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Comparison of plant diversity in protected and communal lands in the Bushbuckridge lowveld savanna, South Africa

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Abstract

Patterns of higher plant species richness and beta diversity were assessed using standard Modified-Whittaker plots in relation to landuse, slope position and mean annual rainfall across a rainfall gradient in the savanna areas of the Bushbuckridge lowveld, South Africa. In particular, comparison of communal areas with adjacent protected areas was important in showing the impacts of potential changes in landuse within an overarching catchment management plan. Although most of the protected areas considered preservation of biodiversity as their primary goal, they were characterised by significantly fewer plant species than the adjacent, highly utilised, communal lands, at both the plot and point scale. Slope position also had a significant effect on plant species richness, with eutrophic bottomlands having c. 30% more species than the dystrophic toplands. This adds weight to the need for greater public awareness for the judicious use and management of the sensitive bottomlands, which fringe the primary drainage lines that are vital for sustained supplies of good quality surface water in this semi-arid environment. The total number of species increased with increasing mean annual rainfall across the rainfall gradient. This suggests that, if the catchment management plan aims to identify additional areas for conservation, the higher rainfall areas should be the first to be assessed. Species turnover was greater along the rainfall gradient than the catenal gradient between toplands and bottomlands. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

In the past two decades the conservation of biodiversity has received ever-increasing expert and lay attention (Noss, 1983; Holdgate, 1996). It has been identified as one of the key indices of sustainable landuse practices, and considerable resources are expended to identify and implement strategies that will reverse the current declines in biodiversity at local, regional and international scales. Most nations are signatories to the 1993 International Convention on Biological Diversity (McNeely, 1995).

One key strategy is the declaration and maintenance of a network of protected areas, albeit recent focus has also shifted to conservation of biodiversity outside conservation areas, especially in agro-ecosystems (Scoones et al., 1992; Halladay and Gilmour, 1995). Protected areas frequently serve to insulate biodiversity from the impacts of human development (e.g. Rai and Sundriyal, 1997), although recent trends are for increasing access to and use of selected resources in protected areas (Wells, 1996; Brown, 1997). Most protected areas in South Africa, as elsewhere in the world, cite (explicitly or implicitly) the preservation of biodiversity as one of the primary reasons for their existence. Yet, by 1989 less than 5% had complete inventories of all groups of fauna and flora within their boundaries, and over 50% had no checklists whatsoever for any group (Siegfried, 1989).

Protected areas are usually surrounded by other landuses and habitats that have been modified by human use to a greater or lesser extent. Nevertheless, often there are strong links (ecological, economic, cultural) between protected areas and adjacent communities which offer constraints and opportunities to both parties (e.g. Wells, 1996; Shyamsundar and Kramer, 1997). It is perceived that the human impacts external to protected areas have inevitably led to a decrease in biodiversity relative to the nearby protected areas,

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although many agro-ecosystems are extremely rich in species (e.g. Alverez-Buylla Roces et al., 1989). Such losses of biodiversity are now also entering the realm of resource economics, with national budgets attempting to account for the costs of biodiversity loss, and the intrinsic value of maintaining genetic biodiversity of currently useful and un-used species (Ehrenfeld, 1988; Aylward, 1991; Adger et al., 1994; Edwards and Abivardi, 1998). These debates contribute to national polices on landuse options and practices.

Despite this concern with biodiversity, there are relatively few studies in southern Africa savannas that have attempted to quantify (i) patterns of alpha and beta diversity, and (ii) the relative decline between protected and adjacent non-protected areas, which would provide a measure of the success or failure of protected areas as one strategy to help prevent the decline of biodiversity worldwide. This is compounded by a lack of standard methodologies and little insight into local-scale patterns of diversity and its determinants, especially in sub-tropical woodlands. Consequently, biodiversity estimates have focussed primarily on estimates of species richness. The majority of these have been compiled from species inventories for entire protected areas, rather than a deliberate strategy to quantify alpha and beta diversity through a systematic and replicated approach, along with potential predictor correlates. Beta diversity has not been assessed in South African savannas (Cowling et al., 1989).

Against this background, a government project was initiated to compile an integrated catchment management plan for the Sand River catchment (South Africa). The catalyst for this was the perceived poor status of the catchment due to poor plantation forestry practices in the upper catchment, and high-density, rural, communal areas boarding on a number of protected areas in the lower catchment. Various assessments (economic, social, ecological) of the different land uses within the catchment were, or remain to be, undertaken (Pollard et al., 1998). Assessment of the patterns of species richness was considered important as it would be one criterion, amongst several, by which the relative sustainability of competing landuses could be assessed. This paper reports on the findings of the assessment with respect to patterns of alpha and beta diversity (i) within the catchment as a whole, (ii) correlation with selected abiotic and biotic variables, and (iii) a comparison between protected and communal areas.

2. Study area

The Bushbuckridge region (c. 2600 km^2) is in the southernmost section of the Northern Province (South Africa), bordering onto the Mpumalanga Province. It is characterised by a west to east gradient in topography, climate, and former political boundaries, which have resulted in several distinct landuse zones. Against the Drakensberg escarpment in the west, the mean annual rainfall (MAR) is c. 1 200 mm, decreasing to 550 mm in the east across a linear distance of 100 km. Mean annual temperature is 22°C, and frost is rare. Except immediately adjacent to the Drakensberg escarpment, the terrain is flat to undulating, being underlain by potassic granites and grandiorite. The most extensive soil types are shallow sandy lithosols, except towards the base of the catena where deeper duplex soils are common. Closer to the escarpment, deep, apedal soils prevail. Paralleling the rainfall gradient, two broad vegetation types are evident; Lowveld Sour Bushveld in the wetter west, grading into Lowveld towards the east (Acocks, 1988). The tree stratum is dominated by members of the Combretaceae (*Terminalia sericea*, *Combretum collinum*, *C. hereroense*, *C. zeyheri* and *C. apiculatum*) and Mimosaceae (*Acacia nilotica*, *A. gerrardii*, *A. ataxacantha*, *A. caffra*, *A. sieberana*, *Albizia harveyi*, *Albizia versicolor* and *Dichrostachys cinerea*), although local dominance varies considerably.

