Impacts of high utilization pressure on biodiversity components in *Colophospermum mopane* savanna

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Abstract

This study aimed to quantify and evaluate the effects of heavy land utilization, mainly grazing, on plant species richness and diversity, species abundance, vegetation structure and soil characteristics in a communal area in *Colophospermum mopane* dominated savanna in southern Africa. The treatment was benchmarked against a relatively lightly stocked neighbouring farm. An assessment of termite richness across the contrasting land-use areas was also made. Significant differences were found mainly in plant structure, with reduced plant canopy cover and plant height on the communal land; thus transforming from woodland to predominantly shrubland physiognomy. There was no significant effect of heavy utilization on richness or diversity of plant or termite taxa. Species compositional shifts were reflected by significant species associations with either land-use type. Forb species formed an important component of the vegetation irrespective of grazing intensity. Cover of annual plants did not increase with heavy utilization owing to the increase of ‘weedy’ annual species being counterbalanced by declining cover of palatable annual plants. Biological soil crusts were markedly less common on the communal land which may result in an increased hydraulic conductivity of the soil. Other soil properties measured appeared to be insensitive to the intense level of land utilization.

Introduction

African rangelands are commonly perceived as undergoing widespread and serious degradation mainly through human population increase and associated land use impacts. This view has been much debated and called into question based on different interpretations of indicators of degradation and insufficient data (Homewood 2004, Ward 2005). In many areas under communal tenure in southern Africa the apparently deleterious effects of degradation through heavy grazing by domestic livestock and fuelwood harvesting (Hoffman and Ashwell 2001, Dovie et al. 2004, Wessels et al. 2007) appear equally contentious (Shackleton 1993a, Ward et al. 1998, Sullivan and Rhode 2002, Vetter and Bond 2010). Land degradation has nevertheless been put forward by Scholes and Biggs (2005) as the main cause of biodiversity loss in the arid savannas of southern Africa. The term land degradation is viewed differently by different stakeholders (Reynolds and Stafford Smith, 2002) and remains notoriously difficult to quantify. Land degradation has commonly been defined as land-uses that lead to a persistent loss of ecosystem productivity (Scholes and Biggs 2005). In southern Africa extensive savannas dominated by *Colophospermum mopane* occupy the semi-arid to arid, generally frost-free areas broadly associated with the hot inland valleys of the Limpopo, Zambezi and Cunene river catchments (Siebert et al. 2003). *C. mopane* (colloquially termed ‘mopane’) is an ecologically and economically important tree or shrub that is heavily used for its durable construction wood and excellent firewood (Mashabane et al. 2001). In addition, mopane may host substantial numbers of caterpillars or ‘mopane worms’ (*Imbrasia belina*), which are in demand and provide a widely sought-after local food supplement (Makhado et al. 2009).

Although mopane savanna has been particularly well conserved through a number of extensive protected areas (Huntley 1978), the savanna type is under pressure outside these areas. Extensive tracts of mopane woodland in Namibia have disappeared over the last century due to demand for building timber and clearing for agriculture (Cunningham and Davis 1997) and in Zimbabwe the mopane resource is in decline and faces continued pressures (Musvoto et al. 2006). Mopane woodlands reportedly suffer from heavy wood poaching in some protected areas in Malawi (Chikuni 1996). In addition, some trees
and branches are broken in the process of harvesting mopane worms (Gondo et al. 2010). In the well-conserved large areas of mopane vegetation within the northern Kruger National Park (KNP) of South Africa (Rutherford et al. 2006a), significant portions are currently subject to land claims from descendants of previously dispossessed groups (Anon 2008). Commendable arrangements have been made with some of the already successful land claimants for continuing conservation. However, in the neighbouring area the settlement expansion rates of mainly rural areas have already exceeded what the rangeland can support, which raises doubt regarding the sustainability of resource extraction (Coetzer et al. 2010). The consequences that future land use intensification and utilization pressure will have on conservation and sustained use of mopane savanna are insufficiently understood and require attention (see Wessels et al. 2003).

