nature Reserve). The trap localities occurred in pairs inside and outside the nature reserve on opposite sides of the boundary. Site II (the comparison between CF2 and NR2) was situated at the high elevation - high precipitation end, Site I (the comparison between NR1 and CF1) at intermediate elevation and Site III (the comparison between the CGA and NR3) at the low elevation - low precipitation end. The grazing intensity and precipitation combined resulted in a large variation in vegetation cover along the elevation gradient (see Chapter 4).

Four trap arrays were positioned at each trap locality, inside and outside the nature reserve at each respective site. A trap array consisted of a 10 m long, 10 cm high plastic drift-fence of which the lower 3 cm was buried. At one end of the fence a bucket was buried flush with the soil surface and at the other end two funnel traps, covered with fine shade-cloth, were positioned side by side, lateral to the fence.

The trap arrays at each trap locality were positioned 150 m apart while the respective pairs of traps were positioned as close together as possible, but further than 100 m from either side of the nature reserve boundary. Care was taken to place pairs of traps at similar elevations, aspects and slopes so that valid numerical comparisons of the data could be made.

Traps were opened for six days a month for six months between October 1993 and March 1994, and the traps were opened and closed at about the same time on the same days. Traps were emptied every day and most specimens were identified, marked and released while some were labelled and fixed in 60% ethanol to be later classified to the species and subspecies level. Recaptured specimens were counted once only when calculating diversity indexes.

For each trap locality the total number of individuals and the number of species were counted, and Hierarchical Richness Indexes or HRIs (French 1994) were calculated. The HRI expressed both abundance and species diversity in a single index, and was found to best express the relative abundance and species richness of the different properties. First, the reptile species collected at a trap were sorted in descending order of abundance. The most abundant species was then allocated a weight or hierarchical index value (*i*) of one, the second most abundant an *i* of two and so on. The hierarchical value of each species was then multiplied by the number of individuals of that species to produce a score *s*. The *s*s were summed for all species at each locality, to produce an $HRI=\sum(si)$ (French 1994). The data for the four traps at each locality were pooled to produce a single HRI for each locality.

To determine which reptile species and which localities were associated with one another, a matrix of reptile species by trap localities was ordinated, using Correspondence Analysis, or CA (Greenacre 1984). The data of the matrix consisted of the number of individuals of each included species which occurred at a locality. Only those species of which at least four individuals were collected in total, with a minimum of three individuals being collected at one or more localities were subjected to CA. This was because of the bias involved in including very low values or many zero frequencies in CA (Beardall, Joubert & Retief 1983).

Small sample sizes precluded the use of chi-square tests to determine the significance of the associations of reptile species with localities. Binomial tests were therefore used to determine whether the observed number of individuals at the CGA differed significantly from the expected number of individuals. The expected number of individuals of a species at the CGA was 1/6 of the total number of individuals of that species, captured at all six localities combined.

RESULTS

A total of 164 specimens belonging to 15 species were collected (Table 1). Only nine of the species were represented by four and more individuals, despite the fact that sampling was done over 864 trap-days.

Table 1. Lizard and snake species and number of specimens collected during the study period. Site I = comparison between the historically overgrazed commercial farm (CF1) and the nature reserve (NR1). Site II = comparison between conservatively stocked commercial farm (CF2) and the nature reserve (NR2). Site III = comparison between the communal grazing area (CGA) and the nature reserve (NR3). Species in bold were included in the Correspondence Analysis, while species not in bold were analysed as supplementary rows

	Site I		Site II		Site III	
	NR1	CF1	NR2	CF2	NR3	CGA
LIZARDS						
Pedioplanis lineoocellata pulchella	17	13	5	1	12	31 **
Mabuya capensis	3	1	1	1	2	11 **
Pachydactylus maculatus	4	1	2	3	4	1
Pachydactylus m. mariequensis	1	1	0	0	2	4 *
Gerrhosaurus typicus	0	0	0	0	0	6 **
Mabuya varia	0	0	0	4	0	0
Cordylus cordylus	0	0	0	3	1	0
Varanus albigularis	0	0	3	0	0	0
Agama a. atra	1	1	0	0	0	2
Mabuya v. variegata	1	1	0	1	0	0
Nucras t. taeniolata	0	0	1	1	0	0
Acontias g. gracilicauda	0	0	1	0	0	0
SNAKES						
Psammophis notostictus	2	0	3	0	3	1
Typhlops lalandei	0	2	0	1	1	0
Prosymna s. sundevallii	0	0	3	0	0	0

** = $P < 0.01$; * = $P < 0.05$ (binomial test)

The respective sites had very similar numbers of lizard and snake species, and, with the exception of the CGA, similar numbers of individuals (Table 2). In the comparison between the CGA and the NR, the CGA had similar numbers of species but more than twice as many individuals, and almost double the HRI value of the NR.

Although 15 species were collected in total, none of the localities contained more than eight species or 55% of the species collected in the study area as a whole. The community similarity between paired sites was not considered because of the low trapping success of many taxa, which made such a calculation both meaningless and misleading.

Table 2. Numbers of lizard and snake species, specimens collected and Hierarchical Richness Indexes (HRI) at three sites. Sites and localities are the same as for Table 1.

	Site I		Site II		Site III	
	NR1	CF1	NR2	CF2	NR3	CGA
Number of species	8	7	8	8	7	8
Number of specimens	29	20	19	15	25	56
HRI	60	42	63	49	60	110

An ordination of a species by localities matrix with data from Table 1 as input (Figure 1) showed that *Gerrhosaurus typicus*, *Mabuya capensis*, *Pachydactylus. m. mariequensis* and *Pedioplanis lineoocellata pulchella* were associated with the CGA, while a variety of single species were associated with the other localities.

This was corroborated by the results of the binomial tests, which showed that the same species had significantly more individuals at the CGA than would be expected if they were evenly distributed (Table 1). All these species are terrestrial and their ranges are centred in the arid western and central parts of South Africa, most of them have large clutch sizes compared to the other species which occur in the study area, and they do not require plant material (litter, bark etc.) to hatch their eggs. This differentiates them from the other species in the study area.

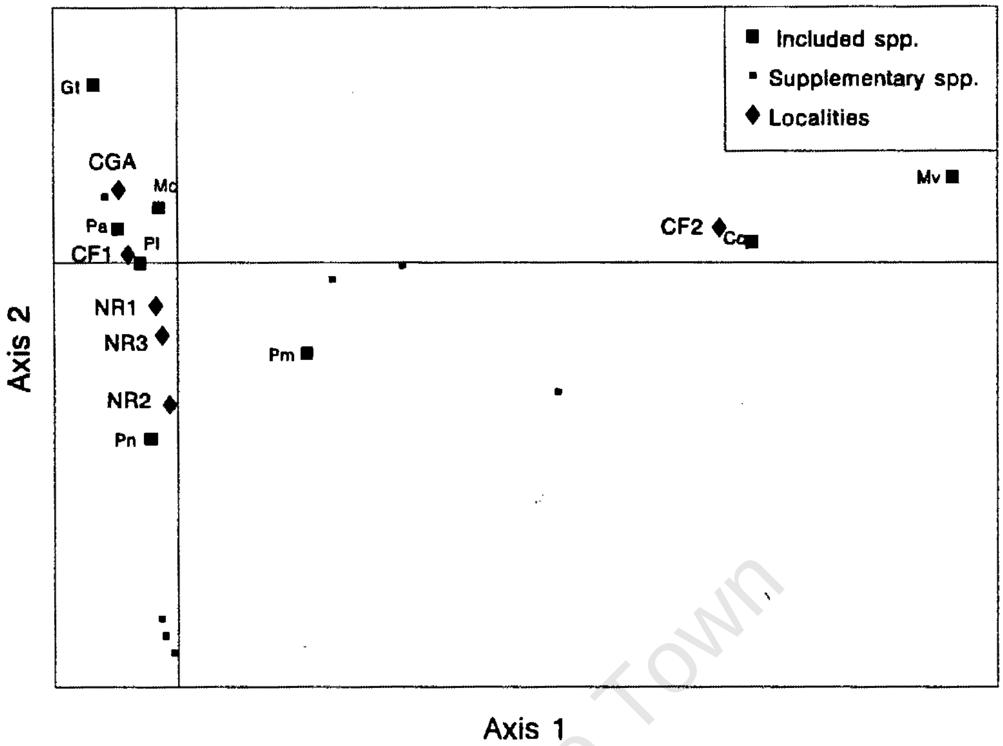


Figure 1. Correspondence Analysis of reptile species and localities. CF1 & 2 = commercial farms, NR1-3 = nature reserve, CGA = communal grazing area, Cc = *Cordylus cordylus*, Gt = *Gerrhosaurus typicus*, Mc = *Mabuya capensis*, Mv = *M. varia*, Pa = *P. maculatus*, Pl = *Pedioplanis lineoocellata pulchella*, Pm = *Pachydactylus m. mariquensis*, Pn = *Psammophis notostictus*. Axis 1 explained 68% of the inertia and Axis 2 a further 23%. Supplementary species, represented by three or less individuals (see Table 1), were not included in the analysis

DISCUSSION

Main implications

Land use seems to have a weaker influence on the biodiversity of terrestrial reptiles than on arthropods in Xeric Succulent Thicket (cf. Chapter 6), except in extreme treatments such as the overutilized Communal Grazing Area, where degradation promotes their abundance and diversity. The apparent insensitivity of reptiles to subtle changes in land use does not however apply to all species. Although heavily degraded areas such as the CGA can make a measurable contribution to the conservation of some terrestrial reptiles, it is most important to maintain areas with high vegetation cover to preserve those species which are not adapted to degraded conditions. Examples of these are arboreal snakes and chameleons, as well as those species which require perennial plant material such as bark and litter to complete their life cycles. In other studies, long-lived stenotopic reptiles such as the desert tortoise *Gopherus agassizi* were sensitive to herbivore-induced land degradation through overgrazing (Berry 1978), while lizard species which are dependent on litter or shade showed a remarkable recovery after the cause of habitat degradation was removed (North, Bullock & Dulloo 1994). Clearing of mesquite reduced the abundance and diversity of lizards in Arizona (Germano & Hungerford 1981).

Causes of greater reptile abundance in the CGA

Possible causes of the higher reptile abundance in the CGA might be greater prey availability, lack of predation, the positive relationship between regional / national distribution and local abundance, facilitation, lack of competition, and improved habitat quality or availability. Greater prey availability can be ruled out as a cause, as the CGA had almost 45% fewer terrestrial arthropods, both in species and abundance, than its corresponding site in the NR (Chapter 6). All the lizard and most of the snake species found in the CGA preyed mainly on invertebrates. It was originally postulated that the large number of reptiles in arid and semi-arid regions was a result of a higher abundance of termites (Pianka 1989). This explanation was rejected in this study because no termites were captured in the CGA (Chapter 6).

Another possible explanation relates to the positive relation between distribution and abundance. Widespread species are more likely to be abundant, at the local level, than species with a restricted distribution (McNaughton & Wolf 1970); a number of likely causes are given by Hanski, Kouki & Halkka (1993), who conclude that the most plausible reason is that widespread species are habitat generalists, and therefore have more resources available at the local level. They also occur at a wider variety of microsites than restricted species, which are mostly stenotopic habitat specialists. We rejected the distribution-abundance relation as a possible cause, because all the species and subspecies collected in this study were widespread in South Africa, with two exceptions (*Nucras taeniolata* and *Gerrhosaurus typicus*).

Predation may also affect the presence or abundance of some species. The CGA has a shortage of predators which prey on squamates, e.g. snakes, certain birds of prey, hornbills and small mammalian carnivores, because it does not contain suitable shelter or perches. In the case of predatory snakes, direct persecution by the local people might have had a negative effect on their populations. The two species of large monitor lizards (*Varanus* spp.) are used for muti or traditional medicine (Simelane 1996) and may be extinct in the CGA.

A feasible explanation for the greater abundance of reptiles in the CGA, in concurrence with the rest of this research programme, relates to improved habitat conditions. The open and barren terrain of the CGA provided suitable foraging habitat for reptiles, with enough sparse vegetation for hiding and darting amongst shrubs (cf. Mushinsky 1992). The CGA was also more strongly associated with arthropod predators (arachnids) than with herbivorous arthropods (Chapter 6). Another possible habitat-related explanation is that the lack of cover at the CGA resulted in superior conditions for thermoregulation of reptiles in winter, which promoted more favourable energy budgets. The positive relation between energy availability and abundance as well as diversity is incorporated in a model by Wright *et al.* (1993), based on an extensive literature review. It could be that reptiles in the CGA searched more for food because of its decreased availability, and were therefore more prone to being trapped there than in the nature reserve.

The increase in lizard richness in response to land degradation is not restricted to Xeric Succulent Thicket. Lizard communities elsewhere have also benefited from apparent land degradation, such as clear-cutting of forests (Greenberg *et al.* 1994); the authors concluded that development of mature forests rather than clear-cutting decreased the diversity of some lizard communities. Sand lizards in the UK were reduced to extinction in habitats where dense undergrowth was maintained, and the highest numbers of these reptiles occurred in "mismanaged" (not from a lizard's point of view!) sparse shrubland. It was postulated that shading of eggs was the main cause of a reduction in sand lizard numbers (Corbett & Tamarind 1979).

The association of a high reptile biodiversity with poorly vegetated areas does not only apply to anthropogenic influences such as overgrazing or land degradation: reptile species richness in the Kalahari semi-desert was negatively correlated with precipitation and, consequently, with vegetation cover (Pianka 1989).

The hypothesis that a greater faunal diversity occurs in habitats with a high patch diversity (Shmida & Wilson 1985) compared to homogenous habitats, does not apply to Squamata in Xeric Succulent Thicket. The CGA had a significantly lower patch diversity, as indicated by the pixel diversity in a SPOT image, than the NR or commercial farms (Chapter 3). The reptiles might have however reacted to patchiness at a finer resolution than the 20 x 20 m patches studied in Chapter 3.

Relationships between species and localities

The common characteristics of the species associated with the CGA was that they were adapted to xeric conditions, being primarily distributed in the arid and semi-arid Western part of South Africa, except *M. capensis* which could be regarded as a generalist with a cosmopolitan distribution. The species which were not associated with the CGA were primarily distributed in the higher rainfall northern and eastern parts of the country (Branch 1988). The association of the degraded CGA with "xeric-adapted" reptile species is ascribed to the increased amount of bare ground and reduced vegetation cover, resembling desertification. These species are likely to have physiological and behavioural adaptations to arid or desertified conditions (Greenberg, Neary & Harris 1994).

In addition to the data recorded during the study, it is possible to speculate about the effects of the different land-use styles on lizard and snake species not sampled during the study period. It may be safely assumed that populations of arboreal species such as dwarf chameleons (*Bradypodion* spp.) and tree snakes (*Dispholidus t. typus*) would be negatively impacted in intensively grazed vegetation such as in the CGA. The CGA is also probably unsuitable for fossorial species (*Acontias* spp.) because of extensive sheet and gully erosion and possible soil compaction in these areas (pers. obs.). The lack of leaf-litter or vegetative debris would negatively effect species which use plant litter for cover, such as the Cape dwarf burrowing skink (*Scelotes caffer*). The small remnant bush-clumps at the CGA are generally devoid of leaf litter because of frequent defoliation by goats, whereas the more lightly browsed bush clumps at other localities provide such micro-habitat.

Procedural shortcomings

The low trapping success was a handicap, and some species could have occurred in areas where they were not collected. It seems as though 864 trap-days are not enough to adequately sample reptiles in Xeric Succulent Thicket; only 15 of the 42 snake and lizard species which are known to occur in the 30' x 30' area which covers the reserve were recorded in this study. Large snakes in particular were reluctant to enter the specially-designed funnel traps.

Conclusion

It appears as though xeric-adapted reptiles could be promoted instead of threatened by overgrazing in Xeric Succulent Thicket. Because of the prevalence of heavily utilised communal areas in the Eastern Cape as a result of the former "homeland" system, there is no need for concern about the conservation status of the species associated with these areas. The species in most need of protection in Xeric Succulent Thicket are not adapted to arid conditions and require dense vegetation cover for survival, such as arboreal and shade-loving species. Less than 55% of the 15 species recorded in this study were collected at any one trap locality, and therefore patches of vegetation with a high cover need to be maintained to ensure the preservation of a high reptile gamma diversity. Because of the trend to overgraze Xeric Succulent Thicket on most commercial farms, conservation areas are essential to maintain such patches and therefore play an important role in preserving lizard diversity.

6. Arthropod Diversity and Land Degradation in Xeric Succulent Thicket

ABSTRACT

The aim of the study was to determine the relation between land management and biodiversity, with a focus on the role of nature reserves in preserving terrestrial arthropods. To achieve this, a nature reserve was compared to an historically overgrazed commercial farm, an intensively managed, conservatively stocked commercial farm and a communal grazing area respectively in Xeric Succulent Thicket in the Eastern Cape, South Africa. Terrestrial arthropods were caught in paired pitfall traps inside and outside the nature reserve respectively. Specimens were sorted into Recognizable Taxonomic Units or RTUs, using rapid assessment techniques. The arthropods which occurred in each land management unit were compared in terms of RTU richness, Hierarchical Richness Indexes (HRIs), community similarity and uniqueness. The nature reserve contained more RTUs and a greater HRI than adjacent land for most arthropod taxonomic groups, and also contained the largest number of unique RTUs which were not collected on unconserved land. The communal grazing area differed most from the nature reserve in terms of richness and community similarity, followed by the conservatively stocked commercial farm. The historically overgrazed commercial farm was most similar to the nature reserve in terms of richness and community similarity. These differences and similarities between localities might be explained by the intermediate disturbance hypothesis. In an ordination, arthropods which were obligate herbivores were associated with well-vegetated localities while predatory arthropods were associated with the localities with poor vegetation cover.

INTRODUCTION

In this chapter the species richness and abundance of arthropods, specifically insects and arachnids, in a nature reserve are compared to that of two commercial farms and a communal grazing area respectively. This study formed part of a more comprehensive project which investigated the impact of land use on biodiversity in relation to landscapes (Chapter 3), vegetation (Chapter 4), reptiles (Chapter 5) and arthropods (this paper).

Invertebrates are important role players in ecosystem health, and the functioning of ecosystems depends to a large degree on the influence of small, unspectacular organisms (Hafernik 1994; Ehrlich 1988). They play a role in altering the structure and fertility of soils, pollination of flowering plants, feeding of predators (Janzen 1987), nutrient cycling and decomposition of organic material (Seastedt & Crossley 1984; Greenslade 1992), and their populations fluctuate episodically which might influence the functioning of unstable ecosystems, e.g. periodic locust outbreaks in semi-deserts (Samways 1994).

Arthropods are potential indicators of subtle habitat change, because they perceive the environment at a finer scale than larger organisms and require smaller habitat patches than larger animals for survival (Wiens & Milne 1989). Arthropods are sensitive to changes at the landscape as well as at the plant community level (Samways 1994). Taxonomic groups with many sub-units (species and subspecies) can be expected to show a high degree of niche differentiation which leads to habitat specificity (stenotopy). Like most organisms, invertebrates react to vegetation and landscape change in different ways. For example, some increase in response to disturbance while others decrease as a result of disturbance (Parmenter & Macmahon 1987).

Arthropods are the most abundant consumers in African savannas and in some instances have a greater biomass than vertebrates (Gandar 1982a,b). Arthropods constitute 85% - 91% of the world's animals and 65% - 79% of known taxa in the world (Kim 1993). Yet they are amongst the most threatened groups in tropical forests (Wilson 1990) and on Pacific islands (Hafernik 1994).

The existence of conservation areas is often defended on the grounds that they are biodiversity banks, and that they protect species which do not occur elsewhere. Surprisingly this conventional dogma is seldom tested. Most data sets on biodiversity in Southern Africa are based on collections, distribution records or from checklists from protected areas, and with a few exceptions (e.g. Moolman & Cowling 1994; Rivers-Moore & Samways 1996) do not include comparisons between protected areas and neighbouring land. The international literature reveals equally few biodiversity studies which incorporate data from both inside and outside protected areas (but see Greenslade 1992).

The objectives of this study were to

1) compare the number of RTUs and Hierarchical Richness Indexes of arthropods in a nature reserve to that of adjacent commercial and communal rangeland;

2) determine the community similarity of arthropods in a nature reserve to that of commercial and communal rangeland;

3) determine the number of unique and shared RTUs in the respective taxonomic groups, in relation to each of the land management units;

4) find out which functional types of arthropods were associated with the respective land management units; and

5) identify taxonomic groups which could act as useful indicators to monitor the effect of land management on biodiversity.

METHODS

Traps were positioned in pairs in each of the three adjacent land management units and at corresponding sites across the boundary fence inside the nature reserve. A *trap* consisted of a 20 cm high and 10 m long drift fence, with a 25 litre plastic bucket, buried flush with the soil surface, at one end of the drift fence and two funnel traps, one on each side of the drift fence, at the other end. Drift fences were buried about 5 cm deep to prevent arthropods from escaping under the fence. Four replicate traps were positioned on each side of the boundary with the reserve for each respective paired trap site. A *trap locality* is defined as a group of four traps in a single land management unit, on one side of the boundary only. A *site* is defined as two paired trap localities on opposite sides of the boundary fence, inside the nature reserve and on an adjacent unconserved property respectively. At Site I the historically overgrazed commercial farm (CF1) was compared to the nature reserve (NR1). At Site II the conservatively stocked and intensively managed commercial farm (CF2) was compared to the nature reserve at NR2. At Site III, the communal grazing area (CGA) was compared to the nature reserve at NR3.

Traps at the same trap locality were positioned about 150 m apart. To avoid a "spill-over" effect (specimens being captured at one trap locality having spent most of their time on the other side of the fence), trap localities were placed further than 100 m from the nature reserve boundary. Every effort was made to ensure that paired traps were positioned at the same slopes, aspects and elevations. The traps (also used for reptiles, Chapter 5) were placed at the same localities as the plots for the landscape analysis (Chapter 3) and the vegetation surveys (Chapter 4). Traps were opened for 6 days a month for 6 months between October 1993 and March 1994. The inspection of traps was synchronized as closely as practically possible.

To avoid misidentification as a result of sex, age and caste polymorphism, training in the identification of RTUs was provided by specialists. All "para-taxonomic" work took place under guidance of trained entomologists. A reference collection of numbered RTUs was compiled and curated. To further validate the use of RTUs in stead of species, spiders and weevils were subsequently identified to the species level by specialized taxonomists (Appendixes 3 and 4).

More than 8500 arthropod specimens were caught during 864 trap-nights. Each specimen was fixed in 60% alcohol, labelled and stored to enable the accurate recording of information at a later stage. A limited number of higher taxonomic groups (Orders and Families) was focused on before the data were analyzed. Groups for further analysis were selected to represent a range of body sizes and feeding strategies. The selection of a taxonomic group to be incorporated in the further analysis of data depended on i) the number of possible finer taxonomic units within the taxon, ii) the number of individual specimens of the taxon collected and iii) the contribution of the taxon to reflecting a range of body sizes and feeding strategies in the study area.

This resulted in the selection of six taxonomic groups for further analysis: grasshoppers (Orthoptera: numerous Families); crickets (Orthoptera: Gryllidae); spiders (Araneae: numerous Families); large arachnids i.e. scorpions (Scorpiones: Scorpionidae and Buthidae), whipscorpions (Amblypygi), solifuges (Solifugae); ants (Hymenoptera: Formicidae) and weevils (Coleoptera: Curculionidae).

Ants were often encountered in large numbers and were not counted individually. Instead, a representative specimen of each ant RTU at each respective trap was collected on each trap-day. Calculations for ants were thus based on daily frequencies of occurrence rather than numerical abundance.

All specimens were classified initially to the Order level, and in some instances to the Family level. Specimens were then categorized, using Rapid Biodiversity Assessment or RBA (Beattie, Majer & Oliver 1993). The main characteristic of RBA is that the use of fine-scaled formal taxonomy down to the species level is avoided as far as possible, provided that the objectives of the study are not compromised. Specimens were distinguished on morphological characteristics and labelled as recognizable units, variously called *morphospecies*, *Operational Taxonomic Units* (OTUs) or *Recognizable Taxonomic Units* (RTUs) (Beattie et al. 1993). The term RTU was used in this study.