The primary landuse in the wetter west, on the foothills of the Drakensberg escarpment, is commercial forestry. This comprises plantations of exotic species, namely *Eucalyptus* and *Pinus*.

The central portion is characterised by relatively high-density, underdeveloped rural villages. It formed part of the Lebowa and Gazankulu homelands under the former apartheid dispensation. The current population density is c. 146 persons per km^2 in the drier east and 303 persons per km^2 in the wetter west. Approximately 60–70% of the potentially economically active population are unemployed. Nearly all households cultivate small areas around the homestead during the rainy season, and 30–40% of households also cultivate demarcated arable fields on the periphery of the village or further afield. Shortage of land prevents more households working an arable plot. The rest of the land is zoned as communal grazing areas. Most households harvest several different kinds of resources from these communal lands, including fruits, thatch grass, fuelwood, mushrooms, reeds and construction wood (Shackleton and Shackleton, 2000). Fuelwood is the primary energy source of >85% of households (Banks et al., 1996), although a considerable mix of other fuel sources is used. Approximately one-third of households possess cattle. The stocking rate is close to ecological carrying capacity at 0.88 ± 0.09 livestock units (LSU) per ha (Parsons et al., 1997). This is >400% of the 'recommended' stocking rate, but the species composition appears resilient (Harrison and Shackleton, 1999). The communal areas are burnt whenever there is sufficient minimum fuel-load, but fire intensities are very low because of the low fuel-loads resulting from the high grazing pressure.

The driest, easternmost section of the region is under conservation in a number of declared state and private protected areas. All have been managed as protected areas for several decades. The primary management objective is preservation of biodiversity, and in the case of the private reserves, income generation. In all instances, the primary source of income is tourism, based mainly on viewing animal species in the wild. Stocking rates with indigenous herbivores vary between reserves, but Parsons et al. (1997) reported a mean for three reserves as 0.33 LSUs per ha. Controlled burning is prescribed in some of the reserves when an adequate fuel-load is apparent. Others simply allow natural (lightning-induced) fires to occur. Currently, none of the protected areas allow significant harvesting of natural resources by neighbouring local communities, although some initiatives are in the planning stages. Most allow some harvesting of thatch grass, reeds, and timber in the construction of buildings within the protected area, and allow limited collection of fuelwood for use by staff and guests.

The Sand River catchment falls entirely within the Bushbuckridge region, but not all the sample sites for this work were within the Sand River catchment.

3. Methods

A two-phase approach was adopted. The first was to characterise the plant species richness across the Sand River catchment, and the second was to test for differences in plant species richness between the two dominant landuses in the region, namely between protected and communal areas.

3.1. *Plant species richness across the Sand River catchment*

During December 1997, two transects were laid out from the foothills of the Drakensberg mountains into Sabi-Sand Game Reserve in the east (diamonds in Fig. 1). This was done several weeks after the first rains of the season, thereby maximising the potential for the detection of annual species. Six locations were identified for sampling at approximately regular intervals along each transect (Fig. 1). At each locality two standard (1000 m^2) Modified-Whittaker plots (Stohlgren et al., 1995) were sited, one at the base of the catena (a regular sequence of soils in relation to topographic position along a slope) (bottomland) and one at the crest (topland), since, in this region, it is well established that toplands and bottomlands are characterised by different plant communities (Fraser et al., 1987; Witkowski and O'Connor, 1996). Thus, there were 12 locations, each with two plots, providing 24 plots in total. The three western-most locations in each transect were in communal lands, the eastern-most localities were in Sabi-Sand Game Reserve, and the ones at the boundary of this reserve (triangles in Fig. 1) had one pair in the reserve and one pair in the adjacent communal land. Given that plant species richness may vary with changes in disturbance related to proximity to human settlement (Shackleton et al., 1994), each location in the communal areas was situated between 0.5 and 1.0 km from the periphery of a village. All of the communal land sites demonstrated some signs of disturbance, such as the canopy being shorter and more open, cut stumps, coppice growth from cut stumps, reduced density of large stems, and the like.

Modified-Whittaker plots quantify species richness at four scales within each 1000 m^2 plot, viz. 1 m^2 (10 replicate quadrats, each 0.5×2.0 m), 10 m^2 (2 replicates, both 2×5 m), 100 m^2 (1 replicate, 5×20 m) and 1000 m^2 (the entire 20×50 m plot). Only the largest (1000 m^2) and the smallest (1 m^2) are discussed in detail. At each scale, species present were classified in the field into a number of functional groups. The grass species present were classified into three categories: tufted perennials, stoloniferous perennials, and annuals, and the percentage contribution of each class to the total for each landuse was determined. The same was done for forb species, by classifying them as perennial legumes, perennial non-legumes, annuals, and geophytes. Woody species were assigned to one of four classes, namely spinescent legumes, non-spinescent legumes, spinescent non-legumes and non-spinescent non-legumes. Additional measurements included grass height, and visual estimates of the percentage herbaceous aerial cover, litter cover and bare ground in each of the ten 1 m^2 quadrats per plot. For the plot as a whole, the percentage woody plant aerial cover was visually estimated, and the number of shrubs (<1.5 m tall) and trees ($>1.5.$ m tall) were counted.