In this study, we focus on assessing the impacts of heavy communal grazing on biodiversity elements of mopane-dominated savanna, in particular that in the lowveld of north-eastern South Africa. The normal consequences of dryland degradation in southern Africa have been well summarized by Scholes (2009) as syndromes, for example, plant species change which can result in structural changes such as bush encroachment. The net effects on biodiversity are less understood. This is also reflected for mopane savanna where most studies appear to concentrate on impacts of herbivore pressure on vegetation structure (for example, Kelly and Walker 1976, Mapaure and Ndeinoma 2011). Moreover, available reports of impacts on plant species diversity or richness in mopane savanna do not appear to quantify grazing intensities (e.g. Richardson-Kageler 2003) and lack information on heavy grazing impacts in this type of savanna. Outside of mopane vegetation, but within the same climatic zone of the lowveld savanna of north-eastern South Africa, studies indicate widely divergent responses of plant species richness to heavy utilization or degradation. Thus local land degradation or heavy utilization led to significantly increased plant species richness (Shackleton 2000), decreased woody plant species richness (Shackleton 1993b, Higgins et al. 1999, see Ward et al. 2000) or increased grass species richness (Shackleton 2000) and diversity (Tefera et al. 2010). Other results in the region have shown neither a significant effect of heavy utilization on richness of woody plant species and forbs (Shackleton 2000) nor on grass species richness (Prendini et al. 1996).

Termites (Isoptera) are particularly species-rich in north-eastern South Africa (Muller et al. 1997). They are also among the dominant role-players in tropical ecosystems (Uys 2002). They contribute greatly to soil quality and fertility as major agents, notably in plant litter decomposition and regulation of soil organic matter in the savannas of Africa (Schothurman 2006). Collective termite biomass in these savannas is comparable with that of the ungulates or megaherbivores (Moe et al. 2009). Studies of grazing impact on termite diversity appear limited, particularly in mopane savanna. The only published study that we located of the impact of high rangeland utilization on termite diversity in mopane vegetation was in Namibia and found no negative effect (Zeidler et al. 2004). Conversely, it has been shown in semi-arid tropical woodland in Australia that heavy grazing can adversely affect termite diversity (Holt et al. 1996). The impact of grazing on diversity of these key ecosystem engineers appears to be surprisingly neglected. More information is needed for developing an effective strategy to conserve termites for maintaining critical ecosystem processes (Muller et al. 1997).

We chose plant species as the primary biodiversity component of study and termites as a secondary and exploratory focus. Our objectives were to test the influence of heavy land utilization on plant species diversity and richness, compositional change, species abundance, plant trait groups (Díaz et al. 2007), and vegetation structure. In addition we sought to make an assessment of the response of termite richness to heavy land utilization. The effects on soil characteristics were also investigated since soil degradation may negatively influence biodiversity (Bridges and Oldeman 1999). This study further contributes to a national pilot research programme on understanding the relationships between mainly plant diversity and land degradation that was instituted by the South African National Biodiversity Institute (see Rutherford and Powrie 2010). This followed the South African National Spatial Biodiversity Assessment (Rouget et al. 2004) that highlighted the inadequate inclusion of the impact of habitat degradation on biodiversity.

Methods

Study area

The Mopane Bioregion of South Africa (Rutherford et al. 2006b) was systematically
scanned using SPOT 5 satellite imagery to detect candidate rangeland sites with major contrasts between communal and other tenure. Of these candidate sites, the area selected for study represented a contrast between a communally and a commercially managed rangeland and was situated at 24°01′ S 31°00′ E near Phalaborwa in the lowveld of Limpopo Province (Figure 1). The selection was carefully ground-checked to ensure no likelihood of any original environmental gradients across the contrast boundary. The site was located at an altitude of 440 m amsl within the Limpopo River catchment. Mean annual precipitation at Phalaborwa was 527 mm of which 85% fell between October and March. Rainfall for the eight growth seasons preceding the study were below average, except for one (Figure 2). In particular, of the four seasons preceding the 2009 study, two experienced approximately 75% of the long-term mean annual rainfall whereas two had below 50%. Mean monthly maximum and minimum temperatures were 38.4 °C and 16.8 °C for January, and 30.7 °C and 5.7 °C for July, respectively. Geology was Mashishimale granite, and soil was loamy sand that varied in depth from shallow lithosols to greater than 30 cm.