Data analysis

The *richness* of a locality is defined as a combination of a) the number of RTUs or taxonomic groups and b) the abundance of individuals in each taxonomic group recorded at a locality (French 1994). After experimenting with various biodiversity indexes it was found that the Hierarchical Richness Index or HRI (French 1994) best reflected the biodiversity patterns and trends recorded in this study. HRIs were calculated for each taxonomic group and each trap separately. First, all RTUs of a particular group collected at a trap were sorted in descending order of abundance. The most abundant RTU was then allocated a weight or hierarchical index value (i) of one, the second most abundant an i of two and so on. The hierarchical value of each RTU was then multiplied by the number of individuals of that RTU to produce a score s. The ss were summed for all RTUs at each locality, to produce an $HRI=\sum(si)$ (French 1994). HRIs were calculated separately for each of the four traps at each locality, and data for the respective trap localities were averaged to obtain means and standard errors.

To determine the degree of similarity between trap localities, Sorenson's index of community or *CC* (Sorenson 1948) was calculated for each paired trap site, for each respective taxonomic group. The formula used was $CC = 2s/(a+b)$ where s is the number of RTUs which are shared by both trap localities, a is the number of RTUs in locality a, and b is the number of RTUs in locality b.

For each trap locality a Uniqueness Index $U = U_r / R_{tot}$ was calculated, where U_r was the number of RTUs which were unique to the trap locality, and R_{tot} was the total number of RTUs captured at a paired trap site.

To determine whether the us were significantly greater than zero, their 90% confidence intervals were calculated, using the formula
90% confidence level = $\pm (z_{(1-\alpha/2k)}(\sqrt{U(1-U)/n})$, where U = the proportion of RTUs unique to the NR (see previous paragraph), k = the number of simultaneous estimates being made, and n = the total number of RTUs for the paired trap site. The purpose of using a Bonferroni normal statistic ($1-\alpha/2k$) instead of the standard normal statistic ($1-\alpha/2$), is to widen the confidence interval to compensate for the fact that more than one simultaneous estimate is involved (Neu, Byers & Peek 1974)[1].

From the uniqueness values it is possible to determine how changes in land use would affect RTU richness, e.g. when one type of land use becomes

---

[1] This results in a slightly more conservative statistic to ensure that when the number of estimates increases, the probability that one of the intervals might be incorrect increases beyond the conventional α. In this instance $k = 3$, consisting of 1) the proportion of RTUs unique to the NR, 2) the proportion of species unique to the adjacent trap locality and 3) the proportion of RTUs shared between the two trap localities. Although the resulting effect on α was severe (if a 90% confidence interval is chosen, α changes from 0.05 to 0.017), the effect on z was moderate. Using the same example, z changed from 1.65 to 2.13.

increasingly prevalent at the expense of other land uses. The rationale is that where significant proportions of unique RTUs occur at a trap locality, the replacement of that type of land use by other types of land use would result in a loss of RTUs in the study area as a whole. A *significant proportion* is defined as a *U* value of which the lower 90% confidence interval is above zero.

One of the goals was to determine which taxonomic groups and which trap localities were associated. A matrix of taxonomic groups (rows) by trap localities (columns) was ordinated by correspondence analysis, or CA (Greenacre 1986). The values in the matrix consisted of the average HRI values calculated for each trap locality and each taxonomic group. The graphical output as well as the row and column contributions of the variables were used to determine which taxonomic group and properties were associated.

The usefullness of a taxonomic group as a biodiversity indicator was calculated as the number of times a group showed a *substantial* difference between paired sites when subjected to the three methods of analysis (CC, HRI and U) specified earlier. The rationale was that a taxonomic group which consistently showed a substantial biodiversity difference between two localities, in response to the three methods of analysis used, would be sensitive to land use and therefore a good indicator. *Substantially different* was defined as: i) HRI values for which the upper and lower standard errors bars did not overlap; ii) *CC* values of 0.75 and smaller; and iii) *U* values for which the lower 90% Bonferroni Z confidence interval was greater than zero.

RESULTS

RTU richness

The greatest difference between the nature reserve and unconserved land, both in terms of number of RTUs and number of individuals trapped, occurred at Site III (comparison between the NR and the CGA). The paired localities at Site I were most similar (Table 1).

Comparative richness

The NR had larger mean HRIs than adjacent land in most taxonomic group (with the exception of ants and grasshoppers at trap site I, the comparison between NR1 and CF1). The most obvious difference in mean HRIs was the comparison between the communal grazing area and the nature reserve (site III) (Table 2). The wide standard errors were expected because of the small number of replicates (four) at each trap locality (Figure 1).

In greater detail, the most noteworthy results were:

i) In a comparison between the nature reserve and the communal grazing area (paired trap site III), the nature reserve had a greater richness than the communal grazing area in all taxonomic groups (Table 2, Figure 1). None of the upper and lower standard error bars overlapped for any of the taxonomic groups at this paired trap site.

Table 1. Number of Recognizable Taxonomic Units (RTUs) and number of individuals (No.) of arthropods trapped at three sites, as well as for the entire nature reserve (NR) and all unconserved localities combined (Uncons). Site I = comparison between the historically overgrazed commercial farm and its corresponding site in the nature reserve. Site II = comparison between conservatively stocked commercial farm and its corresponding site in the nature reserve. Site III = comparison between the communal grazing area and its corresponding site in the nature reserve. CF1 and 2 = commercial farms, NR1 - 3 = nature reserve, CGA = communal grazing area

	Site I				Site II				Site III				Total comparison			
	NR1		CF1		NR2		CF2		NR3		CGA		NR		Uncons.	
	RTU	No.	RTU	No.	RTU	No.	RTU	No.	RTU	No.	RTU	No.	RTU	No.	RTU	No.
Ants *	16	196	19	272	20	310	16	313	18	91	11	62	25	597	20	647
Crickets	3	87	2	46	3	95	3	94	2	91	3	21	3	273	4	161
Grasshoppers	8	42	11	44	12	149	11	150	6	42	6	9	15	233	17	203
Large arachnids	10	151	9	140	7	253	7	87	10	236	7	91	12	640	11	318
Spiders	45	673	39	815	49	629	46	447	39	821	31	292	78	2123	68	1554
Weevils	12	39	9	45	17	122	13	55	12	87	8	46	23	248	19	146

* Daily frequency of occurrence, as opposed to number of individuals

Table 2. Mean Hierarchical Richness Indexes (HRIs) and standard errors for three paired trap sites. Site I = comparison between the historically overgrazed commercial farm and its corresponding site in the nature reserve. Site II = comparison between conservatively stocked commercial farm and its corresponding site in the nature reserve. Site III = comparison between the communal grazing area and its corresponding site in the nature reserve. CF1 and 2 = commercial farms, NR 1 - 3 = nature reserve, CGA = communal grazing area

	Site I				Site II				Site III			
	NR1		CF1		NR2		CF2		NR3		CGA	
	Mean HRI	S.E	Mean HRI	S.E	Mean HRI	S.E	Mean HRI	S.E	Mean HRI	S.E	Mean HRI	S.E
Ants *	175.5	34.0	215.0	39.0	260.5	33.9	209.8	73.3	95.8	8.2	48.5	10.3
Crickets	24.0	2.6	12.8	2.1	32.5	6.0	25.5	5.0	20.0	5.1	6.8	1.3
Grasshoppers	19.8	5.4	25.0	9.1	90.0	16.8	73.0	10.5	35.0	11.0	4.5	2.2
Large arachnids	109.0	12.8	76.8	14.6	87.5	14.5	39.5	14.7	132.5	27.2	48.5	9.9
Spiders	823.8	55.6	757.3	101.8	864.0	146.1	720.0	79.9	876.8	21.5	316.5	47.3
Weevils	24.8	3.8	20.2	5.1	96.5	17.1	36.5	10.2	59.5	3.6	22.3	6.6

* Calculated using daily frequencies as opposed to number of individuals

ii) The richness of large arachnids (scorpions, whipscorpions and solifugids combined) was substantially higher in the nature reserve than on unconserved properties at all paired trap sites.

iii) Weevils displayed a large difference between localities at paired trap site II (the comparison between conservatively grazed commercial farm and the reserve), where the mean HRI recorded at the NR was more than twice as high as the mean HRI recorded at the commercial farm.

iv) The average HRI for crickets at site I was almost twice as high in the nature reserve at NR1 as the average HRI for crickets on CF1 (the heavily grazed commercial farm).

Community similarity

In the *total comparison*, i.e. when all the sites in the nature reserve combined were compared to all unconserved sites, the communities of spiders, ants, crickets, and large arachnids were similar, with *CC* values of 0.82, 0.84, 0.86, and 0.96 respectively (Table 3). Conversely, the grasshopper and weevil communities on the nature reserve differed substantially from the communities on unconserved land, with *CC*s of 0.75 and 0.76 respectively. A *CC* of 0.75 and lower was regarded as the threshold for two sites to be classified as supporting different communities (cf. Whittaker 1972; Cowling, Gibbs Russel, Hoffman & Hilton-Taylor 1989).

When localities at respective *paired trap sites* were compared, the most dissimilar arthropod communities occurred in the comparisons between the NR and CF2 (Site II) and between the NR and the communal grazing area (Site III). At Site II there were different communities of crickets, grasshoppers, large arachnids and weevils. At Site III there were different communities of ants, grasshoppers, spiders and weevils. In the comparison between the nature reserve and commercial farm 1 (Site I), different communities were recorded for one taxonomic group only (spiders).

The taxonomic groups which were be more sensitive than others to land use in terms of their community composition were: grasshoppers, where separate communities occurred at two paired trap sites plus the total comparison; spiders (separate communities at two trap sites); and weevils (separate communities at two trap sites).

Uniqueness

In the *total comparison*, when the entire nature reserve was compared to all surrounding unconserved properties, the taxonomic groups with the largest proportion of RTUs unique to the NR were weevils, ants and spiders (in that order), while grasshoppers had the largest proportion of RTUs unique to adjacent unconserved properties. The largest proportion of shared RTUs occurred in the large arachnids (Table 4).

When *individual trap localities* were compared, i.e. within paired trap sites, spiders and weevils were the most locality-unique. All *U*s for spiders at all localities were significantly larger than zero. The large arachnids and crickets were the least locality-unique: none of their *U* values were significantly larger than zero at any of the trap localities.

The taxonomic groups which stood out as being more unique to the nature reserve than to neighbouring land were the spiders and weevils (in all comparisons) and the ants (with one exception, comparison NR1-CF1). With the exception of the grasshoppers in the total comparison and the ants at NR1-CF1, none of the taxonomic groups contained a significantly larger proportion of unique RTUs on unconserved land than in the nature reserve.

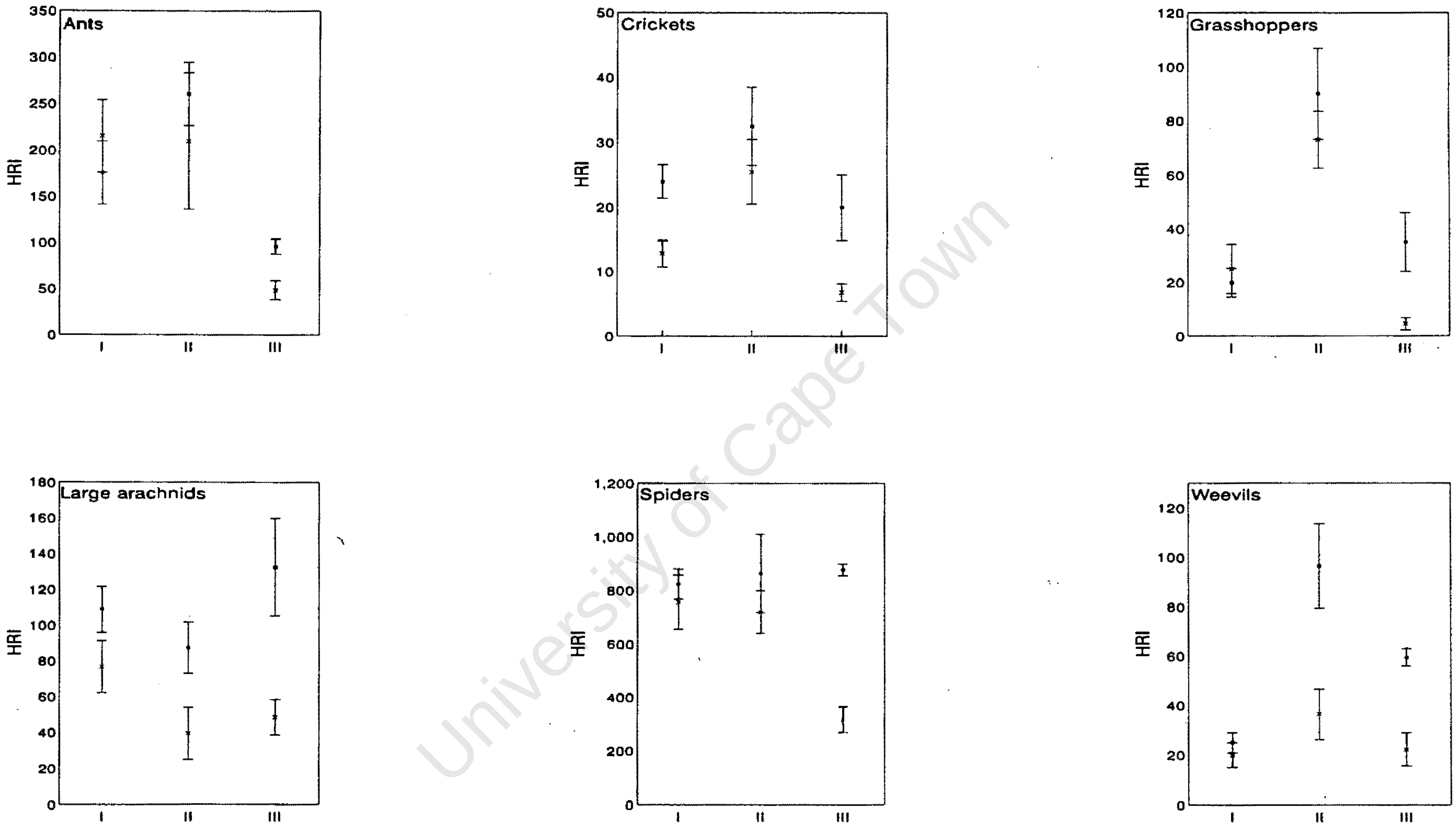


Figure 1. Hierarchical Richness Indexes of arthropod taxonomic groups. I: comparison between historically overgrazed commercial farm and the nature reserve (CF1-NR1). II: comparison between conservatively stocked, intensively managed commercial farm and the nature reserve (CF2-NR2). III: comparison between the communal grazing area and the nature reserve (CGA-NR3). **x** = mean for unconserved land, • = mean for nature reserve. HRIs for ants were calculated using daily frequencies of occurrence rather than numbers of individuals.

Table 3. Community similarities for three paired trap sites, as well as all unconserved localities combined against the nature reserve (Total comparison). Site I = comparison between the historically overgrazed commercial farm and its corresponding site in the nature reserve. Site II = comparison between conservatively stocked commercial farm and its corresponding site in the nature reserve. Site III = comparison between the communal grazing area and its corresponding site in the nature reserve

	Site I	Site II	Site III	Total comparison
Ants	0.86	0.83	0.62	0.84
Crickets	0.80	0.67	0.80	0.86
Grasshoppers	0.84	0.70	0.67	0.75
Large arachnids	0.84	0.71	0.82	0.96
Spiders	0.69	0.76	0.63	0.82
Weevils	0.76	0.60	0.50	0.76

Table 4. *U* values, indicating the proportion of unique RTUs and shared RTUs in the nature reserve (NR) and each respective unconserved locality (Uncons.). *U* = proportions of unique RTUs, relative to the total number of RTUs (n) at each trap locality; 95% conf. limits = 95% Bonferroni-z confidence limits. Site I = comparison between the historically overgrazed commercial farm CF1 and its corresponding site in the nature reserve. Site II = comparison between conservatively stocked commercial farm CF2 and its corresponding site in the nature reserve. Site III = comparison between the communal grazing area CGA and its corresponding site in the nature reserve. Total comparison = all localities on unconserved land compared to all localities in the nature reserve

		Site I			Site II			Site III			Total comparison		
		U	*n*	*95% conf. limits*	*U*	*n*	*95% conf. limits*	*U*	*n*	*95% conf. limits*	*U*	*n*	*95% conf. limits*
Ants	Uncons.	0.20	20	0.19 *	0.05	21	0.10	0.10	20	0.14	0.04	26	0.08
	NR	0.05		0.10	0.24		0.20 *	0.45		0.24 *	0.23		0.18 *
Crickets	Uncons.	0.00	3	0.00	0.25	4	0.46	0.33	3	0.58	0.25	4	0.46
	NR	0.33		0.58	0.25		0.46	0.00		0.00	0.00		0.00
Grasshoppers	Uncons.	0.27	11	0.29	0.20	15	0.22	0.25	8	0.33	0.25	20	0.21 *
	NR	0.00		0.00	0.27		0.24 *	0.25		0.33	0.15		0.17
Large arachnids	Uncons.	0.09	11	0.18	0.22	9	0.30	0.00	10	0.00	0.00	12	0.00
	NR	0.18		0.25	0.22		0.30	0.30		0.31	0.08		0.17
Spiders	Uncons.	0.18	55	0.11 *	0.17	59	0.10 *	0.19	48	0.12 *	0.09	86	0.07 *
	NR	0.29		0.13 *	0.22		0.11 *	0.35		0.15 *	0.21		0.09 *
Weevils	Uncons.	0.08	13	0.16	0.19	21	0.18 *	0.20	15	0.22	0.12	26	0.13
	NR	0.31		0.27 *	0.38		0.23 *	0.47		0.27 *	0.27		0.19 *

* *Lower 90% confidence interval greater than zero*

Increasers and decreasers

The types of land uses which were most likely to become prevalent in the study area were identified as first communal grazing (Ainslie, Fox & Fabricius 1994), and second commercial farming at continuous high stocking rates (La Cock Palmer & Everard 1990). Those taxonomic groups which were unique to the nature reserve and which had *U* values significantly greater than zero were identified. If communal grazing is predicted to become the increasingly prevalent type of land use, at the expense of nature conservation (as at Site III in Table 4), then taxonomic groups which will forfeit RTUs with 95% certainty (only the lower 90% confidence limits were considered) are the ants, spiders and weevils. Likewise, the same taxonomic groups will, with a 95% probability, forfeit RTUs if the nature reserve were to be replaced by the existing combination of land-uses other than conservation ("Total comparison" in Table 4).

Should commercial livestock farming at high stocking rates replace nature conservation (as at Site I in Table 4), then a 95% probability exists that the number of RTUs of spiders and weevils will decrease. Should livestock farming at conservative stocking rates become the predominant land use type (as at Site II in Table 4) at the expense of nature conservation, then the number of RTUs of ants, grasshoppers, spiders and weevils will decrease with a 95% probability.

Association of taxonomic groups and land uses

In a Correspondence Analysis of a trap locality by taxonomic group matrix (Table 5), the respective paired localities at the same trap site were situated closely together in the ordination, which indicated that the sites were suitably selected (Figure 2). Axis 1 displayed a gradient of vegetation density, and sites were arranged from high altitude, high precipitation and low stocking rates (CF2 on the right) to low altitude low precipitation high stocking rates (CGA on the left). In the study area there is a strong positive correlation between altitude and rainfall (Palmer & Avis 1994; Palmer 1981).

Axis 2, which accounted for 29% of the inertia in the data, and axes 3 and 4 which together accounted for 7% of the inertia, contained no known gradients and were therefore not interpreted. To reduce unncessary "noise", the diagram was therefore simplified to display two dimensions only.

Table 5. Matrix of mean Hierarchical Richness Index values, in a trap locality by taxonomic group configuration, which acted as input to the Correspondence Analysis

	CF1	NR1	CF2	NR2	CGA	NR3
Ants	215	175.5	209.8	260.5	48.5	95.8
Crickets	12.8	24	25.5	32.5	6.8	20
Grasshoppers	25	19.8	73	90	4.5	35
Large arachnids	76.8	109	39.5	87.5	48.5	132.5
Spiders	757.3	823.8	720	864	316.5	876.8
Weevils	20	25	36.5	96.5	22.3	59.5

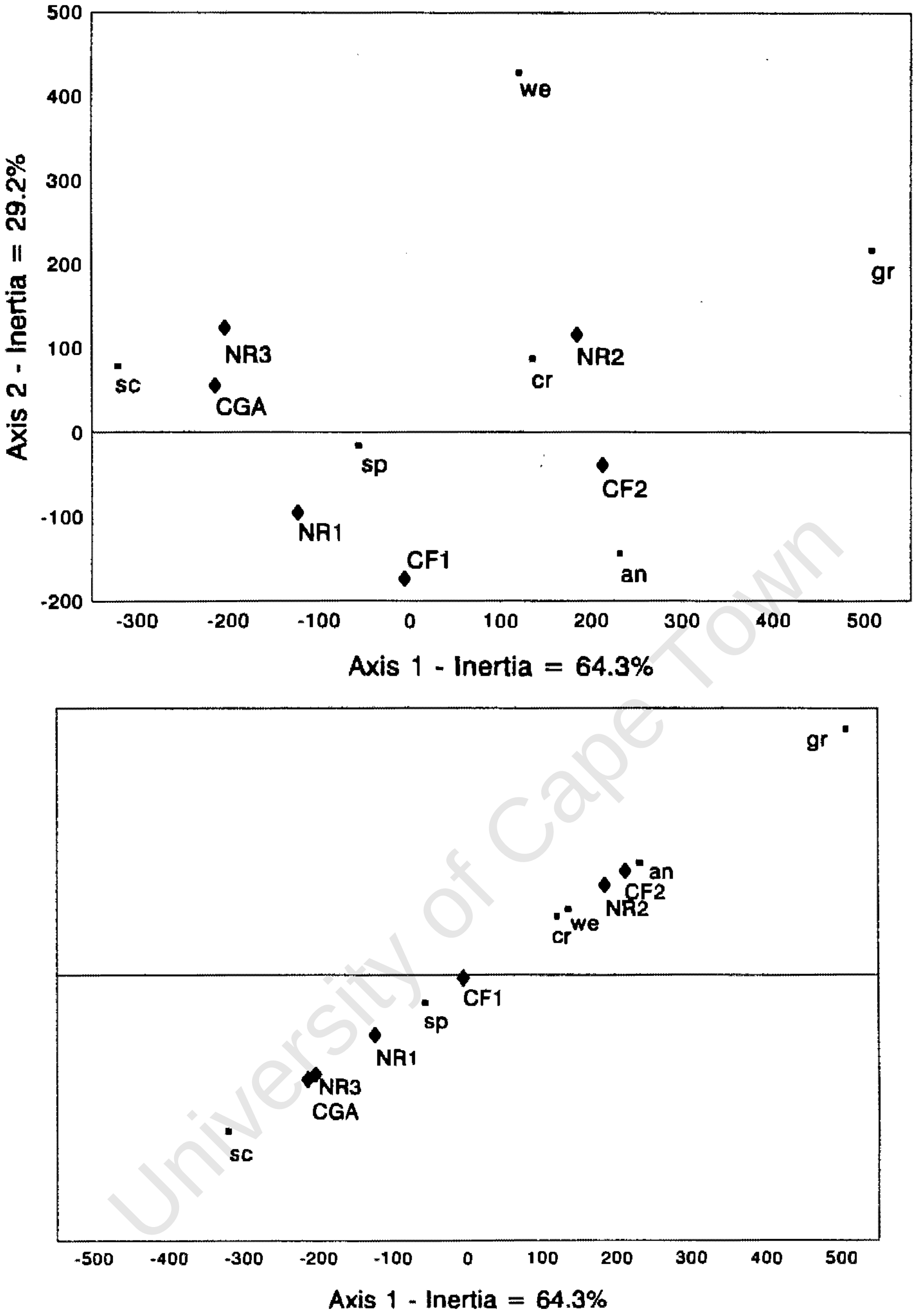


Figure 2. Correspondence analysis of a matrix of taxonomic groups by trap localities. CF1 = historically overgrazed commercial farm, NR1 = its corresponding site in the nature reserve. CF2 = conservatively stocked, intensively managed commercial farm, NR2 = its corresponding site in the nature reserve. CGA = communal grazing area, NR3 = its corresponding site in the nature reserve; an = ants, gr = grasshoppers, cr = crickets, sc = large arachnids, sp = spiders, we = weevils. The bottom diagram is a one-dimensional version of the top diagram. Axis 1 accounted for 64% of the total inertia in the data, and was the only axis which displayed a clear gradient.