Species richness was not assessed in any of the high impact landuses in the catchment, namely plantation forestry and arable farming plots (dry land or irrigated). It was readily apparent that these landuses have severe negative impacts on local species richness of indigenous species, albeit pockets of relatively undisturbed vegetation may be found interspersed throughout areas of intensive landuse.

3.2. *Comparison of protected and communal areas*

During February 1998, an additional five localities were sampled (triangles in Fig. 1), using paired Modified-Whittaker plots as above. At each locality, two plots (one topland and one bottomland) were sited in a protected area, within 0.75 km of a fence separating it from a communal area. Another two plots (one topland and one bottomland) were then sited in the communal area, also within 0.75 km of the fence separating it from

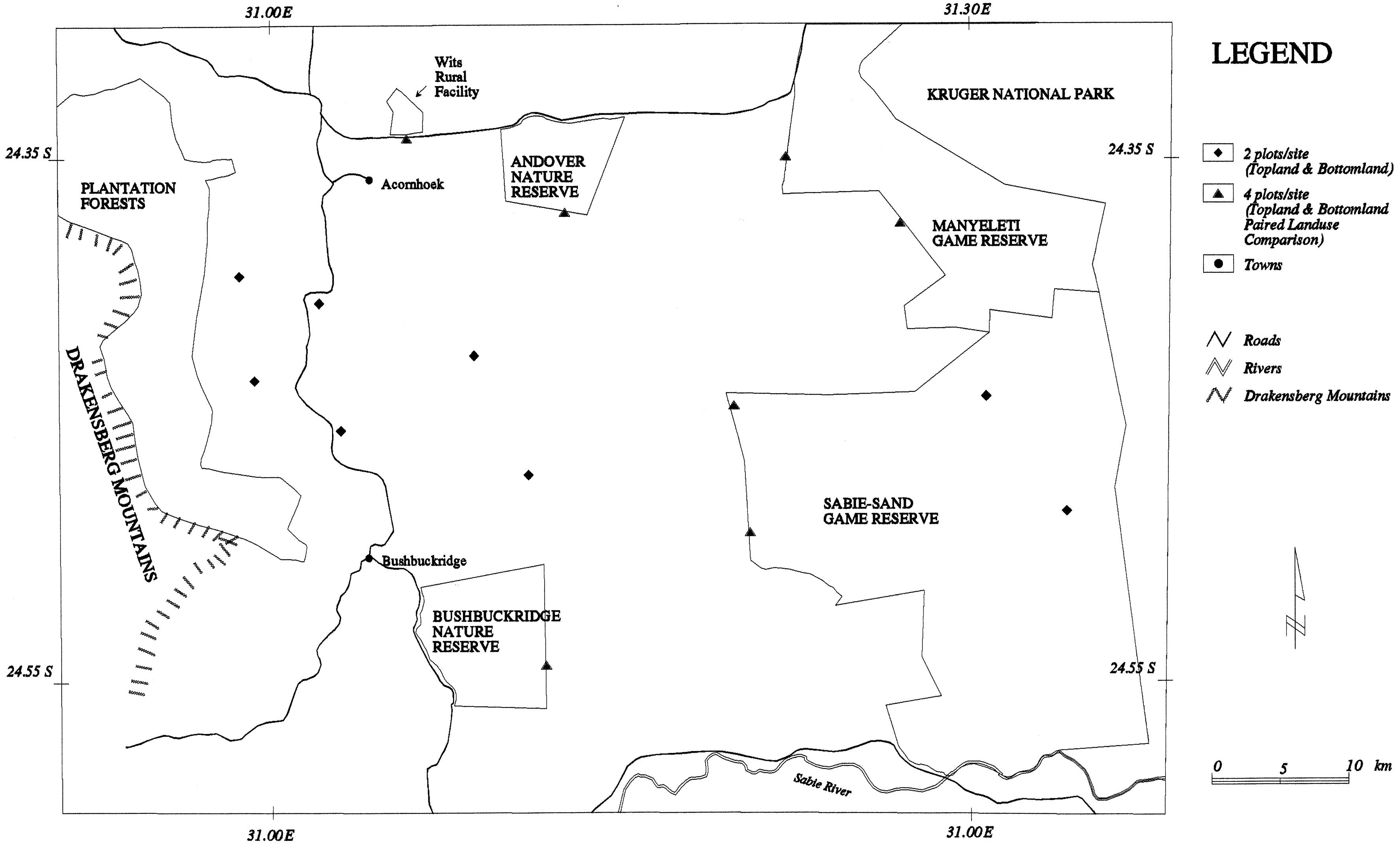

Fig. 1. Study area and location of sample sites.

the protected area. Thus, there were four plots at each locality, giving 20 plots in total, or 10 pairs spanning the landuse change. The protected areas sampled included Bushbuckridge Nature Reserve, Manyeleti Game Reserve, Andover Nature Reserve and Wits Rural Facility (Fig. 1). Two localities (triangles spanning the fence of Sabi-Sand Game Reserve fence in Fig. 1) in phase one of the study conformed to the same design, so the total sample size for the landuse comparison via paired plots was 14 (seven topland and seven bottomland). As with phase one sites, all the communal sites exhibited some degree of disturbance.

3.3. Data analysis

The contribution of each functional group to the total species richness was examined between landuses, catenal position and the rainfall gradient. The proportion of woody species with edible fruits was also assessed relative to landuse and rainfall gradient

Since individual species abundances were not measured, differences in the frequency of occurrence for woody species were assessed as the number of occurrences in plots in the protected area minus the number of occurrences in plots in the communal area. A positive or negative difference of two or more was used to identify species that were encountered more frequently in one landuse or the other, and those species for which frequency of occurrence was relatively independent of landuse.