The vegetation comprised low woodland savanna with a relatively sparse herbaceous layer and formed part of the Phalaborwa-Timbavati Mopaneveld vegetation type (Rutherford et al. 2006a). The site was situated in the relatively termite-rich north-east region and lay immediately adjacent to one of the top 1% richest 15' x 15' latitude x longitude termite grids in South Africa (Muller et al. 1997). The study area comprised the game ranch, Môrelag, separated by a game fence from the adjacent communal rangeland area of Mashishimale which formed part of the former Lebowa ‘homeland’ territory. Formal animal censuses on Môrelag are unavailable. However, stocking density has been estimated by farm staff to lie between 0.08 and 0.09 large stock unit (LSU) equivalents per hectare of which African buffalo made up about 75% and antelope species the remainder. Stocking density on Mashishimale was much higher and was calculated to be between 0.55 and 0.68 LSU ha$^{-1}$ (Ba-Shayi Ditlou Traditional Council). Cattle made up about 93% of the total LSU, followed by goats, donkeys, and a few sheep. The agricultural stocking density guideline for the region was 0.11 LSU ha$^{-1}$ (Peel et al. 2005).

The Ba-Shayi Ditlou Traditional Council provided information indicating that the communal area had an average of over 100 people per km$^2$ of which about 80% relied on locally harvested wood as their source of energy and materials for building and fencing, as was common practice elsewhere in communal areas (Shackleton 1993b). Of the many scattered dwellings and small fields with subsistence crops, few occurred within 300 m of the study fence line. Slash marks on stems and sawn-off stumps of woody plants occurred regularly in the communal area but not in the game ranch. Hereafter, the relatively low utilization on Môrelag is referred to as LU and the

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**Figure 1:** Location of the study area in north eastern South Africa.

**Figure 2:** Annual growth-period rainfall (July–June) at Phalaborwa. Only the rainfall for the first half of the last year preceding the study month is given (unshaded column). Vegetation sampling was in January 2009.
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**Sampling**

**Vegetation**

Thirty 5 m x 10 m plots were sampled, with 15 plots randomly placed on each side of the game fence at distances of 15–20 m from the fence line to avoid possible edge effects associated with the fence, and to not be too far from the fence because environmental conditions can be expected to differ increasingly with greater distances from the fence. Percentage canopy cover and heights of vascular plants were recorded. Time constraints required sampling at two levels of detail. Ten plots were comprehensively sampled for all plant species and used for calculation of plant community properties. The remaining 20 plots were used to record individual species statistics for each woody plant species as well as those herbaceous species with a mean canopy cover of greater than 2% on either LU or HU in the first-mentioned 10-plot sample set. Sampling avoided any distinct drainage lines or bottomlands, which constituted a very small proportion of the area. Plant specimens were identified by the National Herbarium of SANBI. Our sampling took advantage of a natural, pre-existing field experiment in which the resulting logistic problems in avoiding pseudo-replication (Hurlbert 2004) were insurmountable (Hargrove and Pickering 1992). Consequentially, statistical inferences of results such as those of this case study could tend to be local (Stohlgren 2007). See Rutherford and Powrie (2010) for discussion on issues of pseudo-replication in fence-line contrast studies.

**Termites**

Cellulose-based baits, namely paper toilet rolls, were used following Ferrar (1982) and Dawes-Gromadzki and Spain (2003). Sixty baits (10.5 cm diameter by 10 cm long, 500 sheet, single ply, unscented, white) were randomly positioned across the length of the study area about 60 m from the fence, with 30 baits on either side. Sampling was further from the fence than for plants to accommodate termite mobility based on known foraging radii (Darlington 1982, Ferrar 1982, Pearce et al. 1990, Jmhasly and Leuthold 1999, Inoue et al. 2001). Any litter present was first removed to ensure the upright-placed roll was in close contact with the soil surface. Baits were placed in mid-January and termites, particularly soldiers, collected from the baits with an aspirator 36–40 days later following guidelines of Ferrar (1982) and Dawes-Gromadzki and Spain (2003). Identifications to genus were done by V. Uys, Plant Protection Research Institute, Agricultural Research Council in Pretoria. No attempt was made to quantify the very variable number of termite individuals on the baits.

**Soils**

A total of twenty soil samples were taken to a depth of 50 mm, ten from each side of the fence, located randomly between plots. They were analyzed for texture, pH, resistance, carbon, ammonium nitrogen, calcium, magnesium, phosphorus, potassium and sodium by the Provincial Department of Agriculture of the Western Cape (Elsenberg) according to methods given by The Non-affiliated Soil Analysis Work Committee (1990). Unsaturated hydraulic conductivity of the soil was measured using a tension infiltrometer (Lorentz et al. 2001). Physical and biological soil crusts were noted on each sample plot and specimens of associated bryophytes were collected for identification.