The arthropods appeared along the site gradient according to a feeding "gradient", from obligate herbivores on the right through to obligate predators on the left. The order in which they occurred along the gradient was herbivores (grasshoppers); a mixture of omnivores and detritivores (ants, weevils and crickets); small predators (spiders); and large predators (large arachnids). The herbivorous groups (grasshoppers) were associated with the conservatively stocked high elevation locality CF2, while the groups which contained a mixture of omnivores and detritivores (weevils and crickets) were, compared to the grasshoppers, more closely associated with the corresponding paired site on the nature reserve, NR2. The spiders were associated with the intermediate elevation sites NR1 and CF1. The large arachnids were closely associated with the communal grazing area (CGA) as well as its complementary locality in the nature reserve (NR3).

Indicator groups

Table 6 summarizes the number of instances where a taxonomic group "substantially" differed (as defined under Methods) between two trap localities at a paired trap site, when the three different assessment methods, Hierarchical Richness Indexes (*HRI*), Sorenson's Index of Community (*CC*) and Uniqueness Index (*U*), were used.

When all three methods are considered simultaneously (using the column labelled "score") the weevils, spiders and ants seem to be good indicators of habitat change. These groups contained many RTUs and subsequently showed a large degree of niche differentiation. The weevils, which were obligate herbivores and contained many RTUs, were exceptionally good indicators.

The large arachnids and crickets, on the other hand, were poor indicators of habitat change. They contained few RTUs and were not obligate herbivores. When individual methods were considered separately, Uniqueness Indexes were the most effective for taxonomic groups with many RTUs, i.e. the ants, weevils and spiders. Hierarchical Richness Indexes seemed to work best with groups which occurred at high densities (weevils, large arachnids and crickets).

Table 6. Number of instances where a taxonomic group showed a "substantial" difference (see Methods) between two paired trap localities, according to three indexes: Hierarchical Richness (HRI), Sorenson's Index of Community (CC) and Uniqueness (U).

	HRI	CC	U	Score
Ants	1	1	3	5
Crickets	2	1	0	3
Grashoppers	1	3	0	4
Large arachnids	3	1	0	4
Spiders	1	2	4	7
Weevils	2	4	4	10

Main findings

The nature reserve contained more RTUs in total, as well as a higher proportion of unique RTUs, than did adjacent unconserved land. This was true for paired comparisons as well as for a total comparison, when all sites on the NR combined were compared to all unconserved properties combined. The largest difference in richness, in HRI and number of RTUs, was recorded between the nature reserve and the Communal Grazing Area, followed by the nature reserve and the conservatively stocked commercial farm CF2. The historically overgrazed commercial farm CF1 was most similar to the nature reserve, but it nevertheless supported a relatively impoverished arthropod fauna, both in terms of HRI and in RTU numbers, in four of the six taxonomic groups studied.

The same pattern was also observed in the indexes of community (*CC*). The largest community differences were between the nature reserve and the communal grazing area NR3-CGA, and between the conservatively stocked commercial farm and the nature reserve NR2-CF2. The smallest differences in communities (highest *CC* values) were between the nature reserve and the historically overstocked commercial farm NR1-CF1.

DISCUSSION

The influence of land use on biodiversity

From the results it seems as though the lightest grazed and most heavily grazed localities contained significantly lower HRIs and fewer RTUs than the nature reserve. A plausible explanation for this pattern might be the *intermediate disturbance effect* (Connell 1975; Rozenzweig & Abramsky 1993). It predicts that diversity will be lowest at heavily and lightly disturbed sites, with the highest diversity at sites with an intermediate level of disturbance. The amount of disturbance relates to both the rate and intensity of disturbance (Miller 1993). This study should however at best be seen as a weak corroboration of the intermediate disturbance hypothesis because of the many uncontrolled variables and the few replicates.

A possible mechanism is put forward for the relationship between disturbance and biodiversity in Xeric Succulent Thicket. It is postulated that the three unconserved trap localities (CF2, CF1 and CGA) respectively represented points of low, intermediate and high disturbance. The nature reserve represented an intermediately disturbed reference point against which the impact of disturbance could be measured, as a result of its relatively low herbivore density, and the variety of disturbance agents it contained in the form of herbivores of different body sizes. Although the stocking rate on the NR was stable over the long term, i.e. over a 10 year cycle, it displayed short-term (seasonal) fluctuations in the densities of the most abundant mammalian herbivores, warthog and kudu, in response to weather (Eastern Cape Nature Conservation, unpublished data).

The communal grazing area represented a heavily disturbed area as a result of continuous heavy stocking rates and progressive denudation by people who collected plants for consumptive purposes such as firewood and building material. It also had the lowest vegetation cover and diversity, the lowest landscape diversity (Chapter 3) and had more severe soil erosion than other sites (pers. obs.).

The historically overgrazed commercial farm CF1 represented a heavily disturbed area as well, albeit less disturbed than the CGA. Its HRI values, RTU richness and community composition differed the least from the NR of all the unconserved sites. CF1 nevertheless had substantially fewer RTUs and lower HRIs than the NR in four out of the six taxonomic groups sampled.

The commercial farm CF2 was the most conservatively stocked. The management strategy of the land owner led to a much more "predictable" disturbance regime than that of the comparable locality in the nature reserve, and might have explained the lower HRIs and RTU numbers at the former site.

Land use and regional biodiversity (gamma diversity)

Each of the land uses made a unique contribution towards the gamma diversity of the study area. i) In a pair-for-pair comparison, all three paired trap sites contained different communities (CC values of 0.75 and less) for at least one taxonomic group. ii) At each paired trap site there were at least two groups which had substantially larger HRIs than at their complementary localities. iii) Each respective paired trap site supported at least three taxonomic groups with a significant proportion of RTUs which were confined either to the nature reserve or the adjacent unconserved properties. Some examples of significant uniqueness indexes were: 25% of the grasshopper RTUs were unique to unconserved properties, i.e. did not occur on the nature reserve; 23% of all ant RTUs, 27% of all weevil RTUs and 21% of all spider RTUs were unique to the nature reserve and did not occur on unconserved properties. None of the individual trap localities contained more than 62% of the total number of arthropod RTUs collected in the study area. In the most extreme case, the communal grazing area contained only 37% of the total number of arthropod RTUs collected in the study area.

Nature conservation was the single land-use type which made the greatest contribution to arthropod conservation in the study area. Furthermore, it represented the least common form of land use in the Eastern Cape, indeed in the entire country (La Cock, Palmer & Everard 1990), which emphasized its future value as a biodiversity "bank". It is clear that the gamma diversity of arthropods in the area will decrease substantially if any of the other land uses replaced nature conservation. An increase in communal grazing at the cost of nature conservation will have a particularly severe impact on arthropod biodiversity. Under such conditions three of the six taxonomic groups could, with 90% certainty, lose between 19 and 74% of their RTUs. Should communal grazing become the only form of land use at the expense of nature conservation and commercial farming, then Xeric Succulent Thicket might, with a 90% probability, be without 5-40% of the ant RTUs, 12-30% of the spider RTUs and 8-45% of the weevil RTUs recorded in this study[2].

Association of taxonomic groups and land uses

In examining the association between organisms and localities, a relation between trophic groups and vegetation structure became evident. In the ordination the arid, low elevation sites (the communal grazing area and its associated site on the nature reserve) were associated with the predators, i.e. scorpions, whipscorpions and spiders.

---

[2] This is an extreme and unlikely scenario.

The well-vegetated, high-elevation sites (the conservatively grazed commercial farm CF2 and its complementary site on the nature reserve, NR2) were associated with the obligate herbivores and detritivores, grasshoppers, weevils and ants. This was most likely because of an abundance of vegetation and plant litter at these well-vegetated sites. The implication of this is that those arthropod types which are dependent on plant material as an essential part of their life-cycles will most likely be the heaviest impacted when vegetation becomes sparser. This is highly likely to be the future trend as a result of drier climatic cycles (Tyson 1986), coupled with existing continuous heavy levels of grazing in Valley Bushveld.

Indicator groups

The choice of indicator groups will depend on the objectives of the study, the scale of the study, the location of the study area and the available funds (Samways 1994). The taxonomic groups which appeared to be sensitive to the influence of land use were those which i) contained many RTUs, ii) were directly dependent on perennial vegetation during their life-cycles and iii) were incapable of aerial migration, and were therefore poor dispersers (Duelli et al. 1990).

Cicadas were found to be relatively insensitive to the impact of land management practices in the same study area (Villet & Capitao 1996). The choice of taxonomic groups with many RTUs leads to greater variance in the data, but also lead to a greater sensitivity to habitat change, being more stenotopic (habitat-specific) as a result of a higher degree of niche differentiation (Samways 1994). On the other hand, the ideal indicator group needs to be well-known and should not contain such a large number of species and subspecies as to make it impractical to use, from a taxonomic point of view (Samways 1993). A "super-indicator" would be a taxonomic group which met all three the above criteria. Weevils fitted all three criteria well, and proved to be the most efficient indicator of biodiversity change in relation to land-use in this study.

Other authors have found that different taxonomic groups are successful indicators of biodiversity. Duelli et al. (1990) found that spiders showed the greatest dissimilarities between sites, and were the poorest dispersers. According to Dean & Milton (1995), weevil abundance was not significantly different between three old field sites of varying ages, while ants were good indicators of succession and disturbance. Rivers-Moore & Samways (1996) found that weevils were eurytopic and were not affected by land use, whereas other coleoptera were stenotopic and were affected, mainly by differences in animal dung between sites. The structure of the vegetation in the different sites compared by Milton & Dean (1995), as well as that of those compared by Rivers-Moore & Samways (1996), was very similar. It is clear that the taxonomic groups which are suitable indicators of land use vary between vegetation types, and that vegetation structure might be an important determinant of this.

Evaluation of methods

The sampling problems associated with pitfall traps have been well-documented, and it is widely accepted that data collected in this way do not always reflect the real structure of invertebrate communities (e.g. Topping & Sunderland 1992; Marsh 1984). For example, the apparent abundance of arthropod taxa can be confounded by differences in activity patterns and abilities to escape from traps (Topping & Sunderland 1992). The purpose of this study was however to compare arthropod richness between paired trap sites, and not to describe the composition of arthropod communities within trap sites. Because of this and because the same method was used at all localities, errors resulting from different trapping success for different types of arthropods would have been standardized and eliminated. Flying arthropods, which might be good indicators at the biotope level, especially in aquatic systems (Clark & Samways 1996), were also excluded from being sampled.

The adoption of a Rapid Biodiversity Assessment approach was appropriate because i) the objective was to obtain *relative* data to be able to compare sites; ii) within the allocated budget and time-span of the project it would not have been possible to classify arthropods to the species level ; iii) only about 5 - 10% of invertebrates have scientific names (Samways 1994). The disadvantage was that it was not possible to determine the response of different taxa within a taxonomic group to different levels of grazing intensity. Dean & Milton (1995) found that different ant and spider species preferred various successsional stages of old fields because of differences in their feeding strategies and predator avoidance mechanisms.

One of the inadequacies of the study was that data were collected for two seasons only (spring and summer). Factors which affected the temporal density of organisms, such as breeding season and hibernation, could result in different patterns emerging in different seasons (Coombes & Sotherton 1986; Desender & Alderweireldt 1988). For example, a more than 5-fold increase in the abundance of Austrian spiders between May and July in the same year was recorded by Kromp & Steinberger (1992). It was possible that larger differences between land management units would have been recorded during winter, when conditions were harsher and the effects of grazing more extreme, than during summer when this study was done.

CONCLUSIONS

This study found invertebrates to be highly sensitive to landscape and vegetation change as a result of different land uses, and that certain groups such as weevils and spiders could be very useful indicators of ecosystem change. The taxonomic groups which are suitable indicators of land degradation vary between vegetation types. Because of their low profile and present low commercial value in Africa, it is neither feasible to manage protected areas directly for the preservation of arthropods, nor to use invertebrates as umbrella or flagship species to preserve ecosystems. Maximum biodiversity is attained by maintaining a variety of disturbance agents in the form of a diverse mammalian fauna. Megaherbivores such as black rhinoceros can be adopted as umbrella species, and landscapes need to be managed to maintain as many biotopes as possible (Samways 1993). Nature conservation as a form of land use plays a vital role in achieving this. It is therefore important to maintain and expand the existing network of protected areas in Xeric Succulent Thicket. It is also necessary to encourage types of land use other than commercial livestock ranching, which does not result in transformation of the vegetation. In this way not only arthropods, but also many other plants and animals, will be conserved.

7. Biodiversity Change in Response to Land Management in Xeric Succulent Thicket: The Bigger Picture

ABSTRACT

Ecosystems are driven by processes which operate at the landscape, land element, producer community and consumer community levels. Landscapes in Xeric Succulent Thicket consist of land elements (bushclumps) which act as resource patches for plants and animals. These patches are reduced in size and complexity as the intensity of herbivory increases. Current understanding of biodiversity and ecosystem functioning in Xeric Succulent Thicket postulates that these ecosystems degrade according to an integrated process of reduction in patch productivity and within-patch heterogeneity. This leads to a decrease in within-patch species richness, and an increase in nutrient and energy flow from resource patches into the surrounding matrix. In smaller patches, palatable plants are exposed to herbivory, and good light competitors are oucompeted by good colonizers. This further reduces diversity. At the landscape level, landscape complexity is reduced through a decrease in the variety of patch types across the landscape and a reduction in species turnover between patches. Landscapes dominated by small patches are subject to perpetual 'drought' conditions. Arthropod species richness and abundance decrease because of the harsher and more simplified environment, which lead to more severe species interactions and the simplification of trophic and other ecosystem webs. Regression analysis of plant species richness on land element diversity, and arthropod species richness on plant species richness corroborates this paradigm: increasing levels of herbivory leads to a successive loss of species. As the spatial heterogeneity in the environment decreases, all species become rarer and recruitment eventually ceases. The abundance and species richness of weevils are especially well correlated with the diversity of other ecosystem elements higher up the hierarchy. Terrestrial snakes and lizards respond to different resources because of their unique physiology - their resource patches are the warm interclump areas where hunting success is high. They flourish in the degraded areas, especially since avian and mammalian predators are largely absent from such landscapes. Biodiversity at the ecosystem, landscape and community levels in Xeric Succulent Thicket is severely affected by herbivory, primarily because of its influence on bushclump size. The maintenance of large bushclumps is the key to the successful preservation of biodiversity at the landscape and sub-landscape levels in Xeric Succulent Thicket .

INTRODUCTION

The impact of different forms of land management on biodiversity in Xeric Succulent Thicket can be assessed by quantifying landscape diversity in each of the respective land management units (Chapter 3), comparing vegetation (bush clump) structure across land management boundaries (Chapter 4), and comparing the richness, abundance and diversity of various taxonomic groups in the nature reserve with that in neighbouring commercial and subsistence rangeland (Chapters 5 and 6). The relationship, both biological and statistical, between the different hierarchical levels of biodiversity (with the respective sampling localities as replicates) is, however, still unknown. This hierarchical relationship between different levels of biodiversity in Xeric Succulent Thicket needs to be further explored to obtain a better understanding of the effect of ecological events at one spatial scale on biodiversity at other scales.

In this chapter the hierarchical concept of ecosystems (O'Neill et al. 1986; Urban, O'Neill & Shugart 1987; Wiens, Stenseth, Van Horne & Ims 1993) is linked to land degradation by integrating a coarse-grained, landscape / structural approach with a finer-grained community and population approach. Ecosystems (the entire regional mosaic) are conceptualized as an integration of anthropogenic landscapes (land management units with similar management treatments and histories), land elements (smaller-scale patches within anthropogenic landscapes, Bell & McShane 1984), matrix, communities, and populations. This approach is advocated by Turner & O'Neill (1995) and is essential for a thorough understanding of the relation between land degradation and biodiversity. It recognizes that the structural dynamics of land element patches coupled with the community dynamics and interactions of organisms within patches are essential components which explain ecosystem pattern and function (Wiens et al. 1993). An emphasis on structure and pattern alone is insufficient to explain many of the impacts of land degradation on biodiversity, as it does not take into account factors such as co-evolution, species interactions and community dynamics which have been shown to have a profound influence on the number of species in an area (Ehrlich 1994; Tilman & Pacala 1993). A narrow community approach, on the other hand, does not take into account the importance of environmental heterogeneity, landscape dynamics, disturbance and large-scale land use in influencing and maintaining biodiversity (Schluter & Ricklefs 1993; Chen, Franklin & Lowe 1996).

A high level of land element heterogeneity results in a diversity of resource supply rates across the landscape. This increases the number of factors which affect speciation and competition in the environment, allowing a larger number of species to co-exist than in envrironments where spatial heterogeneity is low (Lawton 1994). An increase in land element diversity is also often linked to an increase in the variety of disturbance types and intensities across landscapes. This increases the beta turnover between land elements and consequently the number of species within a landscape (Hobbie, Jensen & Chapin 1994). Spatial (land element) heterogeneity also creates refuges which allow more species to coexist than in homogeneous environments, where diversity can be suppressed through competitive exclusion and excessive predation (McLaughlin & Roughgarden 1993).

Moving lower down the ecological hierarchy, landscape diversity can be linked to the diversity of food web types (Yodzis 1993). Briand (1983) ordinated a variety of food webs, based on their numbers of linkages and species richness, and found distinct groupings among stream foodwebs and those from other habitats. Recent mathematical models of food web structures indicate that the length of food chains and the ratios of top to intermediate to basal species is dependent on the number of species in the system. As can be expected, species-poor food chains are shorter than species-rich food chains (Martinez & Lawton 1995). The 'spill-over' or 'cascade' model (Cohen & Newman 1985) is useful to conceptualize the effect of changes in biodiversity at coarse ecological levels, at the upper end of the hierarchy, on diversity at fine-scale levels lower down the ecological hierarchy (Read & Miller 1989; Yodzis 1993). To put it in the context of this study: anthopogenic landscapes are influenced by disturbance, mainly herbivory. This changes the size and abundance of bushclumps, which impacts on plant species richness and composition within bushclumps, which in turn influences the richness of microbiota such as arthropods as well as micorrhizae and reptiles. Other types of interactive webs, e.g. 'ecosystem engineering webs' and 'mutualism webs' (Martinez 1995) further emphasize the interdependence of different ecosystem elements and the co-evolution of different organisms and abiotic ecosystem elements (Lawton & Brown 1994).

From a conservation management viewpoint, an understanding of the hierarchical relationship between biodiversity at different spatial scales and between different taxa is important to improve conservation decision making. If those biodiversity indicators higher up the hierarchy, which have an effect on biodiversity lower down, could be identified, then monitoring efforts could be directed at the coarse-scale indicators which are often easier and more cost-effective to measure than the fine-scale ones (Franklin 1993). The monitoring of appropriate taxonomic groups or ecosystem elements which might serve as 'umbrella' biodiversity indicators could save conservation managers both time and money. Likewise, this information could be used to devise conservation strategies by identifying new land for protected areas, or by identifying those protected areas or portions of them which require special management because of being biodiversity 'hotspots' (Prendergast, Quinn, Lawton, Eversham & Gibbons 1993; James, Landsberg & Morton 1995).

Key questions in this chapter are:

- what are the relationships between biodiversity indicators at different hierarchical levels; and
- what are the most likely causes of changes in biodiversity in response to land management?

The key management question is:

- what are the most effective and useful indicators of biodiversity for use in monitoring and conservation planning?

METHODS

Linear correlations were sought between the various levels of biodiversity, i.e. the landscapes, vegetation cover, plant species richness, reptile species richness level and the arthropod RTU (Recognizable Taxonomic Unit, Majer et al. 1995) richness. Four localities, viz. NR1, CF1, NR3 and CGA were used as independent replicates.[1]

A matrix (Table 1) was constructed with the rows consisting of the four localities NR1, CF1, NR3 and CGA, and the columns consisting of

- mean CVs of satellite-derived pixel values (Chapter 3);
- mean ground-based diversity indexes (Chapter 3);
- mean bushclump size (Chapter 4);
- mean number of plant species per bushclump (Chapter 4);
- mean number of woody species per clump (Chapter 4);
- the mean Hierarchical Richness Indexes or HRIs (French 1994, and this study Chapter 6) of ants, crickets, grasshoppers, non-spider arachnids, spiders and weevils (Chapter 6) and reptiles (Chapter 5);
- the number of RTUs of ants, crickets, grasshoppers, large arachnids, spiders, and weevils (Chapter 6);
- the abundance, expressed as number individuals captured, of crickets, grasshoppers, large arachnids, spiders and weevils (Chapter 6) and snakes and lizards (Chapter 5). For ants, the frequencies of ant RTUs (Chapter 6) was used, expressed as the sum of the number of trap-days in which each respective ant RTU was collected for each respective locality.

---

[1] Localities at Site 2 (NR2 and CF2) were not included in the analysis because data on vegetation structure and floristics were not recorded for them. These two high elevation localities did not represent typical Xeric Succulent Thicket, as their grass cover was much denser, bushclumps were more widely dispersed and bushclumps contained different plant communities than the other four localities (Palmer 1981).

Table 1. Summary of Hierarchical Richness Indexes (HRIs, Chapter 6), number of Recognizable Taxonomic Units (RTUs, Chapter 6), and abundance of each taxonomic groups. This matrix acted as input for correlation analysis. Values are means for four traps at each locality, but for abundance and RTUs, the totals of four traps were used. CF1 and 2 = commercial farms, NR1-3 = nature reserve, CGA = communal grazing area

	HRIs							RTUs								Abundance									Structure			
	Ants	Crickets	Grass- hoppers	Large arachnids	Spiders	Weevils	Reptiles	Ants	Crickets	Grass- hoppers	Large arachnids	Spiders	Weevils	Total RTUs	Ants	Crickets	Grass- hoppers	Large arachnids	Spiders	Weevils	Total arthropods	Reptiles	Species/ clump	Woodys/ clump	Clump size	Pixel CV
CF1	215	12.8	25	76.8	757.3	20.2	42	19	2	11	9	39	9	89	272	46	44	140	815	45	1362	29	8.2	4.6	5.19	0.04
NR1	175.5	24	19.8	109	823.8	24.8	60	16	3	8	10	45	12	94	196	87	42	151	673	39	1188	20	9.2	6	8.54	0.07
CGA	48.5	6.8	4.5	48.5	316.5	22.3	110	11	3	6	7	31	8	66	62	21	9	91	292	46	521	56	3.8	3	1.7	0.06
NR3	95.8	20	35	132.5	876.8	59.5	60	18	2	6	10	39	12	87	91	91	42	236	821	87	1368	25	11.4	8.1	10.38	0.98

The correlation coefficients between the columns were calculated, with the four localities as the number of replicates. Correlations between the different arthropod groups' abundance, their RTU richness and their HRIs were not included in the output, as such correlations would most likely be spurious and therefore misleading and uninformative. In view of the few degrees of freedom, the biological 'meaningfulness' (where more than 70% of the variance of Y can be attributed to the regression, i.e. $r^2 \geq 0.7$) as well as the statistical significance, i.e.a critical value of $r \geq 0.98$ or 0.90 (in absolute terms) for $n=3$ or $n=4$ respectively, of the data was considered.

RESULTS

Mean bushclump size displayed the strongest correlation with the other indicators of biodiversity (Table 2), notably with:

- mean number of plant species (Figure 1) and woody species (Figure 2) per bushclump;
- either the RTU richness, abundance or mean HRIs of each arthropod taxonomic group; and
- reptile abundance (Figure 7), which was negatively correlated with the mean size of bushclumps as well as with the mean number of plant species per clump.

There was also a strong positive correlation between mean number of plant species per bushclump and the HRIs for grasshoppers, large arachnids, spiders, and the abundance of all arthropods combined (Figure 3).