Species turnover along the two primary gradients (beta diversity), namely the catenal gradient and the rainfall gradient, was calculated using the equation of Wilson and Shmida (1984), as:

$$\beta = (H_g + H_l) \div 2S$$

where H_g is the number of species gained along the gradient; H_l is the number of species lost along the gradient; and S is the mean sample species richness.

Data were tested for normality. Mean annual rainfall was found to have a skewed distribution, which was improved after transformation using the natural log. Since top and bottom plots were paired, a paired *t*-test was used for statistical comparison. Effects of landuse were also assessed via a paired *t*-test. The relationship between species richness and rainfall was determined through linear regression, with subsequent analysis of standardised residuals and examination for outliers.

4. Results

4.1. Alpha diversity (species richness)

4.1.1. Vegetation structure

The higher disturbance of communal lands was reflected in the structural attributes of the herbaceous layer (Table 1). The communal lands had significantly lower herbaceous cover ($P<0.005$), litter cover ($P<0.05$), and herbaceous height ($P<0.0001$). The lower herbaceous and litter covers, resulted in a higher proportion of bare ground in communal areas ($P<0.01$). There was no significant difference in the woody cover per plot between the two landuses.

4.1.2. Total species richness

Communal areas had a statistically significantly ($P<0.05$) higher plant species richness at the 1000 m^2 scale than adjacent protected areas, with c. 11% more species (Table 2). For all life-form groups, the communal areas had a higher species richness than the conservation areas, but this was only significant for grass species richness ($P<0.05$). At the point scale (1 m^2), the communal areas had c. 17% more species, which was a significant difference ($P<0.01$). As at the 1000 m^2 scale, there were more species of all life-forms in the communal areas relative to protected areas, although this was not significant.

4.1.3. Functional groups of species

The percentage contributions of annual and stoloniferous grass species were higher in communal areas relative to protected areas, albeit not significant statistically (Table 3). The protected areas had a greater proportion of tufted perennials.

The percentage of annual forbs was significantly greater in protected areas relative to communal areas

Table 1
Structural characteristics of the vegetation under two landuses (mean ± S.E.)[a]

	Landuse		
Attribute	Protected areas	Communal areas	Significance
Height of herbaceous layer (cm)	48.9 ± 2.82	22.6 ± 3.60	$T=10.61$; $P<0.001$
Herbaceous cover (%)	48.6 ± 1.99	38.0 ± 2.87	$T=3.44$; $P<0.005$
Litter cover (%)	20.7 ± 1.56	14.7 ± 1.66	$T=2.44$; $P<0.05$
Bare ground (%)	30.9 ± 2.70	47.5 ± 2.98	$T=3.35$; $P<0.01$
Woody cover (%)	42.6 ± 6.02	37.1 ± 4.16	$T=0.80$; $P>0.05$

[a] $n=14$ paired plots; plot size = ten 1 m^2 quadrats for herbaceous layer, and one 1000 m^2 plot for woody cover.

($P < 0.05$) (Table 4). There were no significant differences between the two landuses with respect to the percentage contribution of legumes and geophytes.

There were no differences in the different functional groups of woody species between the two landuses (Table 5), and the species composition between landuses was relatively similar. Of the 100 woody species recorded, 10 species were encountered more frequently in protected areas than communal areas (Table 6). It was a mixed group in terms of functional affinities, and included shrubs, dominant and rarer species, as well as leguminous and non-leguminous trees. However, all except *Cissus* sp. were also encountered in communal lands, albeit less frequently. At the opposite end of the spectrum, 21 species were encountered more frequently in communal lands than protected areas. Of these, five were encountered solely in the communal lands during this survey, but I have recorded them in protected areas also during the course of other studies in the region. Thus, they are not exclusive to communal lands, but from these data it can be inferred that there is an apparent change in abundance as indexed through frequency. This group also included trees and shrubs, dominant and rarer species. One species, *Lantana camara*, is an alien invasive, but whilst more frequent in the communal lands, it was also encountered in the protected areas. There was relatively little or no change in frequency for the majority of woody species between the two landuses.

Table 2
Comparison of plant species richness between protected and adjacent communal areas[a]

Sample scale	No. of species	Conservation areas	Communal areas	Significance
1000 m^2	Woody species	24.9 (2.58)	26.1 (2.86)	$T = 1.15$; N.S.[b]
	Grasses	13.4 (0.45)	14.5 (0.48)	$T = 2.81$; *
	Forbs	28.5 (2.36)	32.6 (2.72)	$T = 1.86$; N.S.
	All species	68.3 (4.66)	76.1 (5.13)	$T = 2.18$; *
1 m^2	Woody species	0.7 (0.09)	0.8 (0.12)	$T = 0.12$; N.S.
	Grasses	3.6 (0.16)	4.1 (0.19)	$T = 1.87$; N.S.
	Forbs	2.2 (0.29)	2.8 (0.34)	$T = 1.78$; N.S.
	All species	6.8 (0.38)	8.0 (0.63)	$T = 3.29$; **

[a] Mean ± S.E.; $n = 14$ paired plots.
[b] N.S., $P > 0.05$; *$P < 0.05$; **$P < 0.01$.