**Data analysis**

The comprehensively sampled plots were used to analyze the following properties. Plant canopy cover and soil parameter values were analyzed using two-tailed t-tests after square root transformation of the data (Krebs 1989). The step-up false discovery rate correction was applied to the results of multiple tests where appropriate (Garcia 2004). The Shannon-Wiener index of diversity was calculated as in Krebs (1989) but using loge. The values of this index were also converted to their number equivalents which expresses a species-neutral diversity (Jost 2009). Gamma diversity was calculated for the whole study site by pooling all observations of both treatments. Independent beta diversity across the contrast was calculated assuming the additive partitioning of diversity (Legendre et al. 2005). Species accumulation curves were derived using sample-based rarefaction (Mao Tau expected richness function in EstimateS 8.0) as described by Colwell et al. (2004). Evenness was calculated as the ratio of diversity index to maximum possible diversity index for the given number of species (Krebs 1989).

The expanded sample size of 30 plots was used to analyze results for plant cover and height of species which were also compared with those of the independent Indicator Species Analysis of Dufrêne and Legendre (1997) according to McCune and Grace (2002). Frequency of occurrence was analyzed using the Fisher exact test.
Results

Plant species diversity and vegetation structure

Mean plant species richness did not differ significantly between high and low utilization areas either at sample plot scale (Table 1) or at broader scales as reflected by the remarkably similar species accumulation curves (Figure 3). Mean diversity indices were lower, but not significantly so, on HU due to lower species evenness. Total species numbers were very similar with 105 on LU and 107 on HU and were made up mostly of forb species i.e. 52% and 50% of these totals respectively. Sorenson’s Dissimilarity (distance) Index between LU and HU gave a species turnover of 22%. Beta diversity between LU and HU constituted only 3.6 of the 21.1 for gamma diversity.

Annual species constituted 47% of herbaceous species on LU and 56% on HU but the increase in mean annual species on HU and the decrease in mean perennial herbaceous species on HU was not significant ($p = 0.21$ and $p = 0.66$ respectively). The majority of the forb species were annuals. Mean number of species per life form, growth form, habit and architectural type were not significantly different. Mean woody plant species richness, based on the 30 plot sample