At the landscape level, the CVs of satellite-derived pixel values were significantly correlated with weevil HRIs (Table 2; Fig. 4), but did not correlate well with other biological data.

Reptile abundance (Table 2) was negatively correlated with mean bushclump size (Fig. 7), mean number of plant species per bushclump, and (of less biological significance), with arthropod diversity, viz. either the HRIs or abundance of ants, crickets, spiders, grasshoppers, large arachnids and all arthropods combined.

Amongst arthropods, weevils were singled out as an indicator of the impact of land management on the biodiversity of phytophagous arthropods in Xeric Succulent Thicket. They were also one of the groups for which detailed taxonomic data were available (Appendix 3). Weevil HRIs were significantly correlated with reflectance diversity in a satellite image (Figure 4), while weevil RTU richness was significantly correlated with the number of woody plant species per bushclump (Figure 5) as well as with bushclump size (Figure 6).

Weevils also seem to be sensitive to the impacts of land use: Chapter 6 showed that their HRIs, abundance and RTU richness consistently and substantially differed between adjacent properties. Weevils also contained the largest number of locality-unique taxonomic units, and would therefore be an appropriate focal group to investigate the relations between arthropod diversity and biodiversity change at the landscape, bushclump and plant species level in greater detail.

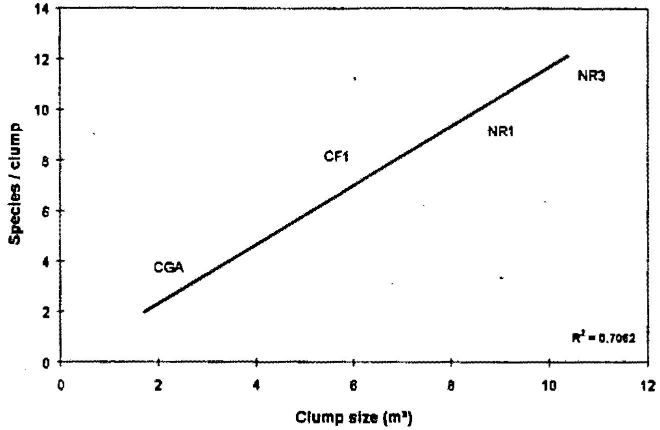


Figure 1. Relation between mean bushclump size and mean number of plant species per clump (r = 0.84). NR1 and 3 = nature reserve, CF = commercial farm 1, CGA = communal grazing area. The r-squared value and regression line were calculated for a zero intercept.

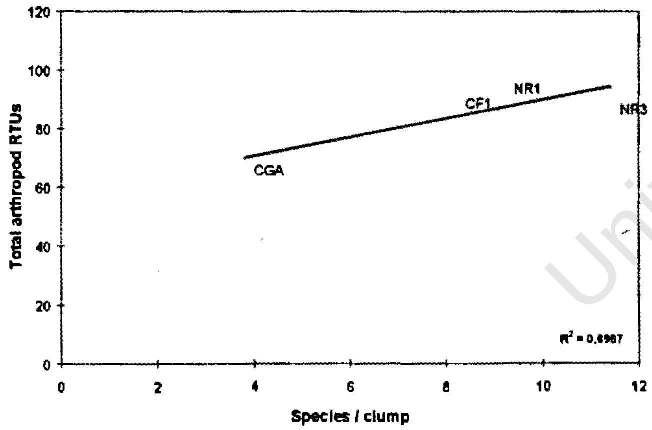


Figure 3. Relation between mean number of plant species per bushclump (Species / clump) and the number of RTUs of all arthropod taxonomic groups combined (r = 0.83). Localities are the same as in Fig. 1.

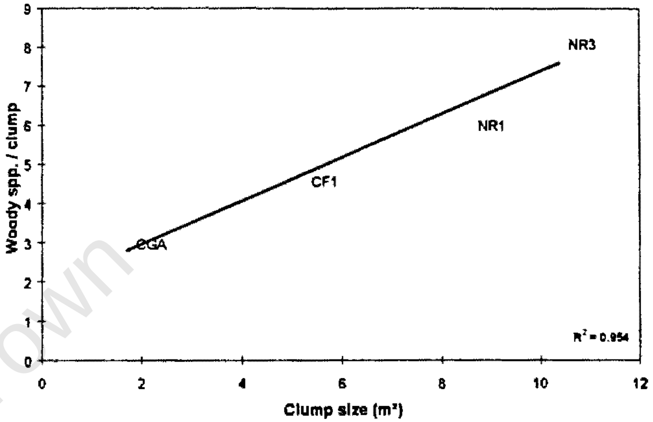


Figure 2. Relation between mean bushclump size and mean number of woody species per clumpm(r = 0.97). Localities are the same as in Fig. 1.

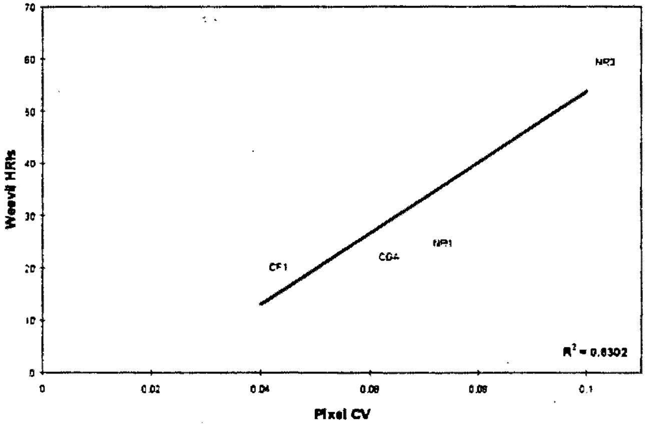


Figure 4. Relation between the coefficients of variation of pixel values in a satellite image (Pixel CV) and the Hierarchical Richness Indexes of weevils (Weevil HRIs) (r = 0.91). Localities are the same as in Fig. 1.

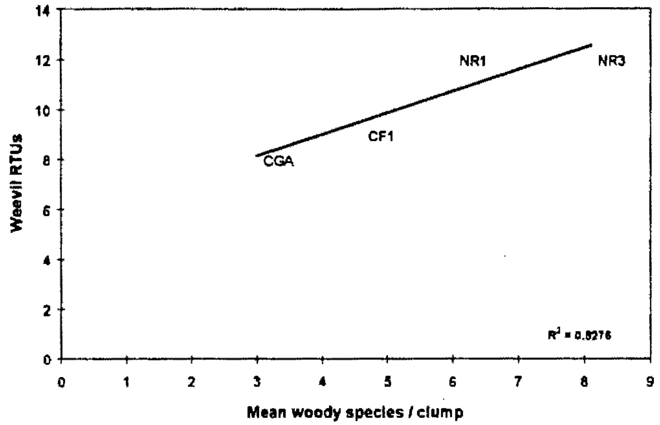


Figure 5. Relation between the mean number of woody plant species per bushclump and the number of weevil RTUs (r=0.91). Localities are the same as in Fig. 1.

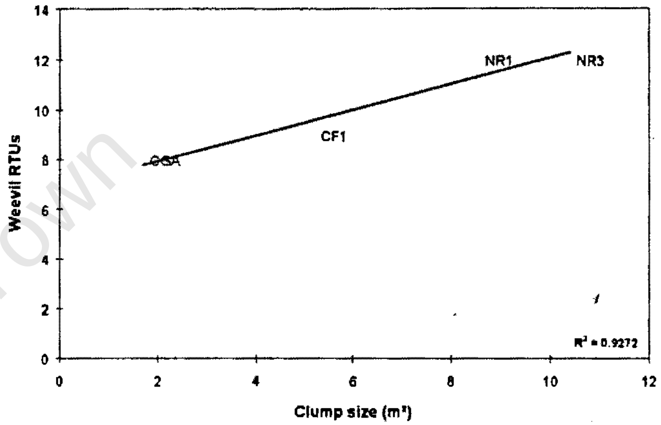


Figure 6. Relation between mean bushclump size (clump size) and the number of weevil RTUs (r=0.96). Localities are the same as in Figure 1.

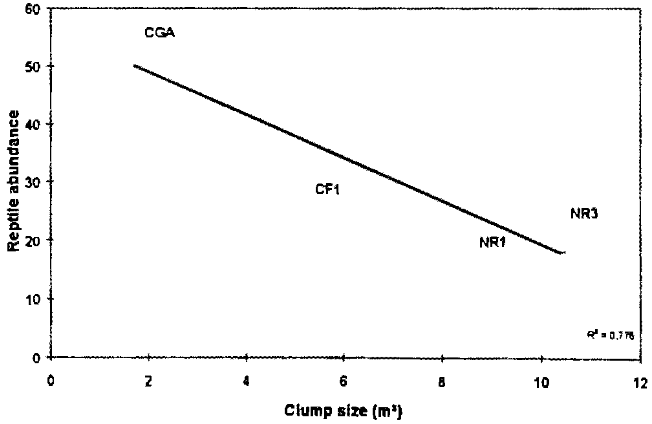


Figure 7. Relation between mean bushclump size and the abundance of reptiles (r=-0.88). Localities are the same as in Figure 1.

Table 2. Correlation coefficients between arthropods, plant species, reptiles, vegetation structure and land element diversity. Bold values: $r^2 \geq 0.70$ ($\geq$ 70% of the variance of Y attributed to the regression). Bold underlined values: one-tailed $P < 0.05$

		Reptile HRI	Reptile abundance	Species/ clump	Woodys/ clump	Clump size	Pixel CV
HRIs	Ants	**-0.86**	-0.69	0.41	0.13	0.28	-0.48
	Crickets	-0.60	**-0.91**	**0.84**	0.81	**0.91**	0.54
	Grasshoppers	-0.81	-0.80	**0.95**	**0.89**	**0.86**	0.49
	Large arachnids	-0.59	**-0.84**	**0.96**	**0.99**	**0.99**	0.76
	Spiders	**-0.89**	**-0.98**	**0.97**	**0.86**	**0.92**	0.38
	Weevils	-0.16	-0.34	0.69	**0.85**	0.72	**0.91**
RTUs	Ants	**-0.97**	-0.83	0.83	0.65	0.68	0.07
	Crickets	0.67	0.39	-0.60	-0.49	-0.40	-0.12
	Grasshoppers	-0.70	-0.37	0.10	-0.19	-0.08	-0.75
	Large arachnids	-0.81	**-0.98**	**0.96**	**0.88**	**0.96**	0.47
	Spiders	-0.76	**-0.95**	0.75	0.61	0.77	0.17
	Weevils	-0.50	**-0.84**	**0.87**	**0.91**	**0.96**	0.73
	All arthropods	**-0.91**	**-0.99**	**0.84**	0.66	0.79	0.13
Abundance	Ants	-0.80	-0.56	0.26	-0.03	0.12	-0.62
	Crickets	-0.59	**-0.88**	**0.92**	**0.94**	**0.99**	0.69
	Grasshoppers	**-0.97**	**-0.96**	**0.89**	0.72	0.80	0.15
	Large arachnids	-0.55	-0.69	**0.93**	**0.98**	**0.91**	0.78
	Spiders	**-0.96**	**-0.88**	**0.90**	0.75	0.78	0.20
	Weevils	-0.13	-0.20	0.60	0.74	0.58	0.81
	All arthropods	**-0.96**	**-0.91**	**0.91**	0.75	0.79	0.20
Reptiles	Reptile HRI	-	**0.88**	-0.78	-0.56	-0.64	0.05
	Reptile abundance		-	**-0.91**	-0.78	**-0.88**	-0.29
Structure	Species /clump			-	**0.96**	**0.97**	0.58
	Woodys/clump				-	**0.98**	0.80
	Clump size					-	0.71
Pixel	CV						-

POSTULATED CAUSES AND EFFECTS OF BIODIVERSITY LOSS IN XERIC SUCCULENT THICKET

The diversity of ecosystem components at different spatial scales is interrelated: a loss of diversity at one level is reflected in some biodiversity loss at other hierarchical levels, but not in all taxonomic groups. Weevil diversity seems particularly sensitive to changes in ecosystem complexity at all hierarchical levels, and is positively correlated with all the higher-level indicators of biodiversity (landscape diversity, bushclump size and plant species richness in bushclumps). Terrestrial snakes and lizards, on the other hand, are negatively correlated with the other measured ecosystem elements. It is also clear that land management has an influence on biodiversity in Xeric Succulent Thicket, and that this influence can be measured and calculated both across land management boundaries (see previous chapters), and within the same land management unit at different spatial scales.

The real causes of these changes in diversity are, however, subject to speculation, and will be difficult to determine with certainty without rigorously designed experiments. In the absence of such experiments, several strong hypotheses (presented in italics) have emerged from this research and that of others. These from the basis for the remainder of this chapter. This study presents strong evidence that land degradation has a cascading impact on biodiversity, mainly through causing a decrease in the size of bushclumps as herbivores and people consume clumps from the edges inward (Stuart-Hill 1992). This reduction in bushclump size is reflected by ecosystem changes at the landscape and community levels.

Landscape level

At the landscape level, the effect of degradation is that land element diversity is reduced, mainly because of an increase in the area of the landscape matrix (bare ground and drought-resistant dwarf shrubs) relative to the area occupied by land element patches (bushclumps and small-scale disturbance features). The hypothesis is that *land elements decrease in size and diversity because of over-utilization of the perennial vegetation and the replacement of natural disturbance agents (wild vertebrates of different body sizes and habits) by domestic livestock.* These land elements can be regarded as 'resource patches' (Huntly 1995) across the landscape and contain anomalies of P, N and organic matter (La Cock 1992). They provide refuges for plants and arthropods against competition and predation (McLaughlin & Roughgarden 1993). (Henceforth the terms 'patch' and 'land element' are used interchangeably). *In anthropogenic landscapes where degradation has not set in, resource and disturbance patches of varying ages and richness across the landscape allow different assemblages of plants to co-exist in each respective patch type, in response to differences in light availability, nutrient availability and moisture availability* (Hobbie, Jensen & Chapin 1994). *When the high-diversity landscape is homogenized through overgrazing, the spatial variability of limiting resources, be it light, nutrients or moisture, decreases across the landscape, and fewer species are able to co-exist* (DeAngelis 1995; Tilman 1982).

The next important effect of a decrease in the size of bushclumps is that *the ratio of edge to patch interior increases rapidly as patch size decreases. This results in an acceleration of energy and nutrient flow from the interior of the patch into the matrix, from where it is diluted into the already impoverished system* (Friedel & James 1995). This results in the patch and its surrounding matrix becoming more and more similar with increasing degradation (Chen, Franklin & Lowe 1976).

This new low-diversity landscape is particularly hostile towards arthropods and other small animals. The risk of being outcompeted by others is high because of a decrease in the number of niches, especially when it is borne in mind that small organisms with a high degree of speciation such as arthropods occupy a particularly high diversity of niches (Lawton & Brown 1994). *As patches become smaller and farther apart, the energy spent by arthropods in moving from one resource patch to another becomes progressively higher. Small organisms such as arthropods are unable to store fat reserves and heat, and their dispersal is impacted to a greater extent than is that of other organisms* (Tilman & Pacala 1993).

Plant community level

At the community and population level the decrease in bushclump size affects species differently. *Plant species richness is negatively affected because of reduction in environmental variability within each clump.* At the core of a large clump there exists a 'high moisture - low light - high nutrient' environment which gradually changes to a 'low moisture - high light - low nutrient' environment at the clump periphery (Palmer 1981; La Cock 1992). This allows a relatively large number of species to co-exist because of weak species interactions between the core of the clump and the edge (Tilman & Pacala 1993). As clumps become smaller the extent of this gradient is reduced until, in very small clumps such as those commonly found in the CGA, the gradient probably does not exist, the number of niches are reduced and species interactions become stronger with a subsequent reduction in species richness. The interiors of large clumps are dominated by good competitors for light (large-seeded, bird-dispersed species, with large leaves, Salisbury 1942), while the periphery is dominated by species with good colonization ability (small-seeded plants with small leaves). In clumps which are reduced in size there is a shift towards a high light - low moisture - low nutrient environment, with the subsequent competitive exclusion of the good light, but poor moisture, competitors (Tilman 1994). The conditions inside small clumps can be equated with perpetual drought, which in itself has a depressing effect on plant species diversity and recruitment (Tilman & Haddi 1992).

There is also a shift in productivity as clumps decrease in size. *The environment inside clumps changes from a productive, 'large-clump' environment with high rates of supply of limiting resources (moisture, N and P, Palmer 1981) to a less productive environment which characterizes the interiors of small clumps.* The unimodal relationship between productivity and species richness is well documented (reviewed in Rozenzweig & Abramsky 1993; see also Tilman & Pacala 1993). In Xeric Succulent Thicket, the decrease in productivity in response to decreasing bushclump size leads to a diagonal shift along the x-axis towards the species-poor end of the productivity gradient.

A further consequence at the plant community level is the exposure of palatable plant species to herbivory as the edges of clumps become progressively eroded. This causes the virtual extinction of palatable plant species in small bushclumps. In the Chilean matorral, which has a similar landscape structure to Xeric Succulent Thicket , i.e. well-defined patches of bush clumps amid a matrix of open or sparsely-vegetated ground, herbivory is responsible for the absence of palatable plant species in open areas where they are not protected by other plants (Jaksic & Fuentes 1980). The eventual removal, either through consumptive utilization for firewood or through herbivory, of 'core' shrubs which are tall enough to act as perches for birds, reduces the amount of 'seed rain' from bird droppings and limits seedling recruitment (Fuentes, Hoffmann, Poiani and Alliende 1986). Those seedlings of palatable plants which do manage to establish have virtually no protection against herbivory, and are either browsed to death or do not form flowers and seeds. Even a low intensity of continuous herbivory is sufficient to prevent many species from establishing, and some species require a temporal refuge during which they are protected against herbivory to establish and grow to the size where they are able to escape herbivory (Huntly 1995). Such rest periods do not exist in the continuously-grazed communal area and are rare on many commercial farms.

Reptiles

The results for terrestrial Squamata demonstrate that different organisms use different criteria to recognize resource patches in the same landscape (Huntly 1995). Reptiles are negatively correlated with vegetation cover and diversity, and become more abundant as both vegetation cover and floristic diversity decreases. *The lower cover probably improves the thermoregulation in reptiles and consequently promotes more favorable energy budgets than does vegetation with high cover* (Pianka 1967; Scheibe 1987). Whiptail lizards in Arizona also occur mostly in open areas (Mitchell 1979). It is also possible that Squamatan hunting success improves because of increased visibility in the open terrain (Chapter 5). In an Australian study, arthropod predators (scorpions) were unaffected by habitat fragmentation (Margules, Milkovits & Smith 1994). Similarly, in this study (Chapter 6), large arachnids were closer in ordination space to the degraded sites than to the well-preserved sites (although their richness was nevertheless significantly lower in the degraded sites). It is thus possible that *resource patches for reptiles are the inverse of those for phytophagous arthropods such as weevils, i.e. they consist of interclump areas instead of bushclumps.*

Another *factor which might promote the abundance of terrestrial Squamata is the absence of avian and mammalian predators from the degraded communal area*, which is probably caused by the lower vegetation cover, a lack of perch sites for avian predators because of overuse of large trees for fuelwood, and the high human population density in the communal grazing area, with subsequent high disturbance levels (Ainslie, Fox & Fabricius 1994). If lack of predators is the cause of a higher reptile diversity in degraded areas, it is unclear why the same effect was not observed in small mammals and larger arachnids (C. Fabricius, unpublished data and Chapter 6).

Arthropods

This reduction in plant species richness and landscape complexity is in turn reflected by a decrease in the abundance and species richness of most arthropods, which are positively and linearly correlated with plant species richness. The lower plant cover causes the microclimate in bushclumps to become drier, and there is less shelter against predation. This results in lower-quality resource patches, which makes the environment less hospitable (Huntly 1994; McLaughlin & Roughgarden 1993). *Species interactions between arthropods become more severe because of the reduced 'microlandscape' diversity within clumps with fewer plant species and diminished environmental gradients* (Lawton & Brown 1994; Wiens et al. 1993). *Host-specific arthropods become locally extinct as plant species richness is reduced* (Zwolfer & Arnold-Rinehart 1994). *The smaller productive space (the size of bushclumps) causes available energy to become limiting, especially for those organisms at the top of the food chain with relatively high energy requirements* (Schoener 1987). *The overall size of the food web becomes smaller, as the physical environment inside bush clumps becomes more variable and less predictable, firstly because of less shade and cover* (Yodzis 1993; May 1973; Pimm & Lawton 1977) and secondly *because the lower community diversity causes the system to become less stable* (Naeem, Thompson, Lawler, Lawton & Woodfin 1994, 1995). Bushclumps become less productive as they become smaller, and they become less species rich (Palmer & Avis 1994; Naeem et al. 1995).

Root symbionts

At the soil micro-organism level there is a decrease in mycorrhizal abundance across the landscape because of the increase in the interclump matrix relative to bushclumps [mycorrhizae are virtually absent from the interclump areas, (Chapter 4)]. Mycorrhizae are particularly effective in raising the P:N ratios in P-deficient soils in environments with high evapotranspiration such as Xeric Succulent Thicket, where the top soil layer becomes saturated with salts and the pH is raised, making P unavailable (Read 1994; Allsopp & Stock 1992). In coniferous forests, the presence of ectomycorrhizae leads to the improved establishment of seedlings and increased rates of litter decomposition (Read 1994) and there is reason to believe that these *symbionts play an important role in the establishment and maintenance of bushclumps in Xeric Succulent Thicket* (N. Allsopp pers. comm.). *Soil micro-organisms such as mycorrhizae can be host specific, and their species richness and density might be affected when certain mutualist plant species become locally extinct* (Read 1994), thereby reducing the recovery of ecosystems after degradation.

DISCUSSION AND CONCLUSIONS

The interdependence of different organisms and abiotic ecosystem components is not limited to food webs. The co-evolution of plants and insects was conceptualized in early models, e.g. Ehrlich & Raven's (1964) hypothesis, which was corroborated more recently by Farrell & Mitter (1994). Martinez (1995) mentions other kinds of ecological webs, e.g. 'ecosystem engineering webs' which consist of interdependent organisms which create physical habitat for each other, for example burrowing mammals such as aardvark which create shelter in which numerous cavity-dwelling animals such as barn owls *Tyto alba* and several bat species take refuge in arid savannas (pers. obs.), or beavers *Castor canadensis*, which construct dams which operate as entire new ecosystems (Pollock, Naiman, Erickson, Johnston, Pastor & Pinay 1995). In the context of evolutionary theory, 'mutualism webs' consist of co-evolved plants and animals (Andre 1985), which has have led to the development of a number of mutualistic and parasitic relationships, some of which might be termed 'loose', e.g. giraffes as pollinators of *Acacias* in African savannas (Du Toit 1990), while others are 'tighter', e.g. *Eurytoma* spp. (Hymenoptera) which are host-specific ecto- and endoparasites of the genus *Urophora* (Diptera), which obligately develop in galls in thistles of the family Cardueae (Zwolfer & Arnold-Rinehart 1994). Another interesting example of a 'mutualist-parasite web' is the interaction between Septobasidiales fungi and scale insects (*Aspidiotus* sp.). The fungi grow in the insects' bodies and eventually form external hyphae which simultaneously envelop the insects and the bark of trees and shrubs (Oberwinkler 1994).

Empirical and theoretical studies which relate diversity at the landscape level to other levels of diversity in the ecological hierarchy are few (James, Landsberg & Morton 1995; C.D. James *in litt.*). Amongst the studies which do indicate that landscape level processes influence diversity at the plant and animal community level is the study of trees, lichens, invertebrates and birds in northern Sweden (Petterson et al. 1995). These authors found that logging of old growth forests resulted in a decrease in the mean size of trees and a reduction in lichen abundance, which in turn affected the diversity and abundance of small invertebrates. This caused a decrease in the abundance of spiders, a major food source for birds, which had a negative effect on the species richness and abundance of tits and nuthatches. Carey (1994) studied the relationship between butterfly egg densities, landscape patch size and plant species richness and found that butterfly egg density was positively correlated only with host species diversity. Bach (1986) found that the abundance of chrysomelid beetles and pentatomid bugs were affected by the size of forest patches as well as the diversity of plant species in patches and in surrounding areas. Forest birds in France selected habitat according to landscape and structural features at a coarse scale, but the floristic composition of forest patches influenced their habitat selection within homogenous habitats (Bersier & Meyer 1994).