Table 3
The percentage contribution of functional grass types for paired protected and communal plots ($n = 14$)

	Tufted perennials		Stoloniferous perennials		Annuals	
	Protected	Communal	Protected	Communal	Protected	Communal
Mean (%)	90.5	87.6	3.3	4.6	6.2	7.8
S.E.	1.46	1.23	1.07	1.30	0.96	0.48
Minimum (%)	82.4	75.0	0	0	0	5.9
Maximum (%)	100.0	92.9	10.0	16.7	11.8	11.8
Median (%)	91.7	87.9	0	6.1	7.4	7.7
Significance	$T = 1.54$; N.S.[a]		$T = 1.02$; N.S.		$T = 1.32$; N.S.	

[a] N.S., $P > 0.05$.

Table 4
The percentage contribution of functional forbs types for paired protected and communal plots ($n = 14$)

	Perennial legumes		Annuals		Geophytes	
	Protected	Communal	Protected	Communal	Protected	Communal
Mean (%)	12.9	14.1	7.7	3.7	7.7	6.7
S.E.	2.45	1.37	1.70	0.74	1.42	0.94
Minimum (%)	3.9	7.3	0	0	0	0
Maximum (%)	33.0	24.0	21.1	8.0	15.8	12.5
Median (%)	12.0	13.5	5.8	3.2	6.2	6.3
Significance	$T = 0.58$; N.S.[a]		$T = 2.57$; *		$T = 0.62$; N.S.	

[a] N.S., $P > 0.05$; *, $P < 0.05$.

Table 5
The percentage contribution (mean ± S.E.)of functional types of woody species for paired protected and communal plots ($n = 14$)

Functional group	Conservation areas	Communal areas	Significance
Legumes			
Spiny	17.2 ± 2.75	15.7 ± 2.54	T = 0.76; N.S.[a]
Not spiny	17.4 ± 1.33	15.0 ± 1.26	T = 1.92; N.S.
Combined	34.6 ± 3.20	30.6 ± 3.12	T = 1.36; N.S.
Non-legumes			
Spiny	14.8 ± 1.45	17.2 ± 1.48	T = 1.48; N.S.
Not spiny	50.6 ± 3.27	52.2 ± 2.39	T = 0.53; N.S.
Combined	65.4 ± 2.61	69.4 ± 2.91	T = 0.98; N.S.
Spinescent (legumes and non-legumes)	32.0 ± 2.79	32.9 ± 1.97	T = 0.45; N.S.
Species with edible fruits	34.7 ± 2.38	34.3 ± 2.54	T = 0.13; N.S.

[a] N.S., $P > 0.05$.

4.1.4. The effect of slope position

At the plot scale (1000 m^2), bottomlands had significantly ($P < 0.05$) more species than toplands, largely as a result of the greater number of woody species (Table 7). On average, there were 30% more woody species in bottomlands than toplands. There was no difference in species richness between toplands and bottomlands at the point scale (Table 7).

4.1.5. The effect of the rainfall gradient

There was a strong relationship between mean annual rainfall (mm) and species richness at the 1000 m^2 scale, summarised as:

$$\text{No. of species}/1000\,\text{m}^2 = 80.03^*\ln(\text{MAR}) - 453.6$$
$$(r^2 = 0.56;\ P < 0.00001;\ n = 44)$$

However, this relationship included four sites that were identified as outliers. Omission of those points provided a relationship in the form:

$$\text{No. of species}/1000\,\text{m}^2 = 80.09^*\ln(\text{MAR}) - 455.57$$
$$(r^2 = 0.67;\ P < 0.00001;\ n = 40)$$

At the point scale the following significant relationship was evident:

$$\text{No. of species}/1\,\text{m}^2 = 8.33^*\ln(\text{MAR}) - 47.12$$
$$(r^2 = 0.37;\ P < 0.00001;\ n = 44).$$

Adjustment for three significant outliers resulted in a relationship of:

$$\text{No. of species}/1\,\text{m}^2 = 8.49^*\ln(\text{MAR}) - 48.47$$
$$(r^2 = 0.49;\ P < 0.0001;\ n = 41).$$

4.1.6. Correlations between plant species richness and vegetation structure

The total number of species was weakly, but significantly, related to the estimated aerial cover of woody plants in the plot ($r^2 = 0.25$; $n = 44$; $P < 0.001$), summarised in the form:

$$\text{Total no. of species}/1000\,\text{m}^2$$
$$= 0.432\,(\%\ \text{aerial cover}) + 58.19$$

There was no relationship between woody plant density and the total number of species per 1000 m^2 plot.

The number of woody species only per plot was correlated with aerial cover of the plot ($r^2 = 0.24$; $n = 44$; $P < 0.001$) in the form:

$$\text{No. of woody species}/1000\,\text{m}^2$$
$$= 0.178\,(\%\ \text{aerial cover}) + 18.44$$

At the point scale, the number of species was not related to attributes of vegetation structure of the plot, such as proportion of aerial cover, shrub density, and the like.

4.2. Beta diversity

There was an approximately 40% turnover in species along the catenal gradient from toplands to bottomlands (Fig. 2). There was no difference ($T = 0.63$; $d.f = 6$; $P > 0.05$) between communal and protected areas in this regard. There was a greater beta diversity associated with the rainfall gradient (Fig. 3), where there was an 85% turnover in species from one end to the other. The rate of turnover along the rainfall gradient between bottomlands and toplands was similar. The number of species recorded more than doubled with a 10-fold increase in sample area (Table 8), suggesting high beta diversity.