Table 1
Species diversity, cover and heights of plants and plant guilds under low and high utilization grazing intensities. LU = low utilization grazing intensity. HU = high utilization grazing intensity. $P =$ probability value. SE = Standard error.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>LU Mean</th>
<th>LU SE</th>
<th>HU Mean</th>
<th>HU SE</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of species</td>
<td>105</td>
<td></td>
<td>107</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Shannon-Wiener Index</td>
<td>2.5</td>
<td>0.05</td>
<td>2.18</td>
<td>0.12</td>
<td>0.18</td>
</tr>
<tr>
<td>Mean Species-neutral diversity index</td>
<td>12.3</td>
<td>0.6</td>
<td>9.5</td>
<td>1.2</td>
<td>0.24</td>
</tr>
<tr>
<td>Mean Evenness Index</td>
<td>0.63</td>
<td>0.01</td>
<td>0.55</td>
<td>0.02</td>
<td>0.051</td>
</tr>
<tr>
<td>Mean species richness per 50 m²</td>
<td>51.4</td>
<td>3.4</td>
<td>52.0</td>
<td>6.8</td>
<td>0.94</td>
</tr>
<tr>
<td>Mean Canopy cover (%)</td>
<td>93.3</td>
<td>1.3</td>
<td>78.3</td>
<td>2.8</td>
<td>$*1.1 \times 10^{-4}$</td>
</tr>
<tr>
<td>Sum of species canopy cover (%)</td>
<td>154.5</td>
<td>10.8</td>
<td>111.9</td>
<td>6.6</td>
<td>*0.010</td>
</tr>
<tr>
<td>Life history: Annual</td>
<td>64.9</td>
<td>6.8</td>
<td>55.6</td>
<td>8.6</td>
<td>0.39</td>
</tr>
<tr>
<td>Perennials</td>
<td>89.5</td>
<td>12.7</td>
<td>56.3</td>
<td>3.9</td>
<td>0.052</td>
</tr>
<tr>
<td>Growth form: Forb</td>
<td>21.5</td>
<td>7.3</td>
<td>8.7</td>
<td>4.1</td>
<td>0.16</td>
</tr>
<tr>
<td>Geophyte</td>
<td>0.3</td>
<td>0.1</td>
<td>0.2</td>
<td>0.1</td>
<td>0.37</td>
</tr>
<tr>
<td>Graminoid</td>
<td>53.9</td>
<td>3.2</td>
<td>52.5</td>
<td>10.3</td>
<td>0.78</td>
</tr>
<tr>
<td>Herbaceous legume</td>
<td>2.1</td>
<td>1.3</td>
<td>0.6</td>
<td>0.3</td>
<td>0.30</td>
</tr>
<tr>
<td>Woody</td>
<td>76.7</td>
<td>10.2</td>
<td>49.9</td>
<td>3.7</td>
<td>0.054</td>
</tr>
<tr>
<td>Habit: Erect</td>
<td>154.5</td>
<td>10.8</td>
<td>111.7</td>
<td>6.5</td>
<td>*0.0095</td>
</tr>
<tr>
<td>Prostrate</td>
<td>0.0</td>
<td>0.0</td>
<td>0.2</td>
<td>0.1</td>
<td>0.18</td>
</tr>
<tr>
<td>Architecture: Leafy stem</td>
<td>100.2</td>
<td>12.8</td>
<td>59.2</td>
<td>6.2</td>
<td>$*0.020$</td>
</tr>
<tr>
<td>Rosette</td>
<td>0.4</td>
<td>0.1</td>
<td>0.2</td>
<td>0.1</td>
<td>0.27</td>
</tr>
<tr>
<td>Stoloniferous</td>
<td>2.6</td>
<td>0.8</td>
<td>0.8</td>
<td>0.6</td>
<td>0.10</td>
</tr>
<tr>
<td>Tussock</td>
<td>51.3</td>
<td>3.6</td>
<td>51.7</td>
<td>10.6</td>
<td>0.90</td>
</tr>
<tr>
<td>Mean heights*, (m): Maximum heights</td>
<td>6.2</td>
<td>0.4</td>
<td>3.3</td>
<td>0.5</td>
<td>*3.9 x 10^{-5}</td>
</tr>
<tr>
<td>Herbaceous layer</td>
<td>0.4</td>
<td>0.03</td>
<td>0.2</td>
<td>0.02</td>
<td>*1.2 x 10^{-5}</td>
</tr>
<tr>
<td>Woody layer</td>
<td>3.5</td>
<td>0.2</td>
<td>1.8</td>
<td>0.08</td>
<td>*7.8 x 10^{-8}</td>
</tr>
</tbody>
</table>

* Significantly different at $P < 0.05$.
† Not significantly different at $P < 0.05$ after False Discovery Rate correction.
* Mean canopy cover (not overlapping) and mean heights from the 30 sample plot set.

Figure 3: Species accumulation curves derived by sample-based rarefaction for (a) low-utilization and (b) high-utilization areas. The dotted lines indicate 95% confidence limits.
Vegetation structure differed significantly between LU and HU. Plant canopy cover and height of herbaceous and woody vegetation were significantly lower on HU compared to that on LU (Table 1). Cover of plants with erect habit declined significantly on HU. There were no significant differences in cover of life forms, growth forms or plant architectures (Table 1). Perennial graminoids constituted only nine percent of total graminoid cover on both LU and HU.

**Individual plant species**

The four woody plant species with the highest cover values on LU were, in descending order, *C. mopane*, *Combretum apiculatum*, *Grewia bicolor* and *Commiphora mollis* (Table 2). This changed on HU to *C. mopane*, * Dichrostachys cinerea*, *Acacia deflexa* and *G. bicolor*. Cover of the woody plant species *C. mopane* and *Clerodendrum ternatum* decreased significantly on HU (Table 2). By contrast, cover of *D. cinerea* increased significantly and more than doubled on HU. Height of *C. mollis* and *G. bicolor* decreased significantly on HU. Cover of the herbaceous annual *Tragus berteronianus* increased significantly on HU (Table 2). Cover of the annual grasses, *Aristida adscensionis* and *Brachiaria deflexa* decreased significantly on HU. Height of *A. adscensionis* and *Melinis repens* decreased significantly on HU. No plant species was found to increase in height on HU. Independent indicator species analysis confirmed the species results above except for, in addition, reporting a significant decrease in cover of *C. mollis* and *M. repens* on HU. The indicator species analysis also showed a non-significant difference in cover of *T. berteronianus* and height of *C. mollis*. Frequent species that appeared to be relatively tolerant of the divergent conditions, i.e. with similar canopy cover on both land-use types, included *Chamaecrista absus*, *Commiphora africana*, *G. bicolor* and *Sclerocarya birrea*, although *G. bicolor* decreased significantly in height on HU (see above).