Bushclump size is an impotant indicator of land degradation in Xeric Succulent Thicket. It is also the easiest and most profitable (in terms of useful data collected per unit effort) to monitor, as it does not require specialist knowledge of plant taxonomy, nor laborious collection of specimens or species counts. Terrestrial snakes and lizards, on the other hand, are poor overall indicators of biodiversity for conservation monitoring purposes and are relatively difficult to collect and identify.

Land degradation in Xeric Succulent Thicket has a cascading effect on the complexity of ecosystems, landscapes and land elements and on the species richness of plant and arthropod communities. An hierarchical approach which integrates data collected at the landscape, land element and community levels is essential to understand the processes which accompany land degradation, and consequently vegetation recovery, in Xeric Succulent Thicket.

8. General discussion and conclusions

A gradient of increasing land degradation and biodiversity loss existed between the nature reserve at the low end, through the two commercial farms, to the communal grazing area at the high degradation end. Based on insights gained during this study and from the literature, degradation is postulated to take place in a step-wise fashion:

1. In well-preserved Xeric Succulent Thicket the bushclumps are large, and the ratio of clump:interclump areas is greater than 0.5. The clumps act as high quality resource patches across the landscape, where a diversity of plant and animal species find refuge from competition and predation (Tilman 1994; Huntly 1995).
2. As the intensity of utilization of the vegetation increases, the mean size of bushclumps decreases (Chapter 4), mainly as a result of increased herbivory by domestic livestock and the replacement of megaherbivores such as black rhinoceros, buffalo and eland by domestic cattle and goats [(cf. Stuart-Hill (1992)].
3. This is mirrored by an increase in the size of open areas between clumps, resulting in a decrease in the ratio of bushclumps to bare areas (Chapter 4).
4. The reduction in bushclump size leads to a decrease in environmental heterogeneity, firstly across the landscape and secondly inside individual clumps. The vertical diversity (diversity of height strata) is reduced, leading to even fewer faunal niches in a vertical dimension (Briand 1983). Competitive interactions between plant species in clumps increases as the diversity of microhabitats decreases (Auerbach & Shmida 1987; Tilman 1994b), and animal species which normally take refuge in bushclumps are exposed to increased levels of predation (Tilman & Pacala 1993).
5. All species in small clumps are more exposed to environmental fluctuations and species interactions than those in large clumps. This increases the probability of local extinction (Tilman & Haddi 1992).
6. The expansion of bare areas leads to an overall decrease in mycorrhizal activity (Chapter 4), which might repress seedling establishment and reduce the rate of nutrient uptake of plants (Read 1994).
7. The small bushclumps have a lower moisture content (Palmer 1981; Palmer, Cook & Lubke 1988) and less soil organic matter, N and P (La Cock 1992; Suzan, Nabhan & Patten 1996). Interclump sites have highly elevated Al concentrations, to the point of possible toxicity, which makes it difficult for seedlings to establish in bare areas (La Cock 1992).
8. The community composition changes. The drier and harsher microclimate within small bushclumps causes the replacement of mesic-adapted, animal-dispersed plant species by xeric-adapted, wind-dispersed plants (Chapter 4).
9. Palatable plant species are replaced by unpalatable ones, because of the lack of protection against herbivory offered by small clumps (Chapter 4). Seedlings do not survive (La Cock 1992).

10. Obligate phytophagous arthropods which are directly dependent on vegetation (e.g. grasshoppers and weevils) are more severely affected by the decrease in clump size than are predatory and omnivorous arthropods (Chapter 6).
11. The decrease in plant species richness in bushclumps decreases the environmental heterogeneity for arthropods. Arthropod abundance and species richness decrease (Chapter 6).
12. Focusing on weevils as a single specific indicator along the degradation gradient, their Hierarchical Richness Index decreases linearly with
    - satellite pixel diversity;
    - mean number of plant and woody species per bushclump; and
    - mean bushclump size (Chapter 7).
13. The open landscape leads to improved thermoregulation by reptiles and increases their hunting success (Mushinsky 1992). Avian and other predators which eat reptiles are excluded because of a lack of perch sites and cover. This is reflected in a negative relationship between the abundance of terrestrial snakes and lizards and mean bushclump size (Chapter 5). The abundance of lizards may depress arthropod numbers in the degraded areas (Dial & Roughgarden 1995).
14. The above process leads to a gradual desertification of the system, with the following possible effects:
    - lower resistance against drought (Tilman & Downing 1994);
    - lower productivity (Naeem, et al. 1995; Tilman & Downing 1994);
    - lower resistance against herbivory (McNaughton 1994);
    - more rapid energy and nutrient transfer from the land elements into the matrix (James, Landsberg & Morton 1995);
    - increased intensity of species interactions such as competition and predation (Tilman 1994a);
    - a change in the composition of plant, arthropod and reptile communities viz.
        - the replacement of animal-dispersed plant species which occur in relatively high rainfall areas by arid-adapted, unpalatable species, which are dispersed either by wind or mechanically (Chapter 4), and
        - the replacement of arboreal Squamata with xeric-adapted terrestrial snake and lizard species (Chapter 5).

DEGRADATION AND DESERTIFICATION

The stepwise degradation process in Xeric Succulent Thicket is consistent with current models of desertification (Milton et al. 1994): reduction of basal cover, change in species composition and finally a change in soil conditions. The replacement of palatable plant species by spiny and poisonous species is also indicative of desertification in other systems (Westoby et al. 1989), while changes in the abundance and composition of the arthropod fauna in response to land degradation have been reported by numerous authors (Dean & Milton 1995; Carey 1994; Milton & Dean 1992, 1993). A similar response by soil fungal symbionts in response to degradation has also been reported elsewhere (Macmahon 1989).

The results of this and other studies (Palmer 1981; La Cock 1992) suggest that if degradation in Xeric Succulent Thicket proceeds beyond a critical threshold level it is often impossible to reverse the process: the farm Hermanuskraal (CF1) has been subject to less intensive herbivory than previously for the past three years, and still has a lower diversity of landscapes, arthropods and plant species than a corresponding site in the nature reserve. The lasting effects of intensive herbivory on vegetation density and physiognomy can be detected across old fence-lines within the nature reserve, in one instance nine years after the fence had been removed (pers. obs.). In arid areas this cut-off occurs at lower intensities of herbivory than in high rainfall areas (Milton et al 1994).

Clearly livestock farming at levels which the commercial farm CF1 is subjected to, and subsistence resource use in the communal areas, do not meet the criteria for sustainable ecosystem management in Xeric Succulent Thicket as defined by Chapin et al. (1996). The main reason for this is the drastic (and possibly irreversible) change in soil resources which occurs when Xeric Succulent Thicket is degraded. In the communal areas the system is probably close to a new, unproductive and species-poor stable state where further degradation is not possible. It is predicted that such a system will consist almost exclusively of arid-adapted plants and animal species, and good colonizers (Tilman & Pacala 1993; Tilman 1994b).

EFFECT OF DISTURBANCE

Although the exact extent of disturbance at each locality in the study area is unknown, the *direction* of disturbance along the disturbance gradient is known from anecdotal and circumstantial evidence. It seemed as though biodiversity was affected in line with predictions of the intermediate disturbance hypothesis (Hobbie et al. 1994). The three unconserved localities (with the nature reserve as a reference site) represented a disturbance gradient, and the levels of biodiversity, particularly in arthropods, followed the predicted unimodal curve (cf. Chapter 6).

A possible mechanism for the intermediate disturbance effect in Xeric Succulent Thicket

In general, there are two main explanations for the mechanism of the intermediate disturbance effect. The first is that the underlying cause of a change in biodiversity in response to disturbance is a combination of direct destruction and competition (Rosenzweig & Abramsky 1993). At very high levels of disturbance, as at the CGA, populations decrease through direct consumption, trampling, soil erosion etc. at a greater rate than they are able to recover. At very low levels of disturbance, as at CF2, infrequent disturbance leads to competition limiting populations. Conditions are so "stable" that competitors can gain a foothold and outcompete some of the less competitive organisms, with a resulting net loss of species. At intermediate levels of disturbance, as on the nature reserve and CF1, competitive species fail to gain dominance between disturbance events. Disturbance is, however, infrequent enough to allow the re-establishment of locally extinct populations through immigration, and a recovery of competitive subdominants.

A second possible explanation for the intermediate disturbance effect relates to the number of microhabitats which are created through different levels and variants of disturbance and rest periods (Rosenzweig 1993). The number of microhabitats or microsites (Samways 1994) at the "barren" communal grazing area might have decreased steadily over time as a result of the continuous removal of the vegetation through direct utilization by humans, continuous heavy grazing and trampling (Lewis 1969). This resulted in a decrease in the number of RTUs and abundance of invertebrates at that site.

At the least disturbed site, i.e. at the intensively managed, conservatively stocked commercial farm CF2, disturbance as a creator of microhabitats was less significant. Disturbance events were less severe and further apart, while grazing and rest periods were fixed in space and time. The type (or agent) of disturbance, i.e. the type of herbivore, was also consistent. Under such conditions the number of microhabitats decreased, with a resulting decrease in diversity. At intermediate levels of disturbance as at CF1, the length and intensity of disturbance events and the length of rest periods were intermediate between the most and least disturbed sites. The disturbance events were varied in space and time, while the length and frequency of "rest periods" between disturbance events were less predictable than at the least disturbed site. This led to an increase in the number of microhabitats and a corresponding increase in diversity, compared to a conservatively managed situation. This effect was exacerbated by a haphazard grazing strategy. Commercial farming which emulates the variety of disturbance agents and events characteristic of the nature reserve will probably be the most beneficial for the maintenance of biodiversity in terrestrial arthropods.

Should competition be the main mechanism underlying disturbance-linked patterns of biodiversity for the intermediate disturbance effect, then the species found at the least disturbed site should be a subset of the species found at the intermediately disturbed site (cf. Rosenzweig & Abramsky 1993). Should, on the other hand, the creation of microhabitats through disturbance be the main mechanism, then each disturbance regime should result in a number of unique RTUs. Table 2 in Chapter 6 shows that there were indeed unique RTUs at the least disturbed site CF2 which did not occur at the complementary intermediately disturbed site NR2, and vice versa: the two sites had different communities in four out of the six taxonomic groups studied. Likewise, CF1 contained RTUs which did not occur at NR1 and vice versa. Competition alone as a mechanism for the intermediate disturbance effect in this study area is therefore rejected. It is more likely that the intermediate disturbance effect on biodiversity was a result of a greater variety of microhabitats being created through intermediate and varied disturbance, and differences in disturbance regimes. This mechanism does not, however, exclude some competitive influence on diversity.

Not all ecosystems have arthropod communities which are as sensitive to grazing as those in Xeric Succulent Thicket. Rivers-Moore & Samways (1996) found no significant differences between numbers of arthropod RTUs inside and outside Hhuluwe-Umfolozi Game Park, Natal, in grassy patches in an open savanna, except adjacent to or inside villages. They nevertheless conclude that land use is a determinant of arthropod biodiversity, but their most important conclusion is that *intensity* of land use, rather than *type* of land use, should be used to group sampling sites. River-Moore & Samways' (1996) study site differed from mine: it was an open grassy savanna with a higher rainfall and therefore a greater resilience than Xeric Succulent Thicket, and the vegetation structure inside and outside the protected area did not differ as much.

In Xeric Succulent Thicket the mechanism through which disturbance affects diversity might be different from that in other ecosystems. Its disturbance threshold seems to be lower (Kerley et al. 1995), i.e. biodiversity may already be negatively affected at stocking rates which might have little or no effect in other vegetation types. Another important difference between Xeric Succulent Thicket and other systems is that the landscape matrix, consisting of interclump areas, represents a far harsher environment than the bushclump patches. No mechanism comes to mind to 'soften' this matrix so that it can play a role in biodiversity preservation as suggested by Franklin (1993).

Apart from acting as corridors for the movement of animals and seed between dense bushclumps, the interclump areas play an unknown, but probably small, role in the preservation of biodiversity in Xeric Succulent Thicket. The herpetiles which are abundant in the degraded communal areas are common in other semi-arid areas of South Africa outside Xeric Succulent Thicket.

Herbivory

Herbivory as a source of disturbance might be as important as interplant competition in determining the structure of plant communities (Sih, Crowley, McPeek, Petranka & Strohmeier 1985). Herbivores normally reduce the diversity of plant communities if inferior competitors are preferentially grazed or browsed, whereas it should increase diversity if competitive dominants are the targets of herbivory (Tilman & Pacala 1993; Hulme 1996a). In Xeric Succulent Thicket, *Portulacaria afra* and *Grewia robusta* are the dominant woody plant species (Chapter 4), but they are also primarily targeted by domestic herbivores (Stuart-Hill & Aucamp 1993). Theoretically, therefore, herbivory should lead to an increase in diversity in Xeric Succulent Thicket, if Hulme's (1996a) argument is valid.

The reason Hulme's (1996a) hypothesis does not explain the direction of diversity change in Xeric Succulent Thicket is that the dominant competitors *P. afra* and *G. robusta* are also the keystone species which form the bulk of bushclumps (Chapter 4). Large clumps are species-rich, despite the dominance of these two species, because of the heterogeneous moisture and light regimes inside large clumps (Tilman 1994); there is a high degree of niche differentiation, and consequently weak competition in these large clumps. Herbivory, which negatively affects the competitive dominants, also reduces environmental heterogeneity and creates an unfavourable microclimate for seedling establishment. Only the most hardy plants are able to establish and survive and the anticipated increase in diversity does not take place.

Indigenous large herbivores

Apart from their intrinsic conservation value, large herbivores and especially megaherbivores play an important role in creating the type of disturbance which promotes natural biodiversity. Browsing by elephant promotes the basal cover of Xeric Succulent Thicket, compared to browsing by domestic browsers (goats) which utilize the fringes of bushclumps, thereby reducing basal cover (Stuart-Hill 1992). Large wild herbivores also increase the number of microhabitats in the landscape by for example

- creating dung middens of different sizes and consistencies, to be used as breeding and feeding sites for arthropods and germination sites for plant species (La Cock 1992; Rivers-Moore & Samways 1996);
- breaking branches and twigs and leaving behind different particle sizes of litter (eland and black rhinoceros), whereby unique and diverse refuge sites are created for arthropods (cf. Huntly 1995);
- creating or maintaining mud or dust wallows (eland, black rhinoceros, buffalo and warthog), thereby contributing to the diversity of land elements (Owen-Smith 1988),
- disturbing the soil through territorial fighting and scraping (Huntly 1995; pers. obs.),
- creating paths of different width which act as corridors for the movement of smaller fauna and dispersal of plant species across the landscape (Forman & Godron 1986);
- distributing seeds of fleshy-fruited plants, e.g. *Pappea capensis* (La Cock 1992), and vegetative parts of some plant species, e.g. *Portulacaria afra* (pers. obs.).

Apart from the types of disturbance created by wild herbivores, the periodic population crashes and natural migrations which characterize the dynamics of wild populations create essential respite periods for the establishment of seedlings (Huntly 1995).

RELATION BETWEEN BIODIVERSITY AT DIFFERENT SPATIAL SCALES

Alpha, beta and gamma diversity are interdependent. Gamma diversity is a product of species richness and beta turnover (Cody 1986; Schluter & Ricklefs 1993), and is the same as coarse-resolution alpha diversity, sampled over more than one land management unit [1]. Topographical or land form diversity is one of the strongest predictors of vegetation species richness, because of this link between alpha, beta and gamma diversity (Cornell 1993; Shmida & Wilson 1985; Lapin & Barnes 1995).

---

[1] In this study, alpha diversity is the number of species recorded in a single land management unit only; beta diversity is the turnover of species between two or more land management units; and gamma diversity is the number of species in an area which spans more than one land management unit.

Terrestrial arthropods should theoretically react to small-scale changes in landscape pattern at a finer grain than the satellite pixel values recorded in Chapter 3, because of their small body size and their relative immobility (especially in flightless arthropods). The characteristic eyesight of arthropods implies that they perceive their environment in terms of their immediate surroundings, and not in terms of the surrounding 'landscape' (as defined in this study) (Samways 1994). It is also dubious whether arthropods make 'decisions' about habitat selection in the same way as mammals do (cf. Senft, Coughenour, Bailey, Rittenbouse, Sala & Swift 1987). Their distribution in relation to habitat elements is probably related to the microclimate of patches through which they move, species interactions such as competition and predation which might affect their survival in a particular habitat patch, and the presence of other individuals of the same species, which can be detected by auditory and olfactory sensors (Samways 1994). The significant positive correrelation between pixel diversity and weevil diversity (Chapter 7) was probably spurious because of autocorrelation.

An important pattern identified in this study was the high beta turnover between localities as a result of different land management treatments, and the high gamma diversity which this generated. This was particularly evident for grasshoppers, spiders and weevils, where the beta turnovers were so high that the arthropod assemblages on adjacent properties could be regarded as separate communities (Chapter 6). In the overall comparison, when the entire nature reserve was compared to all unconserved properties combined, the grasshoppers and weevils showed the highest beta turnover of all taxonomic groups.

The turnover in terrestrial lizards and snakes was also high, although the picture might have been different had trapping continued for a longer period. There was a 50% turnover between the locality NR2 and an adjacent farm CF2, while the CGA was only 67% similar to its paired locality NR3 in terms of reptile species composition. Another surprising result was that none of the localities on their own contained more than 55% of the total number of reptile species collected in the study area as a whole.

The implication of this high beta turnover between anthropogenic landscapes is that each form of land use makes a unique contribution to the preservation of biodiversity in the study area. This elevates the gamma diversity of the region as a result of the mosaic of land use types - one type of land use across the land region would have resulted in a lower overall diversity. Regional diversity also affects local diversity through the migration of species from landscapes where they are present to landscapes where they are extinct (Ricklefs 1987). This of course applies primarily to mobile species such as birds, flying insects, certain spiders and plants with wind-dispersed propagules. These insights would not have been possible without adopting a hierarchical approach, incorporating levels from the regional to that of the plant community (cf. Lapin & Barnes 1995).

Cultural diversity and biodiversity

The mosaic of anthropogenic landscapes has its origins in a variety of cultural beliefs and value systems in the study area (McNeely 1991) and the disparate financial positions of the various land managers (Urban, O'Neill & Shugart

1987). This results in a variety of land management styles because of different types of local knowledge and different social and economic constraints (Fabricius, Ainslie & Burger 1996). In regions where cultural, and hence land use diversity, is low, e.g. the maize fields of the Free State province of S.A., or the wheatbelt of the USA, in the interior of the fomer Transkei and Ciskei, gamma diversity might be lower than if people with a variety of cultural, social and economic value systems owned or managed the land. Cultural diversity might further result in an increase in the economic resilience of an area - a higher diversity of land uses increases the economic options in an area, which makes the area resilient to market fluctuations.

MANAGEMENT AND POLICY RECOMMENDATIONS

Land use policies in South Africa have, until now, not taken cognizance of the impact of land use on biodiversity. This study indicates that the diversity of land use types in the study area leads to a regional mosaic of landscapes and the development of several anthropogenic vegetation types. This in turn leads to a higher gamma diversity than if land use diversity had been low.

Land use policy makers should consider the impact of land use on biodiversity, and should realize that, as far as general policies are concerned:

- a variety of land use types need to be maintained at a regional level to preserve the full spectrum of natural processes and species in a region;
- cultural diversity is the key to the promotion of land use diversity and consequent biodiversity at a regional level;
- resource degradation is directly correlated with human population density in developing rural areas, because more people require more resources e.g. fuelwood, and keep more livestock.

Agricultural policy makers in Xeric Succulent Thicket should take into into account that:

- Xeric Succulent Thicket is extremely sensitive to disturbance by livestock and humans and does not recover once a critical threshold of degradation had been reached.
- farming units need to be of sufficient size to avoid grazing and browsing levels which result in a decline in the size of bushclumps;
- protected areas represent a unique form of land use, which needs to be maintained and promoted.

The value of protected areas

This study has shown that protected areas make a unique contribution to the preservation of biodiversity in Xeric Succulent Thicket by

- preserving a greater richness of landscapes, physiognomic vegetation types and arthropod and plant species than adjacent commercial and subsistence rangeland;
- preserving unique landscapes, species and probably processes which do not occur on unconserved land, thereby elevating gamma diversity;

- making a disproportionate contribution to regional biodiversity, thereby acting as biodiversity 'banks' where genetic material which has become extinct in other forms of land use can be found - [the nature reserve contained 25 medicinal plant species which were absent from the adjacent communal grazing area (Appendix 2)];
- preserving endemic species which might not occur anywhere else - four undescribed weevil species were collected in the nature reserve during this study: no new species were found on unconserved land;
- maintaining the full spectrum of land use options, including the option of large-scale tourism which competes favorably, in economic terms, with alternative land uses (Fabricius & Burger 1994; Kerley et al. 1995).

Implications for protected area management in Xeric Succulent Thicket

It is likely that, in the long term, protected areas will be the only refuges of the mesic-adapted plant and animal component, or those species which co-evolved with the nurse sites provided by large bushclumps in Xeric Succulent Thicket. Protected area managers have a responsibility to manage this particular vegetation type primarily for biodiversity conservation, and to base their management decisions on sound ecological data.

- The contribution that unconserved land, adjacent to protected areas, makes to the preservation of regional biodiversity should be realized. Management plans should include management options and recommendations for unconserved land which adjoins protected areas, and planning should take place in the context of the broader region (Friedman & Zube 1992; Schonewald-Cox, Buechnes, Sauvajot & Wilcox 1992).
- Protected areas should be managed to encompass a mosaic of structural vegetation types along a gradient of cover types. There is, however, no necessity to manage protected areas so that they also contain degraded areas - unconserved land and particularly communal areas contain adequate degraded habitat.
- The most important contribution of protected areas to biodiversity preservation in Xeric Succulent Thicket is in the maintenance of vegetation characterized by large bushclumps.
- Megaherbivores play an important role in creating the types of disturbance which promote a high species richness in arthropods and plants.
- Goals which relate to the preservation of biodiversity should be stated in a measurable way by specifying the desired levels of diversity, relative to that of unconserved land.
- Protected area managers are not able to exercise control over the management of unconserved land, and rely entirely on the willingness and commitment of neighbouring land owners to implement judicial land management strategies to promote biodiversity. The maintenance of good

neighbour relations is essential, and the establishment of bioregional conservation fora need to be encouraged.

Monitoring

The only way to evaluate progress towards the attainment of conservation (or other) goals is through the analysis of relevant data, relative to a benchmark, over time.

- Monitoring programmes should focus on the boundaries between protected areas and unconserved land, to evaluate the *relative* contribution of protected areas to biodiversity preservation on an on-going basis.
- Monitoring programmes should be implemented at appropriate scales. Changes in diversity at the landscape level are not necessarily reflected in corresponding changes in fauna and flora.
- The choice of appropriate indicator species is essential. In this study, weevil HRIs or the number of weevil RTUs were appropriate indicators of biodiversity change at the species level.
- At the structural level, mean bushclump size was a very good and inexpensive indicator of biodiversity at the landscape, plant species and arthropod species level.

The picture which emerges from the research is both encouraging, as far as the value of protected areas is concerned, and disturbing, when the impacts of commercial and subsistence farming are considered. The results should, however, not be used to generalize about the impact of land use on biodiversity in other ecosystems. Xeric Succulent Thicket is a special case of a fragile, low-resilience ecosystem which is probably a relict of a climatic and grazing regime which no longer exist: most arid savannas could probably absorb the impacts of overutilization much better than Xeric Succulent Thicket.

References

ABRAMS P.A. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76: 2019-2027.

ACOCKS J.P.H. 1988. Veld types of Southern Africa. Memoirs of the Botanical Survey of South Africa No. 59, Department of Agriculture Technical Services, Pretoria.

AINSLIE A., FOX R. and FABRICIUS C. 1994. Towards policies for feasible and sustainable natural resource use: the mid-Fish River zonal study, Eastern Cape. Final report to the LAPC Natural Resource Management Programme.