Table 6
Difference in frequency of occurrence of woody species in paired plots in protected and communal areas[a,b]

Difference in frequency of occurrence between paired protected areas ($n = 14$) and communal lands ($n = 14$)						
> +2	+2	+1 to −1			−2	< −2
Higher frequency of occurrence in protected areas		Approximately equal frequency of occurrence			Higher frequency of occurrence in communal lands	
Cissus sp. *Dalbergia melanoxylon* *Gardenia spatulifolia* *Grewia bicolor*	*Albizia harveyii* *Combretum apiculatum* *Dombeya rotundifolia* *Pterocarpus rotundifolius* *Rhoicissus tridentata* *Strychnos spinosa*	*Acacia burkeii* *Acacia caffra* *Acacia exuvialis* *Acacia gerrardii* *Acacia nigrescens* *Acacia nilotica* *Acacia robusta* *Acacia swazica* *Acokanthera oppositifolia* *Albizia versicolor* *Annona senegalensis* *Antidesma venosum* *Apodytes dimidiata* *Bercehmia zeyheri* *Bolosanthus speciosus* *Canthium inerme* *Clerodendrum glabrum* *Combretum collinum* *Combretum hereroense* *Combretum imberbe* *Combretum molle* *Commiphera schimperii* *Cordia ovalis*	*Crotolaria obscura* *Dichrostachys cinerea* *Diospyros mespiliformis* *Ehretia amoena* *Euclea divinorum* *Faurea saligna* *Ficus* sp. *Gardenia amoena* *Grewia flavescens* *Grewia hexamita* *Grewia monticolor* *Heteropyxis natalensis* *Hippocratea* sp. *Jasminum* sp. *Lannea discolor* *Lannea stuhlmannii* *Lippea javanica* *Lonchocarpus capassa* *Maerua caffra* *Maytenus heterophylla* *Maytenus undata* *Mundelea sericea* *Ochna* sp. *Olea europeana*	*Ormocarpum trichocarpum* *Ozoroa sphaerocarpa* *Parinari curatellifolia* *Peltaphorum africanum* *Piliostigma thonningii* *Pterocarpus angolensis* *Rhus chirendensis* *Rhus dentata* *Rhus leptodictya* *Rhus* sp. *Sclerocarya birrea* *Senna petersiana* *Strychnos madagascariensis* *Syzygium guineense* *Terminalia sericea* *Turraea nilotica* Unidentified species *Xanthocercis zambesiaca* *Xeromphis obovata* *Ximenia caffra* *Zanthoxylum capense* *Ziziphus mucronata*	*Abutilon* sp. *Canthium mundianum* *Carissa edulis* *Cassine aethiopica* *Cassine tranvaalensis* *Diospyros lyciodes* *Ehretia rigida* *Euclea natalensis* *Flacourtia indica* *Fluggaea virosa* *Grewia flava* *Lantana camara* *Maytenus polyacantha* *Maytenus senegalensis* *Pappea capensis* *Pavetta schumanniana* *Vangueria infausta*	*Aloe ferrox* *Coddia rudis* *Euclea crispa* *Schotia brachypetala*

[a] Score = frequency of species in protected plots ($n = 14$) minus frequency in communal plots ($n = 14$).

[b] Nomenclature follows Gibbs Russell et al. (1985).

5. Discussion

This study has provided replicated quantitative estimates for alpha and beta diversity within the savannas of the central lowveld, as well as established interpretative frameworks for explaining changes in diversity in relation to prevailing environmental gradients, and landuses.

Table 7
Comparison of plant species richness between paired topland and bottomland sites (irrespective of land use)[a]

Sample scale	No. of species	Toplands	Bottomlands	Significance
1000 m^2	Woody species	22.4 (1.42)	29.0 (1.99)	$T=3.05$; **
	Grasses	13.6 (0.52)	13.9 (0.53)	$T=0.44$; N.S.[b]
	Forbs	32.5 (2.82)	34.3 (2.58)	$T=0.88$; N.S.
	All species	71.3 (4.13)	80.1 (4.51)	$T=2.48$; *
1 m^2	Woody species	0.7 (0.09)	0.8 (0.07)	$T=0.88$; N.S.
	Grasses	3.8 (0.17)	3.8 (0.17)	$T=0.35$; N.S.
	Forbs	2.9 (0.39)	3.0 (0.32)	$T=0.27$; N.S.
	All species	7.9 (0.59)	8.2 (0.53)	$T=0.69$; N.S.

[a] Mean ± S.E.; 22 plots paired plots.

[b] N.S., $P>0.05$; *, $P<0.05$; **, $P<0.01$.

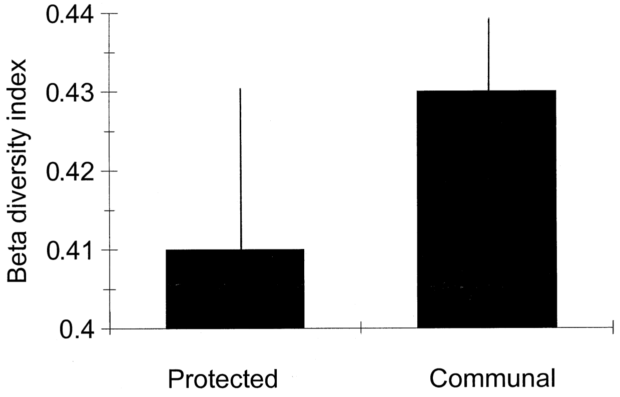

Fig. 2. Mean beta diversity along the catenal gradient in protected and communal areas.

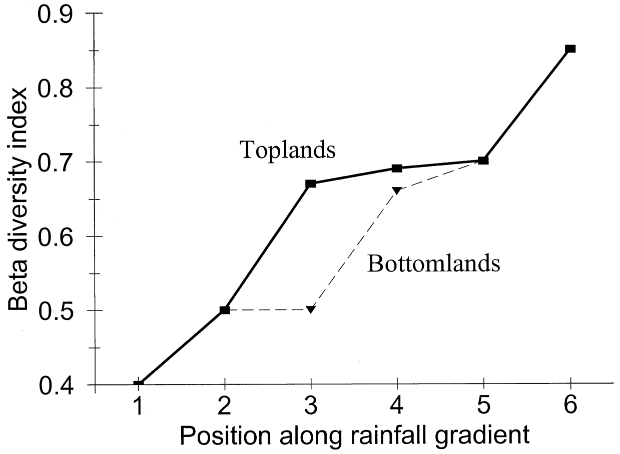

Fig. 3. Mean beta diversity along the rainfall gradient across the catchment.

It is clear from the results that the communal lands of the Bushbuckridge region, whilst having a lower vegetation structure and more bare ground, are not depauperate in species relative to adjacent protected areas, as is often presumed. Indeed, they support significantly more species than protected areas at the scale of measurement. This is not an unusual finding. In southern Africa, several studies have found a positive effect, or no effect, of greater intensity of human use in rural areas on species richness across a range of taxa relative to less impacted areas. For example, Dahlberg (1996), in comparing a communal area with an adjacent protected area in arid woodlands in Botswana, found no difference in herbaceous species richness between the two landuses. Similarly, Vermeulen (1996) reported no difference in tree species richness between a communal area and a protected state forest in central Zimbabwe, even though there was a much lower woody basal area and density in the communal area. Prendini et al. (1996) recorded a higher species richness of grasshoppers in Timbavati communal lands relative to adjacent protected areas in the Bushbuckridge lowveld. Cumming et al. (1997) found reduced species richness of trees, woodland birds, bats, ants and mantisses in protected woodland areas with high elephant densities relative to adjacent unprotected areas with higher human impacts, but lower elephant densities. In the succulent karroo of the northern Cape, South Africa, Todd et al. (1998) found no differences in species richness of plants and invertebrates between an intensely used communal land and adjacent commercial land. There was a reduction in bird species richness on the communal land.

Similar findings have been reported from elsewhere in the world and different vegetation types. For example, Pandey and Singh (1992) reported a higher herbaceous species richness in grazed savannas relative to ungrazed savannas. The same was found by Nabhan et al. (1982) in comparing a protected and a utilised area of the Sonoran Desert. Salick et al. (1995) recorded a higher plant species richness in logged forests in Nicaragua than adjacent unlogged forests. Goguen and Mathews (1998) found no change in abundance or species richness of songbirds in a heavily grazed pinyon–juniper woodland relative to adjacent ungrazed areas, and Aigner et al. (1998) reported that experimental firewood harvesting in an oak–pine woodland led to an increased

Table 8
Mean number of species (±S.E.) per area from 44 Modified-Whittaker plots

Plot size (m^2)	Mean no. of species
1	8.0 ± 0.39
10	18.2 ± 0.76
100	37.4 ± 1.66
1000	75.7 ± 3.10

abundance of ten bird species, a decrease in abundance of two species, and had no effect on 50 species.

However, other studies have indicated the opposite, i.e. disturbed sites have a reduced species richness (fauna and flora) across a range of species functional groups (e.g. Rao et al., 1990; Daniels et al., 1995; Lewis, 1997). There is a large constituency arguing that diversity is greatest at intermediate levels of disturbance (e.g. Grime, 1979; Armesto and Pickett, 1985; Huston, 1994). Clearly, there is a need for more study of the role of the intensity and duration of disturbance and its effects on species richness, particularly in savannas, rather than to simply diagnose disturbance as inevitably leading to losses of biodiversity. A uniform methodology is required.

It may be hypothesised that the higher species richness at the scale of measurement in the communal areas is a result of increased levels of disturbance by humans and livestock (as reflected in the reduced height of the woody stratum and increased proportion of bare ground), which (i) provides niches for establishment of weedy species, and (ii) increases patchiness in the environment (beta diversity) thereby providing opportunities for different functional groups of species. However, the results from this study are not consistent with either of these hypotheses. The majority of weedy species in semiarid savannas are annual forbs, although not exclusively so. In this study, the protected areas had significantly more annual forbs than the communal lands. Thus, the protected areas have a higher profile of potential weedy species than do the communal lands. The communal lands had a greater number of woody species exclusive to it (for this study) than vice versa. These exclusive species included weedy type species (e.g. *L. camara*), as well as community dominant and less abundant species.

In terms of beta diversity, there was no difference between the communal and protected areas along the primary environmental gradients present in the study area. However, I did not sample along a gradient in potential human disturbance and livestock grazing radiating out from local settlements. It is probable that this is the primary mechanism towards increased beta diversity. Shackleton et al. (1994) found that attributes of woody community structure and plot species richness within the region increased with increasing distance from human settlement.

With respect to the conservation significance of the findings of this study, a true evaluation of the higher species richness in communal lands was hindered by the absence of species identities for all but the woody plants. Noss (1983) stressed that all species should not be considered equal, and therefore numbers alone provide an incomplete picture. Examination of the identities of the woody plants did not reveal any major losses in species functional types. There were several woody species where a change in frequency was detected. However, within the landuse mosaic in the region, the species affected remain well represented. Several authors have commented on the importance of scale in assessing and evaluating species richness data (Margules and Usher, 1981; Auerbach and Schmida, 1987), and O'Connell and Noss (1992) comment that from a regional conservation perspective, the loss of a species from a specific locality need not necessarily be cause for concern. Thus, consideration of species identities to the exclusion of numerical comparisons, also provides an incomplete perspective. Therefore, a methodological approach is required that balances the quantitative and qualitative components of diversity assessments. In many areas of the species-rich developing world, there is inadequate information on the autecology of large numbers of species, hindering a good appraisal of shifts in species dominance and diversity. In these instances, emphasis is better placed on the numerical aspects of diversity assessment as a first phase. This also applies to examination of patterns of diversity at large geographic scales (Cowling et al., 1989). Grime (1998) recently argued the important role of dominant species in assessing the benefits of plant diversity to ecosystem function. Thus, the loss of a dominant would be more significant than the loss of a transient or subordinate species. There has been little change in patterns of dominance within the Sand River catchment communal lands.