ALLSOPP N. and STOCK W.D. 1993. Mycorrhizal status of plants growing in the Cape Floristic Region, South Africa. Bothalia 23: 91-104

ANDRé H.M. 1985. Associations between corticolous microarthropod communities and epiphytic cover on bark. Holartic Ecology 8: 113-119.

ARDRI 1994. A description and analysis of the agricultural land use systems in the mid-Fish river area. Report to the LAPC, Agricultural and Rural Development Research Institute, University of Fort Hare.

AUCAMP A.J. and TAINTON N.M. 1984. Veld management in the Valley Bushveld of the Eastern Cape. Dept. of Agriculture, Pretoria.

AUERBACH M. and SHMIDA A. 1987. Spatial scale and the determinants of plant species richness. TREE 2: 238-242

BACH C.E. 1986. A comparison of the responses of two tropical specialist herbivores to host plant patch size. Oecologia 68: 580-584.

BAKER W.L. and CAI Y. 1992. The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. Landscape Ecology 7: 291-302.

BATTEN A. and BOKELMANN H. 1966. Wild flowers of the Eastern Cape Province. Books of Africa, Cape Town.

BEARDALL G.M., JOUBERT S.C.J. and RETIEF P. 1984. An evaluation of the use of correspondence analysis for the analysis of herbivore-habitat selection. South African Journal of Wildlife Research 14: 79-89.

BEATTIE A.J., MAJER J.D. and OLIVER I. 1993. Rapid biodiversity assessment: a review. Pp. 4-14 in: Rapid Biodiversity Assessment - Proceedings of the Biodiversity Assessment Workshop, 3-4 May 1993. Macquarie University, Sydney, Australia.

BELL R.H.V. and MCSHANE T. 1984. Landscape classification. Pp. 93-106 in: Conservation and wildlife management in Africa, edited by R.H.V. Bell and E. McShane-Caluzi. U.S. Peace Corps, Washington.

BENNETT R.M. 1992. The use of 'economic' quantitative modelling techniques in livestock health and disease-control decision making: a review. Preventative Veterinary Medicine 13: 63-76.

BENSON D.E. 1991. Values and management of wildlife and recreation on private land in South Africa. Wildlife Society Bulletin 19: 497-510.

BERRY K.H. 1978. Livestock grazing and the desert tortoise. Transactions of the 43rd North American Wildlife and Natural Resources Conference: 505-519.

BERSIER L.-F. and MEYER, D.R. 1994. Bird assemblages in mosaic forests: the relative importance of vegetation structure and floristic composition along the successional gradient. Acta Oecologia 15: 561-576.

BISHOP R.C. and WELSH M.P. 1992. Existence values in benefit-cost analysis and damage assessment. Land Economics 68: 405-417.

BOND W.R. 1994. Keystone species. Pp. 237-253 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

BOND W.R. 1989. The dynamic nature of biotic diversity. Pp. 2-18 in: Biotic diversity in southern Africa, edited by B.J. Huntley. Oxford University Press, Cape Town.

BRANCH W.R. 1988. Field guide to the snakes and other reptiles of Southern Africa. Struik, Johannesburg.

BRIAND F. 1983. Environmental control of food web structure. Ecology 64: 253-263.

BRUNDRETT M., MELVILLE L. and PETERSON L. 1994. Practical methods in mycorrhizae research. Mycologue Publications, Canada.

CAREY D.B. 1994. Patch dynamics of *Glaucopsyche lygdamus* (Lycaenidae): correlations between butterfly density and host species diversity. Oecologia 99: 337-342.

CARPENTER S.R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 76: 677-680.

CHAPIN F.S., TORN M.S. and TATENO M. 1996. Principles of ecological sustainability. The American Naturalist 148: 1016-1037.

CHEN J., FRANKLIN J.F. and LOWE S. 1996. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conservation Biology 10: 854-861.

CLARK T.E. and SAMWAYS M.J. 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. Journal of Applied Ecology 33: 1001-1012.

CODY M.L. 1986. Diversity, rarity and conservation in Mediterranean-climate regions. Pp. 122-52 in: Conservation biology - the science of scarcity and diversity, edited by M.E. Soulé. Sunderland, Massachusets: Sinauer and Associates.

COETZEE C.G. 1994. Forts of the Eastern Cape - securing a frontier, 1799 - 1878. Published by the author, Grahamstown.

COHEN J.E. and NEWMAN C.M. 1985. A stochastic theory of community food webs. I Models and aggregated data. Proceedings of the Royal Society (London) B 224: 412-428.

CONNELL J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

CONNELL J.H. 1975. Some mechanisms producing structure in natural communities - model and evidence from field experiments. Pp. 460-490 in: Ecology and Evolution of Communities, edited by M.L. Cody and J. Diamond. Harvard University Press.

COOMBES D.S. and SOTHERTON N.W. 1986. The dispersal and distribution of polyphagous predatory Coleoptera in cereals. Annals of Applied Biology 108: 461-474.

CORBETT K.F. and TAMARIND D.L. 1979. Conservation of the sand lizard, *Lacerta agilis*, by habitat management. British Journal of Herpetology 5: 799-823.

CORNELL H. 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. Pp. 243-252 in: Species diversity in ecological communities, edited by R.E. Ricklefs and D. Schluter. Univ. of Chicago Press, Chicago.

COWLING R.M. 1983. Diversity relations in Cape shrublands and other vegetation in the south-eastern Cape, South Africa. Vegetatio 54: 103-127.

COWLING R.M., GIBBS RUSSEL G.E., HOFFMAN M.T. and HILTON-TAYLOR C. 1989. Patterns of plant species diversity in southern Africa. Pp. 19-50 in: Biotic diversity in southern Africa, edited by B.J. Huntley. Oxford University Press, Cape Town.

COWLING R.M. and HOLMES P.M. 1991. Subtropical Thicket in the south Eastern Cape: a biogeographical perspective. Pp. 3-4 in: Proceedings of the first Valley Bushveld / Subtropical Thicket Symposium. Grassland Society of Southern Africa.

CRAWLEY M.J. 1993. GLIM for ecologists. Blackwell Scientific Publications, London.

CULLINAN V.I. and THOMAS J.M. 1992. A comparison of quantitative methods for examining landscape pattern and scale. Landscape Ecology 7: 211-227.

CUNNINGHAM A.B. 1994. Integrating local plant resources and habitat management. Biodiversity and Conservation 3: 104-115.

CUNNINGHAM A.B. 1989. Indigenous plant use: balancing human needs and resources. Pp. 93-106 in: Biotic diversity in southern Africa, edited by B.J. Huntley. Oxford University Press, Cape Town.

DANCKWERTS J.E. and TEAGUE W.R. (Eds.) 1989. Veld management in the Eastern Cape. Dept. of Agriculture and Water Supply, Pretoria.

DEAN W.R.J. and MILTON S.J. 1995. Plant and invertebrate assemblages on old fields in the arid southern Karoo, South Africa. African Journal of Ecology 33: 1-13.

DEANGELIS D. 1995. Relationship between the energetics of species and large-scale species richness. Pp. 263-272 in: Linking species and ecosystems, edited by C.G. Jones and J.H. Lawton. Chapman and Hall, New York.

DESENDER K. and ALDERWEIRELDT M. 1988. Population dynamics of adult and larval Carabid beetles in a maize field and its boundary. Journal of Applied Entomology 106: 13-19.

DIAL R. and ROUGHGARDEN J. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. Ecology 76: 1821-1834

DIAMOND J. and CASE T.J. (Eds.) 1986. Community Ecology. Harper and Row, New York.

DU TOIT J.T. 1990. Giraffe feeding on Acacia flowers: predation or pollination? African Journal of Ecology 28: 63-68.

DUELLI P., STUDER M., MARCHAND I. and JACOB S. 1992. Population movements of arthropods between natural and cultivated areas. Biological Conservation 54: 193-207.

EASTERN CAPE NATURE CONSERVATION AND CONTOUR 1996. Great Fish River Reserve Management Plan. Eastern Cape Nature Conservation, Port Elizabeth.

EHRENFELD D. 1990. Why put a value on diversity? Pp. 212-216 in: Biodiversity, edited by E.O. Wilson. National Academy Press, Washington.

EHRLICH P.R. 1988. The loss of diversity - causes and consequences. Pp. 21-27 in: Biodiversity, edited by Wilson E.O.. National Academy Press, Washington.

EHRLICH P.R. 1994. Foreword - Biodiversity and ecosystem function: need we know more? Pp. IX-XI in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

EHRLICH P.R. and EHRLICH A.H. 1992. The value of biodiversity. Ambio 21: 219-226.

EHRLICH P.R. and RAVEN P.H. 1964. Butterflies and plants: a study in coevolution. Evolution 18: 586-608.

EVERARD D.A. 1987. A classification of Subtropical Transitional Thicket in the Eastern Cape, based on syntaxonomic and structural attributes. South African Journal of Botany 53: 329-338.

FABRICIUS C. 1994. Kudu density and resource dispersion in arid savanna. African Journal of Range and Forage Science 11: 7-10.

FABRICIUS C. and BURGER M. 1994. The relation between land management and biodiversity: comparing commercial and communal livestock farming to nature conservation in the mid-Fish River valley. Report to the LAPC, East Cape Nature Conservation, Port Elizabeth.

FABRICIUS C. and BURGER M. 1997 (in press). A comparison between a nature reserve and adjacent communal land in Xeric Succulent Thicket: an indigenous plant user's perspective. South African Journal of Science 00: 00-00.

FARRELL B.D. and MITTER C. 1994. Adaptive radiation in insects and plants: time and opportunity. American Zoologist 34: 57-69.

FORBES R.G. and TROLLOPE W.S.W. 1991. Veld management in the communal areas of the Ciskei. Journal of the Grassland Society of Southern Africa 8: 147-152.

FORMAN R.T. and GODRON M. 1986. Landscape Ecology. Jon Wiley and Sons, New York.

FRANKLIN J.F. 1993. Preserving biodiversity: species, ecosystems or landscapes? Ecological Applications 3: 202-205.

FRENCH D.D 1994. Hierarchical Richness Index (HRI): a simple procedure for scoring 'richness', for use with grouped data. Biological Conservation 69: 207-212.

FRIEDEL M.H. and JAMES C.D. 1995. How does grazing of native pastures affect their biodiversity? Pp. 249-259 in: Conserving biodiversity - threats and solutions, edited by R.A. Bradstock, T.D. Auld, D.A. Keith, R.T. Kingford, D. Lunney and D.P. Sivertsen. Surrey Beatty and Sons, Adelaide.

FRIEDMAN S.K. and ZUBE E.H. 1992. Assessing landscape dynamics in a protected area. Environmental Management 16: 363-370.

FUENTES E.R., HOFFMANN A.J., POIANI A. and ALLIENDE M.C. 1986. Vegetation change in large clearings: patterns in Chilean matorral. Oecologia (Berlin) 68: 358-366.

GADGILL M., BERKES F. and FOLKE C. 1993. Indigenous knowledge for biodiversity conservation. Ambio 22: 151-156.

GANDAR M.V. 1982a. Trophic ecology and plant-herbivore energetics. Pp. 514-534 in: The Ecology of Tropical Savannas, edited by B.J. Huntley and B.H. Walker. Springer-Verlag, Berlin.

GANDAR M.V. 1982b. The dynamics and trophic ecology of grasshoppers (Acridoidea) in a South African savanna. Oecologia (Berlin) 54: 370-378.

GERMANO D.J. and HUNGERFORD C.R. 1981. Reptile population changes with manipulation of Sonoran desert shrub. Great Basin Naturalist 41: 129-138.

GITAY H., WILSON J.B. and LEE W.G. 1996. Species redundancy: a redundant concept? Journal of Ecology 121-124.

GRAINGER A. 1982. Desertification. Earthscan, London.

GREENACRE M.J. 1986. SIMCA: a program to perform simple correspondence analysis. American Statistician 40: 230-231.

GREENBERG C.H., NEARY D.G. and HARRIS L.D. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. Conservation Biology 8: 1047-1057.

GREENSLADE P. 1992. Conserving invertebrate diversity in agricultural, forestry and natural ecosystems in Australia. Agriculture Ecosystems and Environment 40: 297-312.

GRIMM N.B. 1995. Why link species and ecosystems? A perspective from ecosystem ecology. Pp. 5-15 in: Linking species and ecosystems, edited by C.J. Jones and J.H. Lawton. Chapman and Hall.

GUTIéREREZ R.J. and CAREY A.B. 1985. Ecology and management of the Spotted Owl in the Pacific Northwest. General Technical Report PNW-185, Portland OR: US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experimental Station.

HAFERNIK J.E. 1992. Threats to invertebrate biodiversity: implications for conservation strategies. Pp. 41-49 in: Conservation biology - the theory and practice of nature conservation, preservation and management, edited by P.L. Fiedler P.L. and S.K. Jain. Chapman and Hall, New York.

HANSELL M.H. 1993. The ecological impact of animal nests and burrows. Functional Ecology 7: 5-12.

HANSKI I., KOUKI J. and HALKKA A. 1993. Three explanations of the positive relationship between distribution and abundance. Pp. 108-116 in: Species Diversity in Ecological Communities, edited by R.E. Ricklefs and D. Schluter. University of Chicago Press, Chicago.

HARLEY J.L. 1989. The significance of mycorrhizas. Mycological Research 92: 129-139.

HART D.D. and HORWITZ R.J. 1991. Habitat diversity and species-area relationships: alternative models and tests. Pp. 47-68 in: Habitat structure: the physical arrangement of objects in space, edited by S.S. Bell, E.D. McCoy and H.R. Mushinsky. Chapman and Hall, New York.

HARTWIG E.K. 1955. Control of snouted harvester termites. Farming in South Africa 30: 361-366.

HENGEVELD R. 1987. Scales of variation: their distribution and ecological importance. Annales Zoologici Fennici 24: 195-202.

HOBBIE S.E., JENSEN D.B. and CHAPIN F.S. 1994. Resource supply and disturbance as controls over present and future plant diversity. Pp. 385-408 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

HOLT R.D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pp. 77-88 in: Species diversity in ecological communities, edited by R.E. Ricklefs and D. Schluter. Univ. of Chicago Press.

HULME P.E. 1996a. Herbivory, plant regeneration and species coexistence. Journal of Ecology 84: 609-615.

HULME P.E. 1996b. Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory. Journal of Ecology 84: 43-51.

HUNTLY N. 1995. How important are consumer species to ecosystem functioning? Pp. 72-83 in: Linking species and ecosystems, edited by C.G. Jones and J.H. Lawton. Chapman and Hall, New York.

HURLBERT S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

JAKSIC M. and FUENTES E.R. 1980. Why are native herbs in Chilean matorral more abundant beneath bushes: microclimate or grazing? Journal of Ecology 665-669.

JAMES C.D., LANDSBERG J. and MORTON S.R. 1995. Ecological functioning in arid Australia and research to assist conservation of biodiversity. Pacific Conservation Biology 2: 126-142.

JANZEN D.H. 1987. Insect diversity of a Costa Rican dry forest: why keep it and how? Biological Journal of the Linnean Society 30: 343-356.

KERLEY G.I.H., HASCHICK S.L., FABRICIUS C. and LA COCK G.D. (eds.) 1997. Proceedings of the Second Valley Bushveld Symposium. Grassland Society of Southern Africa Special Publication, 1-84.

KERLEY G.I.H., KNIGHT M.H. and DE KOCK M. 1995. Desertification of Subtropical Thicket in the Eastern Cape, South Africa: are there alternatives? Environmental Monitoring and Assessment 37: 211-230.

KIM K.C. 1993. Biodiversity, conservation and inventory: why insects matter. Biodiversity and Conservation 2: 191-214.

KROMP B. and STEINBERGER K-H. 1992. Grassy field margins and arthropod diversity: a case study on ground beetles and spiders in eastern Austria (Coleoptera: Carabidae; Arachnida: Aranei, Opiliones). Agriculture Ecosystems and Environment 40: 71-93.

LA COCK G.D. 1992. The conservation status of Subtropical Transitional Thicket, and regeneration through seeding of shrubs in the Xeric Succulent Thicket of the Eastern Cape. M.Sc. thesis, Rhodes University, Grahamstown.

LA COCK G.D., PALMER A.R. and EVERARD D.A. 1990. Re-assessment of the area and conservation status of Subtropical Transitional Thicket (Valley Bushveld) in the eastern Cape, South Africa. South African Journal of Photogrammetry, Remote Sensing and Cartography 15: 231-235.

LAPIN M. and BARNES B.V. 1995. Using the landscape ecosystem approach to assess species and ecosystem diversity. Conservation Biology 9: 1148-1158.

LAWTON J.H. and JONES C.G. 1995. Linking species and ecosystems: organisms as ecosystem engineers. Pp. 194-208 in: Linking species and ecosystems, edited by C.G. Jones and J.H. Lawton. Chapman and Hall, New York.

LAWTON J.H. and BROWN V.K. 1994. Redundancy in ecosystems. Pp. 255-270 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

LEVIN S.A. and PAINE R.T. 1974. Disturbance, patch formation and community structure. Proceedings of the National Academy of Science, USA 71: 2744-2777.

LEWIS T. 1969. The diversity of insect fauna in a hedgerow and neighbouring field. Journal of Applied Ecology 6: 453-458.

LILLESAND T.M. and KIEFER R.W. 1987. Remote sensing and image interpretation. John Wiley and Sons, New York.

MACARTHUR R.H. 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36: 533-536.

MACMAHON J.A. 1987. Disturbed land and ecological theory: an essay about a mutualistic association. Pp. 221-238 in: Restoration Ecology - a synthetic approach to ecological research, edited by W.R. Jordan, M.E. Gilpin and J.D. Aber. Cambridge Univ. Press, London.

MAEHR D.S. and COX J.A. 1995. Landscape features and panthers in Florida. Conservation Biology 9: 1008-1019.

MAILLE P. and MENDELSOHN R. 1993. Valuing ecotourism in Madagascar. Journal of Environmental Management 38: 213-218.

MAJER J.D. 1993. Costs of biodiversity assessment. Pp. 35-39 in: Rapid Biodiversity Assessment. Proceedings of the Biodiversity Assessment Workshop, 3-4 May 1993, Macquarie University, Sydney, Australia.

MARGULES C.R., MILKOVITS, G.A. and SMITH, G.T. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. Ecology 75: 2033-2042

MARSH A.C. 1984. The efficacy of pitfall traps for determining the structure of a desert ant community. Journal of the Entomological Society of Southern Africa 47: 115-120.

MARTIN P.S. 1990. 40 000 years of extinction on the 'planet of doom'. Paleogeography, Paleoclimatology and Paleoecology 82: 187-201.

MARTINEZ L. 1995. Unifying ecological subdisciplines with ecosystem food webs. Pp. 166-175 in: Linking species and ecosystems, edited by C.G. Jones and J.H. Lawton. Chapman and Hall, New York.

MARTINEZ N.D. and LAWTON, J.H. 1995. Scale and food-web structure - from local to global. Oikos 73: 148-154.

MAY R.M. 1973. Stability and complexity in model ecosystems. Princeton University Press.

MCLAUGHLIN J.F. and ROUGHGARDEN J. 1993. Species interactions in space. Pp. 89-98 in: Species diversity in ecological communities, edited by R.E. Ricklefs and D. Schluter. University of Chicago Press.

MCNAUGHTON S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. The American Naturalist 111: 515-525.

MCNAUGHTON S.J. 1994. Biodiversity and function of grazing ecosystems. Pp. 361-384 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

MCNAUGHTON S.J. and WOLF L.L. 1970. Dominance and the niche in ecological systems. Science 167: 131-139.

MCNEELY J.A. 1988. Economics and biological diversity: developing and using economic incentives to preserve biological resources. IUCN, Gland, Switzerland.

MCNEELY J. 1991. Conserving cultural diversity: how the variety of human experience can help promote sustainable forms of using natural resources. Sustainable Development 1: 55-64.

MCNEELY J.A., MILLER K.R., REID W.V.C., MITTERMEIER R.A. and WERNER T.B. 1990. Conserving the world's biological diversity. IUCN, WRI, World Bank, WWF, Washington.

MIDGLEY J.J. and COWLING R.M. 1993. Regeneration patterns in Cape subtropical transitional thicket: where are all the seedlings? South African Journal of Botany 59: 496-499.

MILLER J.C. 1993. Insect natural history, multi-species interactions and biodiversity in ecosystems. Biodiversity and Conservation 2: 233-241.

MILNE B.T. 1992. Spatial aggregation and neutral models in fractal landscapes. The American Naturalist. 139: 32-57.

MILTON S.J. and DEAN W.R.J. 1992. An underground index of rangeland degradation: cicadas in arid southern Africa. Oecologia 91: 288-291.

MILTON S.J. and DEAN W.R.J. 1993. Selection of seeds by harvester ants (*Messor capensis*) in relation to condition of arid rangeland. Journal of Arid Environments 24: 63-74.

MILTON S.J., DEAN R.J. DU PLESSIS M.A. and SIEGFRIED W.R. 1994. A conceptual model of arid rangeland degradation: the escalating cost of declining productivity. BioScience 44: 70-76.

MILTON S.J. and HOFFMAN M.T. 1994. The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. African Journal of Range and Forage Science 11: 18-26.

MITCHELL J.C. 1979. Ecology of southeastern Arizona whiptail lizards (*Cnemidophorus*: Teiidae): population densities, resource partitioning, and niche overlap. Canadian Journal of Zoology 57: 1487-1499.

MLADENOFF D.J., WHIT M.A. and PASTOR J. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3: 294-306.

MOOLMAN H.J. and COWLING R.M. 1994. The impact of elephant and goat grazing on the endemic flora of South African succulent thicket. Biological Conservation 68: 53-63.

MORTON S.R. 1994. Determinants of diversity in animal communities of arid Australia. Pp. 159-169 in: Species Diversity in Ecological Communities, edited by R.E. Ricklefs and D. Schluter. Univ. of Chicago Press.

MUSHINSKY H.R. 1992. Natural history and abundance of southeastern five-lined skinks, *Eumeces inexpectatus*, on a periodically burned sandhill in Florida. Herpetologica 48: 307-312.

NAEEM S., THOMPSON L.J., LAWLER S.P., LAWTON J.H. and WOODFIN R.M. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368: 734-736.

NAEEM S., THOMPSON L.J., LAWLER S.P., LAWTON J.H. and WOODFIN R.M. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Philosophical Transactions of the Royal Society of London B 347: 249-262.

NEU C.W., BYERS C.R. and J.M. PEEK 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38: 541-545.

NILSSON C. and GRELSSON G. 1995. The fragility of ecosystems: a review. Journal of Applied Ecology 32: 677-692.

NORTON B.G. (Ed.) 1986. The preservation of species: the value of biological diversity. Princeton University Press, New Jersey.

NORTH S.G., BULLOCK D.J. and DULLOO M.E. 1994. Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. Biological Conservation 67: 21-28.

NORTON B.G. and ULANOWICZ R.E. 1992. Scale and biodiversity policy: a hierarchical approach. Ambio 21: 244-249.

NOSS R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4: 355-364.

NOVELLIE P. 1990. Habitat use by indigenous ungulates in relation to sward structure and veld condition. Journal of the Grassland Society of Southern Africa 7: 16-21.

O'NEILL R.V., DEANGELIS D.L., WAIDE J.B. and ALLEN T.F.H. 1986. A hierarchical concept of ecosystems. Princeton University Press.

O'NEILL R.V., KRUMMEL J.R., GARDNER R.H., SUGIHARA G., JACKSON B., DEANGELIS D.L. and MILNE B. 1988. Indexes of landscape pattern. Landscape Ecology 1: 153-162.

O'NEILL R.V., TURNER S.J., CULLINAN V.I., COFFIN D.P., COOK T., CONLEY W., BRUNT J. and THOMAS,1991. Multiple landscape scales: an intersite comparison. Landscape Ecology 5: 137-144.

OBERWINKLER F. 1994. Evolution of functional groups in Basidiomycetes (Fungi). Pp. 143-164 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

OKSANEN J. 1996. Is the hump-shaped relationship between species richness and biomass an artefact due to plot size? Journal of Ecology 84: 293-295.

OWEN-SMITH R.N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge.

PALMER A.R. 1981. A study of the vegetation of the Andries Vosloo Kudu reserve, Cape Province. M.Sc. thesis, Rhodes University, Grahamstown.

PALMER A.R. 1990. A qualitative model of vegetation history in the Eastern Cape midlands, South Africa. Journal of Biogeography 17: 35-46.

PALMER A.R. and AVIS A. 1994. The description, mapping and evaluation of recent changes in the contemporary vegetation patterns. Report to the LAPC, Roodeplaat Grassland Institute, Grahamstown.

PALMER A.R., COOK B.J.S. and LUBKE R.A. 1988. Aspects of the vegetation and soil relationships in the Andries Vosloo Kudu Reserve, Cape Province. South African Journal of Botany 54: 309-314.

PARMENTER R.R. and MACMAHON J.A. 1987. Early successional patterns of arthropod recolonization on reclaimed strip mines in Southwestern Wyoming: the ground-dwelling beetle fauna (Coleoptera). Environmental Entomology 16: 168-177.

PEARCE D. and MORAN D. 1994. The economic value of biodiversity. Earthscan Publications, London.

PELLEW R.A. 1983. The giraffe and its food resource in the Serengetti. I.Composition, biomass and production of available browse. African Journal of Ecology 21: 241-267.

PETTERSON R.B., BALL J.P., RENHORN K., ESSEEN P. and SJOBERG K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. Biological Conservation 74: 57-63.

PIANKA E.R. 1967. On lizard species diversity: North American flatland lizards. Ecology 48: 333-351.

PIANKA E.R. 1989. Desert lizard diversity: additional comments and some data. The American Naturalist 134: 344-364.

PICKETT S.T.A., PARKER V.T. and FIEDLER P.L. 1992. The new paradigm in ecology: implications for conservation biology above the species level. Pp. 64-86 in: Conservation biology: the theory and practice of nature conservation, preservation and management, edited by P.L. Fiedler and S.K. Jain, Chapman and Hall, New York.

PIMBERT M.P and PRETTY J.N. 1995. Parks, people and professionals. UNRISD Discussion Paper DP 57, UNRISD, Geneva.

PIMM S.L. and LAWTON J.H. 1977. The number of trophic levels in ecological communities. Nature 268: 329-331.

POLIS G.A. and STRONG D.R. 1996. Food web complexity and community dynamics. The American Naturalist 147: 813-846.

POLLOCK M.M., NAIMAN R.J., ERICKSON H.E., JOHNSTON C.A., PASTOR J. and PINAY G. 1995. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pp. 117-126 in: Linking species and ecosystems, edited by C.G. Jones and J.H. Lawton. Chapman and Hall, New York.

POOLEY E. 1993. The complete guide to trees of Natal, Zululand and Transkei. Natal Flora Publications Trust, Durban.

PRENDERGAST J.R., QUINN R.M., LAWTON, J.H., EVERSHAM B.C. and GIBBONS D.W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365: 335-337.

READ D.J. 1994. Plant-microbe mutualisms and community structure. Pp. 181-210 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

RECHER 1969. Bird species diversity and habitat diversity in Australia and North America. The American Naturalist 103: 75-80.

REID W.V. and MILLER K.R. 1989. Keeping options alive - the scientific basis for conserving biodiversity. WRI, Washington D.C.

RICKELFS R.E. and SCHLUTER D. (Eds.) 1993a. Species diversity in ecological communities. Univ. of Chicago Press.

RICKLEFS R.E. and SCHLUTER D. 1993b. Species diversity: regional and historical influences. Pp. 350-364 in: Species diversity in ecological communities, edited by R.E. Ricklefs and D. Schluter. Univ. of Chicago Press.

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

RIVERS-MOORE J.L. and SAMWAYS M.J. 1996. Game and cattle trampling, and impacts of human dwellings on arthropods at a game park. Biodiversity and Conservation 5: 1545-1557.

ROMME W.H. and KNIGHT D.H. 1982. Landscape ecology: the concept applied to Yellowstone National Park. BioScience 32: 664-670.

ROZENZWEIG M.L. and ABRAMSKY Z. 1993. How are diversity and productivity related? Pp. 52-65 in: Species Diversity in Ecological Communities, edited by R.E. Ricklefs and D. Schluter. University of Chicago Press, Chicago.

RUTHERFORD M.C. and WESTFALL R.H. 1986. Biomes of southern Africa - an objective categorization. Memoirs of the Botanical Survey of Southern Africa 54, Botanical Research Institute, Dept. of Agriculture, Pretoria.

SALISBURY E.J. 1942. The reproductive capacity of plants. G. Bell, London.

SAMWAYS M.J. 1993. Insects in biodiversity conservation: some perspectives and directives. Biodiversity and Conservation 2: 258-282.

SAMWAYS M.J. 1994. Insect Conservation Biology. Chapman and Hall, London.

SCHEIBE J.S. 1987. Climate, competition and the structure of temperate zone lizard communities. Ecology 68: 1424-36.

SCHEINER S.M. 1992. Measuring pattern diversity. Ecology 73: 1860-1867.

SCHLUTER D. and RICKLEFS R.E. 1993. Species diversity: an introduction to the problem. Pp. 1-10 in: Species diversity in ecological communities, edited by R.E. Ricklefs and D. Schluter. University of Chicago Press.

SCHOENER T.W. 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. American Zoologist 27: 259-291.

SCHONEWALD-COX C., BUECHNER M., SAUVAJOT R. and WILCOX B.A. 1992. Cross-boundary management between national parks and surrounding lands: a review and discussion. Environmental Management 16: 273-282.

SCHULZE E.-D and MOONEY H.A. (Eds.) 1994. Biodiversity and ecosystem function. Springer-Verlag, Berlin.

SEASTEDT T.R. and CROSSLEY D.A. (jr.) 1984. The influence of arthropods on ecosystems. Bioscience 34: 157-161.

SENFT R.L., COUGHENOUR M.B., BAILEY D.W., RITTENHOUSE L.R., SALA O.E. and SWIFT D.M. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37: 789-799.

SHERMAN P.B. and DIXON J.A. 1991. The economics of nature tourism: determining if it pays. Pp. 89-131 in: Nature tourism, edited by T. Whelan. Island Press, Washington.

SHMIDA A. and WILSON M.V. 1985. Biological determinants of species diversity. Journal of Biogeography 12: 1-20.

SIH A., CROWLEY P., MCPEEK P., PETRANKA J. and STROHMEIER K. 1985. Predation, competition and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16: 269-311.

SIMELANE T.S. 1996. The traditional use of indigenous vertebrates. M.Sc. Thesis, University of Port Elizabeth.

SOLBRIG O. 1994. Plant traits and adaptive strategies: their role in ecosystem function. Pp. 97-116 in: Biodiversity and ecosystem function, Edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

SORENSON T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity in species content. Biol. Skr. K. Danske Vidensk. Selsk. 5: 1-34.

SPLASH C.L. and SIMPSON I.A. 1993. Protecting sites of species scientific interest - intrinsic and utilitarian values. Journal of Environmental Management 39: 213- 227

STUART-HILL G.C. 1992. Effects of elephants and goats on the Kaffrarian succulent thicket of the Eastern Cape, South Africa. Journal of Applied Ecology 29: 699-710.

STUART-HILL G.C. and AUCAMP A.J. 1993. Carrying capacity of the succulent Valley Bushveld of the Eastern Cape. African Journal of Range and Forage Science 10: 1-10.

STUART-HILL G.C., AUCAMP A.J., LE ROUX C.J.G. and TEAGUE W.R. 1986. Towards a method of assessing the veld condition of the Valley Bushveld in the Eastern Cape. Journal of the Grassland Society of Southern Africa 3: 19-24.

STUART-HILL G.C. and DANCKWERTS J.E. 1988. Influence of domestic livestock and wild animals on the future of succulent Valley Bushveld. Pelea 7: 45-56.

SUZAN, H., NABHAN G.P. and PATTEN D.T. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran desert. Journal of Vegetation Science 7: 635-644.

SWANSON T.M. 1992. Economics of a biodiversity convention. Ambio 21: 250-257.

TAINTON N.M. (Ed.) 1981. Veld and pasture management in South Africa. Shuter and Shooter, Pietermaritzburg.

TAINTON N.M., ZACHARIAS P.J.K. and HARDY M.B. 1989. The contribution of veld diversity to the agricultural economy. Pp. 107-120 in: Biotic diversity in southern Africa, edited by B.J. Huntley. Oxford University Press, Cape Town.

TILMAN D. 1982. Resource competition and community structure. Princeton University Press, Princeton.

TILMAN D. 1994a. Community diversity and succession: the roles of competition, dispersal and habitat modification. Pp. 327-346 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

TILMAN D. 1994b. Competition and biodiversity in spatially structured habitats. Ecology 75: 2-16

TILMAN D. and DOWNING J.A. 1994. Biodiversity and stability in grasslands. Nature 367: 363-365

TILMAN D. and HADDI A.E. 1992. Drought and biodiversity in Grasslands. Oecologia 89: 257-264

TILMAN D. and PACALA S. 1993. The maintenance of species richness in plant communities. Pp. 13-25 in: Species diversity in ecological communities, edited by R.E. Ricklefs and D. Schluter. University of Chicago Press.

TOPPING C.J. and SUNDERLAND K.D. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29: 485-491.

TURNER M.V. and O'NEILL R.V. 1995. Exploring aggregation in space and time. Pp. 194-208 in: Linking species and ecosystems, edited by C.G. Jones and J.H. Lawton. Chapman and Hall, New York.

TYSON P.D. 1986. Climatic change and variability in Southern Africa. Oxford University Press, Cape Town.

URBAN D.L., O'NEILL R.V. and SHUGART H.H. 1987. Landscape ecology - a hierarchical perspective can help scientists understand spatial patterns. BioScience 37: 119-127.

USACERL 1994. GRASS 4.1 Geographic Resources Analysis Support System. USA Corps of Engineers Research Laboratory. Champaign, Illinois.

VILLET M.H. and CAPITAO I.R. 1996 (in press). Cicadas (Homoptera: Cicadidae) as indicators of habitat and veld condition in Valley Bushveld in the Great Fish River Valley. African Entomology 00: 00-00.

WALKER B.H. 1989. Diversity and stability in ecosystem conservation. Pp. 121-130 in: Conservation for the Twenty-first century, edited by D. Western and M. Pearl. Oxford University Press, New York.

WALKER B.H. 1992. Biodiversity and ecological redundancy. Conservation Biology 6: 18-23.

WARREN P.H. 1990. Variation in food-web structure: the determinants of connectance. The American Naturalist 136: 689-700.

WATTS D.B. 1996. Landscape configuration and density hotspots in wintering sparrows. Oecologia 108: 512-517.

WERGER M.J.A. 1972. Specie-area relationships and plot size, with some examples from Southern African vegetation. Bothalia 10: 583-594

WESTERN D. 1989. Wildlife without parks: wildlife in the rural landscape. Pp. 158-165 in: Conservation for the Twenty-first century, edited by D. Western and M. Pearl. Oxford University Press, New York.

WESTOBY M., WALKER B. and NOY-MEIR I. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42: 266-274.

WHEELER Q.D. 1990. Insect diversity and cladistic constraints. Annals of the Entomological Society of America 83: 1031-1047.

WHITE P.S. and PICKET S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. Pp. 3-13 in: The ecology of natural disturbance and patch dynamics, edited by S.T.A. Picket and P.S. White. Academic Press, New York.

WHITFORD W.G., DICK-PEDDIE D., WALTERS D and LUDWIG J. 1978. Effect of shrub defoliation on grass cover and rodent species in a Chihuahuan desert ecosystem. Journal of Arid Environments 1: 237-242.

WHITTAKER R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

WIENS J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

WIENS J.A., CRIST T.O., WITH K.A. and MILNE B.T. 1995. Fractal patens of insect movement in microlandscape mosaics. Ecology 76: 663-666.

WIENS J.A. and MILNE B.T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology 3: 87-96.

WIENS J.A., STENSETH N.C., VAN HORNE B. and IMS R.A. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369-380.

WILSON E.O. 1990. The current state of biological diversity. Pp. 3-20 in: Biodiversity, edited by E.O. Wilson. National Academy Press, Washington.

WOODWARD F.I. 1994. How many species are required for a functional system? Pp. 271-292 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

YEATON R.I. 1988. Porcupines, fires and the dynamics of the tree layer of the Burkea africana savanna. Journal of Ecology 76: 1017-1029.

YODZIS P. 1993. Environment and trophodiversity. Pp. 26-38 in: Species diversity in ecological communities, edited by R.E. Ricklefs and D. Schluter. University of Chicago Press.

ZWOLFER H. and ARNOLD-RINEHART J. 1994. The evolution of interactions and diversity in plant-insect systems: the *Urophora-Eurytoma* food web in galls on Palearctic Cardue. Pp. 211-236 in: Biodiversity and ecosystem function, edited by E.-D. Schulze and H.A. Mooney. Springer-Verlag, Berlin.

APPENDIX 1.

Scientific names of large animals mentioned in the text

Porcupine	*Hystrix africaeaustralis*
Leopard	*Panthera pardus*
Caracal	*Felis caracal*
Black-backed jackal	*Canis mesomelas*
Aardvark	*Orycteropus afer*
African elephant / elephant	*Loxodonta africana*
Black rhinoceros	*Diceros bicornis*
Zebra / Burchell's zebra	*Equus zebra zebra*
Warthog	*Phacochoerus aethiopicus*
Hippopotamus	*Hippopotamus amphibius*
Red hartebeest	*Alcelaphus buselaphus*
Blue duiker	*Philantomba monticola*
Springbok	*Antidorcas marsupialis*
Grey duiker	*Sylvicapra grimmia*
Steenbok	*Raphiceros campestris*
Buffalo / African buffalo	*Syncerus caffer*
Kudu	*Tragelaphus strepsiceros*
Bushbuck	*Tragelaphus scriptus*
Eland	*Taurotragus oryx*

APPENDIX 2.

A Comparison between a Nature Reserve and Adjacent Communal Land in Xeric Succulent Thicket: an indigenous plant user's perspective [1]

ABSTRACT

Local people with knowledge of indigenous plants could contribute to the management of protected areas while simultaneously improving their options for employment. Members of a local Xhosa community who lived adjacent to the Great Fish River nature reserve in the former Ciskei, Eastern Cape, were employed to assist me with an inventory of locally useful plants. The survey was designed to quantify differences in plant diversity between the nature reserve and the adjacent communal area, from the point of view of local indigenous plant users. Traditional healers and rural villagers who were experienced users of indigenous plants were recruited with the aid of a local community organization. Plants which were used for physical and spiritual healing, fuel, food and construction were identified along paired transects in the nature reserve and the communal area respectively. Hierarchical Richness Indices (HRIs) and the number of recognisable plants as well as their abundance at each site were used to compare the nature reserve to the communal area. Altogether, 122 utilised plant types were recorded, of which 68 % had medicinal or spiritual value, 12 % were used for food, 13 % for fuel and 7 % for building purposes. These ratios were similar for both the nature reserve and the communal area. One hundred and eight (108) useful types of plants were recorded on the nature reserve and 97 at the communal area. The nature reserve contained 25 'unique' recognisable plants which were not recorded in the communal area, whereas the communal area contained 14. Useful plants were more abundant on the nature reserve than at the communal area, and the average HRI for the nature reserve was almost double the average HRI of the communal area. The advantages to the community were limited: temporary employment was created and local skills were developed which might have improved the people's prospects for future employment. The conservation benefits were more substantial: information became available which would otherwise have remained hidden, relations between the community and conservation agencies improved, and credible education programmes in sustainable resource use could be developed through a participatory approach. The next step from a management point of view is to provide opportunities for the community to interpret and apply the results, and to, with the local people, explore small business opportunities based on the cultivation of useful plants. Participatory research and monitoring could be furthered by putting greater emphasis on the participatory process than on results, by actively involving local

---

[1] Adapted from FABRICIUS C. and BURGER M. 1997 (in press). A comparison between a nature reserve and adjacent communal land in Xeric Succulent Thicket: an indigenous plant user's perspective. South African Journal of Science 00: 00-00.

people in the development of monitoring programmes from the outset, and by interpreting and deliberating the results of monitoring with them in an interactive way.

INTRODUCTION

Indigenous people in rural areas have knowledge and skills which could contribute to the improved management of protected areas. It is important for conservationists to recognise that this knowledge exists, and to harness it for the benefit of conservation and social development. Impoverished rural people, especially those who live adjacent to protected areas, should be made aware that their knowledge of natural resources is valuable and a potential source of income.

In developing countries, the skills of local people (people who reside within the boundaries of a pre-defined study area) have been incorporated into land use planning (Selin & Chavez 1995), agricultural management planning (Coppock 1994), tourism development projects (Drake 1991), wildlife monitoring (Marks 1994), gathering and providing information about biomedicines (Martin 1995), law enforcement (Lober 1992) and data collection for biological inventories in conservation projects (Phillips, Gentry, Reynel, Wilkin & Galvés-Durand 1994). The involvement of local people in the management and research of natural resources invariably results in a learning experience which enriches all participants (Chambers 1994; Pimbert & Pretty 1995).

In South Africa the participation of local indigenous people in conservation projects was unusual before 1993, but currently it is commonplace for local communities to be recognized as important stakeholders in the management of protected areas (Pimbert & Pretty 1995; Eastern Cape Nature Consevation 1995; Fabricius 1994a; Fabricius 1994b). Although "functional" and "interactive" community participation (Pimbert & Pretty 1995) in conservation is limited to a few exceptional cases, almost all conservation institutions have community relations sections, and most protected area managers strive to provide some tangible benefits from protected areas to neighbouring communities, e.g. firewood, building material, meat, jobs and business opportunities (Shackleton 1993; Wells & Brandon 1992).

Local communities should be involved and participate in conservation management and research in a meaningful way. They possess wisdom and skills which can be applied to improve the sustainable use of natural resources. They should be compensated for their contribution, as are other consultants, and should be encouraged to develop small businesses, linked to protected areas, to capitalise on their unique knowledge and abilities.

In this preliminary study I co-operated with Xhosa people who lived in the former Ciskei, adjacent to the Great Fish River nature reserve in the Eastern Cape Province. They assisted me in evaluating the role of the nature reserve in preserving useful plant species. In the process much-needed but short-term local employment was created and opportunities for small businesses became evident, based on the utilisation and cultivation of indigenous biota. The project was part of a larger programme to assess the potential of protected areas to preserve biodiversity and contribute to sustainable development in the Eastern Cape.

METHODS

Project participants were recruited with the aid of the local Civic Organisation, which endorsed the project. The rationale for the project was fully explained to all participants and other interested community members. I employed nine local people, consisting of three qualified traditional healers (*amagqirha*), three "unqualified" male indigenous plant users and three "unqualified" female indigenous plant users. All these people had lived in the area for twenty years or more and regularly made use of indigenous plants.

The participants were divided into three groups of 3 people each, consisting of a traditional healer, a man and a woman respectively. Participants were selected to represent the main indigenous plant user groups in the community. Each group was accompanied by a field ranger who recorded the data and acted as interpreter. A pilot study was first conducted to familiarise the participants with the research process. The pilot transects were 400 m long and 10 m wide and were located inside and outside the nature reserve. All three groups combined participated in this part of the study. In the main study each of the groups walked along a transect 450 m long and 10 m wide at each of the two localities, in areas which were selected for their representativeness of a particular land use type. Surveys on the nature reserve and the communal area employed the same methods and the same people, and I made every effort to ensure that the paired sampling areas were in comparable landscapes with the same elevations, substrates, slopes and aspects. All plant species within the transect which were regarded as useful as spiritual or physical medicines, fuel or building materials were recorded. The various uses and the Xhosa names of identified plants were also recorded.

The data collected by the three groups were cross-checked for contradictions between groups and then pooled into a single sample, together with the results of the pilot study. The numbers of plant species in different utilisation categories (medicinal, food, fuel and building material) were counted for the two sites and Hierarchical Richness Indices or HRIs (French 1994) were calculated to express diversity. The average HRI and standard errors for the four transects at each respective locality were calculated to compare the two sites. The HRI combines abundance and species richness into a single index, and assigns hierarchical weights to taxa to ensure that rare taxa contribute disproportionately more to the total index. The percentage similarity between the two sites was calculated according to the formula of Sorenson (1948).

RESULTS

Results are summarised in Table 1. The average Hierarchical Richness Index for useful plants was more than 45% lower for the communal area than for the nature reserve, and the abundance of useful plants was much higher in the nature reserve than in the communal area. A total of 122 plant species were identified as useful. Most of the species (68 %) were used for physical and spiritual healing purposes, while 12 % were food plants, 13 % were used for fuel and 7 % were used for building material. One hundred and eight (108) species were recorded in the nature reserve, and 97 at the communal area. While the proportions of different utilisation classes at the two areas were similar, the plants used for fuel and building purposes in the communal area were mostly copicing stumps, whereas the same species in the nature reserve consisted of undamaged trees or shrubs.

While the nature reserves contained almost twice as many unique plants (types which were recorded at that locality only) than the communal area, it was nevertheless surprising that there were unique plants in the degraded communal area, and that the community similarity of the nature reserve and the communal area was as high as 80%. The two plant communities were therefore very similar, from an indigenous plant user's perspective, if the conventional 75% which characterises separate communities is used as a yardstick (Whittaker 1972; Cowling, Gibbs Russel, Hoffman & Hilton-Taylor 1989).

Table 1. Useful plants identified by local indigenous plant users in the Great Fish River nature reserve and in the communal area. HRI = Hierarchical Richness Index. The number of plant types used for various purposes do not add up to the total number of plant types, because some plants were used for more than one purpose. Unique plant types are plants which were recorded at one locality only. S.E. = standard error

	Nature Reserve	Communal Area
No. of plant types	108	97
Medicinal	94	84
Fuel	18	16
Food	16	15
Building	9	8
Unique plant types	25	14
Shared plant types	83	-
% Similarity	80	-
Mean HRI	12282	6877
S.E.	2649	1896
Mean no. of useful plants per 100 m	340	238
S.E.	14	31

DISCUSSION

The involvement of local people in research and management is becoming part of the new conservation paradigm in South Africa, in accordance with world-wide trends. This study has demonstrated that local communities can contribute to inventory-type information about parks and nature reserves while simultaneously earning an income. Conservation professionals need to be encouraged and trained to involve local communities in the management and monitoring of protected areas in a constructive and mutually beneficial way (Pimbert & Pretty 1995).

Even from this limited sample it became clear that the communal area was biologically impoverished relative to the nature reserve, especially in relation to the abundance of plants. This emphasised the role of protected areas as gene banks, and the participants remarked on that while collecting data. More than 20 % (25) of the plants were unique to the nature reserve, whereas 11% (14) were restricted to the communal area, which was equally noteworthy and unexpected. In Chapter 6 I found that the nature reserve contained more than twice as many ant, weevil and spider species as the communal area, and that between 23% and 45% of arthropod species were unique to the reserve. It should however be borne in mind that the unique plants in the nature reserve occurred at relatively high densities, while the species which were restricted to the communal area occurred at very low densities, often as single, copicing individuals (C. Fabricius, unpublished data). It is also expected that the participants were more acquainted with the rare plants of the communal grazing area than with those of the nature reserve.

As with most participatory research and monitoring exercises, the scientific merits of the study might be questionable since a) participants were accustomed to the plants growing in the communal area, and probably did not recognise all the useful plants which were restricted to the nature reserve; b) differences in vegetation cover made plants in the nature reserve less visible than those in the communal area, and some species might have not been detected in the nature reserve; c) participants deviated from the prescribed transect width in some instances, but the deviation was consistent for the two areas. On the other hand, it was not desirable to force the rigid protocols of scientific sampling on the participants, as this would have hampered the free flow of knowledge because of a lack of spontaneity.

The project benefited both conservation and the community, although the former benefits outweighed the latter.

Conservation benefits

- Inventory type information about the relative occurrence of useful plant species was obtained which would not have been possible under other circumstances. The local people had an intimate awareness of every plant species which grew in the area, including those which were recorded exclusively in the nature reserve.
- Information about the use of medicinal and other plants was accessed which is lacking for the eastern Cape. Although some of the plants used by the local people for medicinal purposes do not have pharmacological properties, others might have, and these are highly sought after by pharmaceutical companies (M. Hirst, Kaffrarian Museum, P.O. King Williams Town, pers. comm.).