The higher species richness in the communal lands does not mean that there should be no concern about potential loss of species from communal areas in the Sand River catchment. Samples were in the communal grazing lands surrounding villages, and not immediately adjacent to, or within, the villages. It is quite probable that species richness is reduced in the more intensively managed areas of communal systems, especially the arable fields. If such areas are expanding, then species richness for the catchment as a whole will be negatively affected, although many useful edible herbs species are concentrated in disturbed areas, including arable fields (Shackleton et al., 1998). Most households retain useful indigenous fruit tree species in fields cultivated for annual crops. The scale of measurement during this study does not include gamma diversity within each landuse, and thus it is possible that full plant species inventories may not be different between the two landuses.

The correlations between plant species richness and other more easily measured variables, namely mean annual rainfall, and woody plant cover, allow for rapid estimates of anticipated species richness for any site within the catchment. This is a useful first stage identification of potential priority areas for conservation of species richness within the ambit of the total catchment management plan, and recommendations regarding changes in landuses (Pollard et al., 1998). High rainfall localities within the catchment supported a higher plant species richness, as do bottomland sites. Such areas must, therefore, be regarded as the most sensitive in terms of landuse from a biodiversity perspective (which may be at odds with other perspectives). The absolute number of woody plants with edible fruits increased with increasing rainfall, but this was simply a reflection of the greater species richness of all woody plants in relation to increasing rainfall, as the proportion of species with edible fruits was unrelated to rainfall. O'Brien (1988) found a strong relationship between the number of edible woody plant species and rainfall at a national scale, but did not assess it as a proportion of all woody species. Cowling et al. (1997) evaluated patterns of regional species diversity for all South African biomes against a number of explanatory variables. Regional species diversity for savannas was found to be significantly correlated with length of the growing season, modelled potential primary productivity, and the range in minimum July temperatures. There was no relationship with mean annual rainfall at the regional scale for savannas, but one was evident for the fynbos and karroo biomes. Knight et al. (1982), examined regional species richness of woody plants and found strong correlations with a number of environmental variables. The strongest was a positive correlation with mean annual rainfall, and a negative correlation with annual solar radiation. Thus, the positive relationship between plant species richness and mean annual rainfall established at the catchment scale in this study, mirrors that at a regional scale.

The International Convention on Biodiversity places considerable emphasis on the conservation of biodiversity external to formally declared protected areas. Thus, although this study has found that species richness of communal grazing lands is significantly higher than in protected areas, it does not mean that protected areas are failing to achieve their primary objective, but rather that communal land use does not automatically lead to a loss of species. Moreover, it is easy to become complacent when much still remains to be done to integrate biodiversity conservation into management objectives and strategies for intensive landuses such as forestry, arable farming and communal grazing and resource harvesting. A range of strategies can be evaluated for the various landusers within the Bushbuckridge region, such as broad contour banks of indigenous vegetation across sloping arable lands, and between different fields, agro-forestry practices, replacement of wire fences with hedgerows of indigenous thorny species, plans for sustainable harvesting of communal resources, designation of riparian corridors, maintenance of strips of natural vegetation adjacent to roadsides, and the like.

There are relatively few published data on plant species richness and beta diversity in southern African savannas collected from standardised plots. At the 1000 m^2 scale, the Bushbuckridge region appears to be relatively typical of southern African savannas from the data at hand (Table 9), although a wider range of species richness between plots was recorded during this survey than previous studies. The plots at the moister sites had more species than previous studies, all of which were in more arid localities. The mean number of species at the point scale was less than previous studies, but the range overlaps with that recorded in previous studies.

This study has focussed on quantifying and maximising plant species richness within the catchment, largely at the scale of a plant community. The status and dynamics of individual species are altered through different landuse management practices, and whilst total species richness may be relatively consistent, there could be loss of individual key species of disproportionate value to local communities, or conservation authorities. The only declared protected species widely distributed throughout the catchment is *Pterocarpus angolensis* which is harvested by woodworkers. It is reported by local woodworkers and village inhabitants that the abundance of this species is declining throughout the region (Shackleton, 1996). The same applies to several high value medicinal species (Mander, 1997) and other

Table 9
Plant species richness in southern African savannas

Reference	Region	Scale (m^2)	Sample size	Mean no. of species	Range
This study	Bushbuckridge lowveld	1	44	8.0	3.0–13.9
		1000	44	75.7	34–119
Cowling et al. (1989)	South-eastern Cape thicket communities,	1	15	9.9	4–15
	Northern Province and Mpumalanga	1000	15	67.0	43–102
Dahlberg (1996)	North-east Botswana	1	12	8.8	7–12
Whittaker et al. (1984)	Kruger National Park	1	4	12.0	–
	(*Combretum zeyherii–C. apiculatum* community)	1000	4	93	–
Whittaker et al. (1984)	Kruger National Park	1	5	10.1	–
	(*Combretum zeyherii–Pterocarpus angolensis* community)	1000	5	78	–
Whittaker et al. (1984)	Nylsvley Nature Reserve	1	10	8.8	4.7–12.8
	(10 different plant communities)	1000	10	65.1	42–100

carving species. Specific management plans for individual threatened species need to be derived and encompassed within the broader catchment management plan, with support and participation of local communities (Tidsell, 1995).

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