- Following initiatives by reserve management staff the relationship between conservationists and the Glenmore villagers greatly improved. This should be seen against the backdrop of political change in the country, which no doubt played a role in changing people's attitudes. Reserve staff became more active in Glenmore and communication improved. Poaching has decreased, and the number of local people visiting the reserve has increased. A recent attitude survey found that the Glenmore villagers were much more positive towards the nature reserve and conservation than any of the other villages where there were no participatory projects. In a questionnaire survey, 89% of Glenmore respondents (n=28) indicated that they "liked" the nature reserve, compared to 18% of respondents from other neighbouring villages (n=60). Likewise, 96% of Glenmore residents thought it was important to conserve plants and animals, compared to 66% of residents of other villages (Ainslie 1995). Before these results are rigidly interpreted, it should be borne in mind Glenmore is a "special case" and not comparable to the other villages in some respects. It is a resettlement village and therefore contains more advanced infrastructure, and the people are less reliant on livestock farming. Its inhabitants do not have the same grievances about land as do those of the other villages.
- The results clearly demonstrated the value of protected areas in conserving traditionally useful plants. Credible data on this and other aspects were obtained for environmental education purposes, to demonstrate the value of protected areas to local people. Because the data were collected by the people themselves, their validity is less likely to be challenged than the validity of data collected by formally-trained biologists.

Advantages to the community

- Limited employment was provided, which nevertheless resulted in an increase in cash flow to and in the village. The amount of R 45 / day (the maximum prescribed by government, who employed both authors) might sound trivial, but in an impoverished area such as Glenmore it was regarded as a fortune. As a result of this and other research projects initiated by the authors R 8000 was brought into the small community over a period of a few months, of which a large proportion was probably spent locally because of the relative remoteness of the area and the relatively weak transport links to other centres. This should be seen within the context of the high unemployment rate and the low household incomes which characterize the area (Ainslie, Fox & Fabricius 1994). The sustainability of this source of income depends on continued research of a similar type in the area, coupled with on-going participatory monitoring programmes.
- The foundation was layed for local small business operators to possibly grow and sell medicinal plants to outside markets. Pharmaceutical companies might even in future franchise the cultivation of medicinal plants to local people, as they move into the highly lucrative herbal plant market (M. Hirst, Kaffrarian Museum, P.O. King Williams Town, pers. comm.). This depends to a large extent on the commitment of the conservation institutions to facilitate such franchises, for example by making the nature reserve available for the sustainable harvesting of genetic material by local people.

- Skills were discovered which might lead to the participants finding other employment, for example in the specialized nature tourism market.

It is obvious that rural people appreciate the value of ecosystems consisting of a wide variety of useful plant species. It is however unclear how they perceive the link between resource degradation, plant species diversity and long-term "ecosystem health", and how that perception compares to the views of formally-trained scientists. This needs to be explored if solutions are sought for sustainable resource use in rural areas. The next scheduled step is to present the outcome of the study to the participants and other members of the community. After feasibility studies, plans for small community-based businesses, based on the cultivation and sustainable harvesting of natural resources, could be developed. Conservation institutions should seriously consider formalizing participatory monitoring programmes, by involving indigenous plant users in an interactive way from the outset of projects.

The project described here should not be confused with true participatory research, as the participants acted more like employees than like partners. Participatory ecological research could be improved by

- incorporating participatory research and monitoring as part of a total process of local participation in conservation projects and initiatives;
- putting greater emphasis on the research *process* rather than on results;
- limiting external design to a minimum, within the constraints of the conservation management objectives;
- linking the research to an activity at the local level, i.e. avoiding monitoring for the sake of information gathering only;
- incorporating flexibility into participatory programmes (Shah 1995).

The involvement of indigenous plant users as described in this paper was nevertheless a step closer to the ideal of true local participation in conservation initiatives, and should be encouraged.

Acknowledgements

Field rangers Wellington Phongolo and Johannes Mvane, and indigenous plant users S.D. Quma, W. Mologweni, N. Ngxonde, M. Gqomone, Joyce Tyileka, Nobantu Mpolweni, V. Manke, M.Z. Wulana, and Nokwando Mnyofo are thanked for their able assistance.

REFERENCES

Ainslie A. 1995. The attitudes of neighbours towards nature conservation at two East Cape nature reserves. Unpublished report commissioned by Eastern Cape Nature Conservation, ISER, Rhodes University, 48 pages.

Ainslie A., Fox R. & Fabricius C. 1994. Towards policies for feasible and sustainable natural resource use: the mid-Fish River zonal study, Eastern Cape. Final report to the LAPC Natural Resource Management Programme.

Chambers R. 1994. Participatory Rural Appraisal (PRA): analysis of experience. World Development 22: 1253-1268.

Coppock L. 1994. The Borana Plateau of Southern Ethiopia: synthesis of pastoral research, development and change, 1980-91. International Livestock Centre for Africa (ILCA), Addis Ababa, Ethiopia.

Cowling R.M., Gibbs Russel G.E., Hoffman M.T. & Hilton-Taylor C. 1989. Patterns of plant species diversity in southern Africa. Pp. 19-50 in: Biotic diversity in southern Africa, edited by B.J. Huntley. Oxford University Press, Cape Town.

Drake S. (1991). Local participation in ecotourism projects. Pp.132-164 In: Nature tourism, edited by T. Whelan. Island Press, Washington.

Eastern Cape Nature Conservation 1995. Management plan for Karoo Nature Reserve. Eastern Cape Nature Conservation, Graaff Reinet.

Fabricius C. (ed.) 1994a. Groendal Wilderness Area: integrating nature conservation and livestock grazing with community participation - an ad hoc report. Eastern Cape Nature Conservation.

Fabricius C. 1994b. People-park conflicts at Dwesa and Cwebe nature reserves - emergency interim report. Eastern Cape Nature Conservation.

French D.D. 1994. Hierarchical Richness Index (HRI): a simple procedure for scoring 'richness', for use with grouped data. Biological Conservation 69: 207-212.

La Cock G.D., Palmer A.R. & Everard D.A. 1990. Re-assessment of the area and conservation status of Subtropical Transitional Thicket (Valley Bushveld) in the eastern Cape, South Africa. South African Journal of Photogrammetry, Remote Sensing and Cartography 15: 231-235.

Lober D.J. (1992). Using forest guards to protect a biological reserve in Costa Rica: one step towards linking parks to people. Journal of Environmental Planning and Management 35: 17-41.

Marks S. A. 1994. Local hunters and wilflife surveys: a design to enhance participation. African Journal of Ecology 32:233-254

Martin G.J. 1995. Ethnobotany: a methods manual. Chapman & Hall, London.

Phillips O., Gentry A.H., Reynel C., Wilkin P. & Galvéz-Durand C. 1994. Quantitative ethnobotany and Amazonian conservation. Conservation Biology 8: 225-248.

Pimbert M.P. & Pretty J.N. 1995. Parks, people and professionals: putting "participation" into protected area management. UNRISD, IIED and WWF discussion paper DP 57, UNRISD, Switzerland.

Selin S. & Chavez D. 1995. Developing a collaborative model for environmental planning and management. Environmental Management 19: 189-195.

Shackleton C.M. (1993). Fuelwood harvesting and sustainable utilisation in a communal grazing land and protected area in the Eastern Transvaal lowveld. Biological Conservation 63: 247-254.

Shah M. 1995. Participatory monitoring: some reflections. Paper presented at the ODA Social Development Colloquium, London, December 1995.

Sorenson T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity in species content. Biol. Skr. K. Danske Vidensk. Selsk. 5: 1-34.

Wells M. & Brandon K. 1992. People and parks - linking protected area management with local communities. World Bank, WWF, USAID Washington.

Whittaker R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

APPENDIX 3.

Checklist of weevils (Curculionidae) collected from the Great Fish River Nature Reserve, the commercial farms Bucklands and Hermanuskraal, and Ndwayana in the communal area

The following weevil identifications were supplied by Dr. Rolf Oberprieler of the Plant Protection Research Unit at Pretoria. In most cases specimens were only identified at the genus level. In total 40 different taxa were distinguished, at least six of which appear to be new species, all of which occur only in the nature reserve. Of particular taxonomic importance is a specimen of an undescribed species of the genus *Euretus* which, up until now, was regarded as a monotypic genus.

Adoxini indet.
Brachycerus cordiger
Brachycerus productus
Brachycerus sp. 1
Brachycerus sp. 2
Brachycerus sp. 3
Brachycerus sp. 4
Brachycerus sp. 5
Brachycerus sp. 6
Brachycerus sp. 7
Brachycerus sp. 8
Calodemas cf *prolixum* ?
Diaphna sp. 1
Diaphna sp. 2
Elassonyx sp. 1
Episus sp. 1
Euretus sp. nov.
Euretus aurivillii
Hipporhinus sp. 1
Hipporhinus sp. 2
Hypocolobus sp. 1
Hypocolobus sp. 2
Hypocolobus sp. 3
Ithyporina indet.
Ithyporus sp. 1
Microcerus sp. 1
Microcerus sp. 2
Neocleonus sannio
Notogronops sp. 1
Ocladius cf *obliquesetosus* ?
Ocladius sp. 1
Origenes praetor
Origenes sp. 1
Pseudocolaspis sp. 1
Pseudocolaspis sp. 2
Rhytirhinini indet.
Rhyparosomus sp. 1
Spartecerus sp. 1
Spartecerus sp. 2
Zygopini indet.

APPENDIX 4.

Checklist of arachnids collected from the Great Fish River Nature Reserve, the commercial farms Bucklands and Hermanuskraal, and Ndwayana in the communal area

The following arachnid identifications were supplied by Dr. Ansie Dippenaar of the Plant Protection Research Unit at Pretoria. In most cases specimens were only identified at the genus level. Some of the material collected may prove to be undescribed species.

ORDER: ARANEAE (Spiders)

FAMILY	**GENUS**	**SPECIES**
Agelenidae	*Benoitia*	sp. 1
Ammoxenidae	*Ammoxenus*	*kalaharicus*
Araneidae	*Araneus*	*nigroquadratus*
	Argiope	*nigrovittata*
	Larinia	sp. 1
Barychelidae	*Sipalolasma*	sp. 1
Caponiidae	*Caponia*	sp. 1
Clubionidae	*Cheiracanthium*	sp. 1
	Clubiona	sp. 1
	Clubiona	sp. 2
	Clubiona	sp. 3
Corinnidae	*Castianeira*	sp. 1
	Copa	sp. 1
	Trachelas	sp. 1
	Trachelas	sp. 2
	Unidentified genus	sp. 3
	Unidentified genus	sp. 4
Cryptothelidae	*Cryptothele*	sp. 1
Cyrtaucheniidae	*Ancylotrypa*	sp. 1
Dipluridae	*Allothele*	sp. 1
Eresidae	*Dresserus*	sp. 1
	Gandanameno	sp. 1
Gnaphosidae	*Callilepis*	sp. 1
	Megamyrmeceon	sp. 1
	Xerophaeus	sp. 1
	Unidentified genus	sp. 1
	Unidentified genus	sp. 2
	Unidentified genus	sp. 3
	Unidentified genus	sp. 4
	Unidentified genus	sp. 5

	Unidentified genus	sp. 6
Heteropodidae	*Olios*	*correvoni*
	Olios	sp. 1
	Orchestrella	sp. 1
	Palystes	sp. 1

FAMILY	**GENUS**	**SPECIES**
Lycosidae	*Pardosa*	sp. 1
	Pardosa	sp. 2
	Unidentified genus 1 (Venoniinae)	
	Unidentified genus 2 (Venoniinae)	
	Unidentified genus 3	
	Unidentified genus 4	
	Unidentified genus 5	
Migidae	*Moggridgea*	sp. 1
	Moggridgea	sp. 2
Nemesiidae	*Lepthercus*	sp. 1
Oxyopidae	*Oxyopes*	sp. 1
	Oxyopes	sp. 2
	Oxyopes	sp. 3
	Peucetia	*maculifera*
Palpimanidae	*Ikuma*	sp. 1
	Ikuma	sp. 2
	Ikuma	sp. 3
Philodromidae	*Philodromus*	*brachycephalus*
	Philodromus	sp. 1
Pholcidae	*Smeringopus*	sp. 1
	Spermaphora	sp. 1
Pisauridae	*Chiasmopes*	sp. 1
	Cispius	sp. 1
	Perenethis	sp. 1
Salticidae	*Afrobeata*	sp. 1
	Baryphas	sp. 1
	Baryphas	sp. 2
	Cembalea	sp. 1
	Cyrba	sp. 1
	Myrmarachne	sp. 1
	Myrmarachne	sp. 2
	Myrmarachne	sp. 3
	Neaethea	sp. 1
	Natta	sp. 1
	Thyene	*inflata*
	Thyene	sp. 1
	Theynula	*ogdeni*
	Unidentified genus 1	
	Unidentified genus 2	

	Unidentified genus 3	
Scytodidae	*Scytodes*	sp. 1
	Scytodes	sp. 2
	Scytodes	sp. 3

FAMILY	**GENUS**	**SPECIES**
Segestriidae	*Ariadna*	sp. 1
	Ariadna	sp. 2
Selenopidae	*Anyphops*	*minutus*
Sicariidae	*Loxosceles*	sp. 1
Theraphosidae	*Harpactirella*	sp. 1
	Harpactira	sp. 1
Theridiidae	*Latrodectus*	*geometricus*
	Steatoda	sp. 1
	Steatoda	sp. 2
	Unidentified genus 1	
Thomisidae	*Oxyptila*	sp. 1
	Oxyptila	sp. 2
	Simorcus	*capensis*
	Stiphropus	sp. 1
	Suemus	sp. 1
Trochanteriidae	*Platyoides*	sp. 1
Zodariidae	*Cydrela*	sp. 1
	Diores	sp. 1
	Ranops	sp. 1
	Thaumastochilus	sp. 1
	Unidentified genus 1	
	Unidentified genus 2	

ORDER: AMBLYPYGI

FAMILY	**GENUS**	**SPECIES**
Tarantulidae	*Damon*	*variegatus*
	Phrynichus	sp. 1

ORDER: SOLIFUGAE (Sunspiders)

FAMILY	**GENUS**	**SPECIES**
Ceromidae	Unidentified genus	sp. 1
Melanoblossiidae	Unidentified genus	sp. 1
Solpugidae	Unidentified genus	sp. 1
	Unidentified genus	sp. 2
	Unidentified genus	sp. 3

ORDER: OPILIONES (Harvestmen)
Suborder Liniatores sp. 1
Suborder Palpatores sp. 1
Suborder Palpatores sp. 2

ORDER: SCORPIONES (Scorpions)

FAMILY	**GENUS**	**SPECIES**
Buthidae	*Lychas*	sp. 1
	Parabuthus	sp. 1
Scorpionidae	*Opistophthalmus*	sp. 1

ORDER: PSEUDOSCORPIONES (Pseudoscorpions)
Unidentified genus

APPENDIX 5.

Coordinates of plots for landscape diversity indexes. NR1-3 = nature reserve, CF1&2 = commercial farm, CGA = communal grazing area. E = degrees longitude, S = degrees latitude. Figures are expressed as ddmmss where d=degrees, m=minutes and s=seconds

NR1		CF1		NR2		CF2		NR3		CGA[1]	
S	E	S	E	S	E	S	E	S	E	S	E
330845	263942	330852	263937	330739	264277	330733	264271	330654	264807	330818	265521
330847	263940	330848	263932	330739	264276	330735	264275	330654	264811	330818	265523
330848	263938	330848	263932	330741	264275	330736	264275	330654	264815	330818	265526
330848	263938	330848	263933	330739	264268	330736	264277	330654	264819	330818	265529
330847	263935	330847	263930	330742	264272	330736	264270	330654	264823	330818	265532
330847	263937	330850	263933	330742	264276	330736	264269	330657	264807	330821	265521
330845	263937	330850	263932	330739	264271	330735	264278	330657	264811	330821	265523
330847	263940	330850	263932	330738	264275	330736	264280	330657	264815	330821	265526
330850	263938	330850	263933	330744	264279	330735	264277	330657	264819	330821	265529
330845	263935	330850	263933	330743	264276	330734	264274	330657	264823	330821	265532
				330745	264277	330734	264273				
330843	263935	330847	263930	330745	264276	330736	264272	330210	265753	330212	265756
330840	263933	330843	263928					330212	265753	330214	265756
330838	263935	330843	263928	330717	264280	330734	264281	330215	265753	330216	265756
330838	263933	330845	263928	330724	264278	330737	264284	330217	265751	330219	265754
330835	263932	330845	263928	330746	264262	330737	264279	330220	265751	330221	265754
330835	263935	330843	263927	330746	264261	330733	264277	330223	265751	330224	265754
330835	263935	330845	263927	330747	264264	330732	264274	330226	265749	330227	265753
330833	263935	330845	263925	330742	264284	330733	264280	330229	265749	330229	265753
330835	263937	330845	263927	330739	264284	330734	264282	330232	265749	330232	265753
330838	263935	330845	263930	330737	264286	330734	264281	330234	265749	330234	265753
				330738	264288	330733	264279				
330838	263937	330845	263928	330739	264287	330730	264273	330338	265736	330341	265739
330839	263941	330843	263928	330740	264286	330730	264271	330341	265735	330344	265738
330837	263937	330842	263928	330742	264283	330732	264274	330345	265733	330346	265737
330841	263933	330838	263927					330347	265731	330349	265736
330840	263934	330843	263920	330718	264297	330733	264286	330350	265730	330351	265735
330840	263935	330843	263927	330719	264296	330731	264283	330353	265729	330354	265734
330840	263939	330843	263928	330717	264295	330732	264283	330355	265728	330357	265733
330844	263936	330849	263931	330707	264281	330734	264283	330358	265727	330400	265731
330841	263941	330851	263935	330707	264282	330734	264282	330401	265726	330402	265729
330845	263941	330846	263930	330709	264283	330733	264283	330404	265725	330404	265727
330842	263939	330849	263926	330707	264286	330732	264284				
330839	263938	330850	263928	330707	264290	330731	264285	335656	264612	335656	264613
				330713	264295	330729	264283	335658	264613	335658	264613
330835	263930	330843	263926	330714	264296	330729	264280	335701	264613	335701	264615
330836	263930	330840	263925	330715	264292	330730	264281	335703	264615	335703	264617
330836	263927	330839	263929	330715	264295	330732	264280	335705	264617	335704	264619
330837	263926	330839	263925					335707	264618	335706	264619

---

[1] This column is incomplete. Dr. A.R. Palmer, Agricultural Research Council, Range & Forage Institute, Grahamstown is in posession of a more extensive list of coordinates for the CGA [C. Fabricius, 13 October 1997].

330834	263925	330842	263924	330723	264291	330726	264292	335709	264620	335708	264621
330834	263926	330846	263926	330722	264292	330729	264287	335712	264622	335711	264623
330836	263926	330844	263928	330724	264289	330728	264284	335715	264622	335714	264625
330835	263929	330843	263927	330725	264290	330736	264290	335717	264623	335716	264627
330837	263932	330843	263926	330728	264290	330730	264285				
330837	263931	330842	263924	330730	264291	330729	264286	335731	264832	335730	264832
330837	263927	330842	263925	330730	264292	330728	264288	335731	264835	335730	264835
330836	263931	330842	263924	330728	264294	330726	264289	335733	264838	335732	264837
				330731	264302	330721	264289	335733	264841	335732	264840
330833	263930	330838	263925	330731	264293	330727	264288	335733	264844	335735	264843
330830	263925	330839	263923	330733	264291	330726	264287	335736	264847	335735	264845
330834	263929	330834	263922	330735	264288	330733	264286	335736	264851	335735	264848
330835	263929	330835	263923					335736	264855	335737	264852
330831	263928	330838	263919	330729	264293	330730	264291	335738	264859	335737	264855
330830	263926	330833	263922	330729	264294	330728	264292	335738	264901	335737	264859
330838	263931	330837	263921	330728	264291	330727	264291				
330836	263930	330838	263924	330732	264291	330732	264289				
330831	263928	330837	263923	330730	264292	330730	264289				
330833	263929	330833	263922	330727	264293	330731	264289				
330831	263927	330837	263921	330726	264295	330729	264292				
330828	263925	330838	263920	330724	264298	330724	264294				
				330726	264299	330723	264292				
330826	263921	330832	263922	330728	264297	330728	264291				
330830	263924	330831	263920	330729	264296	330725	264291				
330827	263921	330830	263921	330728	264300	330726	264290				
330824	263921	330828	263918								
330827	263923	330833	263915	330732	264307	330721	264295				
330826	263925	330828	263922	330731	264208	330722	264295				
330829	263928	330837	263922	330727	264299	330721	264298				
330826	263931	330837	263924	330734	264303	330719	264304				
330830	263934	330837	263923	330734	264302	330718	264204				
330826	263926	330832	263919	330738	264202	330724	264200				
330824	263924	330836	263920	330736	264204	330721	264297				
330824	263924	330833	263916	330733	264203	330722	264299				
				330731	264203	330722	264297				
330821	263924	330833	263914	330731	264204	330719	264298				
330821	263923	330829	263918	330726	264300	330722	264299				
330824	263920	330827	263918	330726	264299	330722	264302				
330823	263919	330827	263920								
330821	263921	330825	263922	330722	264299	330717	264299				
330821	263922	330828	263925	330723	264301	330715	264300				
330825	263921	330828	263919	330728	264304	330716	264302				
330826	263922	330830	263919	330725	264204	330714	264203				
330825	263925	330828	263915	330725	264203	330713	264201				
330823	263924	330829	263916	330724	264202	330715	264201				
330819	263923	330829	263915	330727	264208	330716	264200				
330820	263920	330827	263914	330731	264208	330715	264297				
				330724	264210	330724	264303				
330824	263925	330829	263918	330722	264209	330721	264297				
330825	263921	330827	263915	330724	264211	330719	264295				
330824	263921	330828	263915	330721	264210	330725	264292				
330822	263918	330826	263916								
330820	263918	330827	263914	330719	264304	330721	264302				
330822	263921	330828	263914	330718	264205	330719	264201				
330823	263924	330828	263915	330716	264206	330720	264204				

330822 263922	330829 263917	330715 264207	330719 264209		
330821 263922	330828 263918	330716 264208	330716 264298		
330818 263921	330830 263914	330716 264207	330721 264302		
330819 263923	330830 263911	330717 264207	330721 264299		
330820 263925	330829 263912	330718 264206	330719 264298		
		330719 264204	330720 264299		
330825 263921	330823 263913	330715 264204	330717 264295		
330821 263917	330820 263914	330715 264208	330717 264296		
330820 263918	330822 263911	330718 264208	330717 264298		
330819 263917	330818 263912				
330823 263920	330819 263912	330713 264305	330718 264304		
330822 263921	330822 263913	330715 264207	330715 264210		
330819 263921	330824 263912	330711 264208	330715 264206		
330824 263925	330822 263912	330709 264211	330713 264211		
330824 263923	330821 263912	330711 264208	330709 264217		
330822 263923	330822 263912	330714 264211	330707 264204		
330819 263920	330821 263911	330713 264208	330706 264203		
330817 263920	330819 263911	330718 264214	330709 264206		
		330720 264216	330712 264209		
330821 263919	330812 263908	330718 264216	330709 264207		
330818 263915	330817 263910	330716 264215	330710 264207		
330812 263914	330817 263909	330715 264215	330708 264210		
330814 263914	330817 263905				
330813 263915	330816 263907	330719 264313	330807 264308		
330812 263914	330818 263908	330714 264217	330709 264213		
330816 263917	330818 263907	330708 264212	330706 264211		
330817 263917	330819 263910	330709 264215	330709 264215		
330814 263919	330823 263910	330713 264218	330704 264214		
330817 263919	330820 263903	330717 264213	330706 264211		
330812 263914	330823 263907	330716 264218	330708 264209		
330814 263915	330823 263911	330716 264213	330711 264215		
		330717 264213	330713 264213		
		330719 264217	330709 264211		
		330712 264216	330712 264212		
		330707 264219	330705 264212		