**Termites**

At the time of sampling five bait rolls were missing on HU, possibly removed by local people. Forty-five of the remaining 55 baits were attacked by termites. Twenty-five baits were attacked on LU (83%) and 20 on HU (80%). Seven baits (three on LU and four on HU) were either partially or completely consumed and abandoned by termites at sampling and no termites could be collected. Species of five genera were found on the remaining 38 baits (Table 3) with about two thirds belonging to species of *Microtermes*. A single genus was found using each bait, except for one bait on which two genera were found. Fungus-growing termites (Subfamily Macrotermitinae) were overwhelmingly dominant (97%), and comprised the mound-building *Macrotermes* species and the subterranean-nesting *Allodontermes*, *Microtermes* and *Odontotermes* species. The relatively low occurrence of *Macrotermes* species accorded with the relatively low cover of their mounds. No significant differences in occurrence of genera were revealed between LU and HU with only *Allodontermes* possibly favouring LU (Table 3). Sorensen’s Dissimilarity Index for genera was 25% between LU and HU.

**Soils, water infiltration and soil crusts**

None of the physical and chemical soil properties measured on LU and HU were significantly different although pH and cations tended to decrease on HU (Table 4). While only two replicate points were sampled for unsaturated hydraulic conductance, large differences were evident with higher but more variable infiltration rates on HU (Figure 4). Soil surface biological crusts were common, occurring on all sample plots in LU. Crusts were dominated by the bryophytes *Bryum bicolor* Dicks. and *Riccia c.f. runssorensis* Steph. Black crusts were common and seemed to be mostly associated with *R. c.f. runssorensis* but cyanobacteria may also have been present. Biological crusts were virtually absent on six plots on HU and were limited on most of the remaining plots on HU to occasional areas under shrubs.
### Table 2

Frequency, canopy cover and heights on low or high utilization intensity plots. LU = low utilization intensity. HU = high utilization intensity. 

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency (number of plots)</th>
<th>Canopy cover (%)</th>
<th>Height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L</td>
<td>H</td>
<td>P</td>
</tr>
<tr>
<td>Woody species with highest canopy cover *</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia nigrescens Oliv.</td>
<td>11</td>
<td>7</td>
<td>0.26</td>
</tr>
<tr>
<td>Cissus cornifolia (Baker) Planch.</td>
<td>4</td>
<td>3</td>
<td>1.00</td>
</tr>
<tr>
<td>Clerodendrum ternatum Schinz</td>
<td>8</td>
<td>4</td>
<td>0.26</td>
</tr>
<tr>
<td>Colophospermum mopane (J.Kirk ex Benth.) J.Kirk ex J.Léonard</td>
<td>15</td>
<td>14</td>
<td>1.00</td>
</tr>
<tr>
<td>Combretum apiculatum Sond.</td>
<td>15</td>
<td>13</td>
<td>0.48</td>
</tr>
<tr>
<td>Commiphora africana (A.Rich.) Engl. var. africana</td>
<td>7</td>
<td>7</td>
<td>1.00</td>
</tr>
<tr>
<td>Commiphora mollis (Oliv.) Engl.</td>
<td>12</td>
<td>7</td>
<td>0.13</td>
</tr>
<tr>
<td>Dalbergia melanoxylon Guill. &amp; Perr.</td>
<td>5</td>
<td>4</td>
<td>1.00</td>
</tr>
<tr>
<td>Dichrostachys cinerea (L.) Wight &amp; Arn.</td>
<td>13</td>
<td>15</td>
<td>0.48</td>
</tr>
<tr>
<td>Flueggea virosa (Roxb. ex Willd.) Voigt subsp. virosa</td>
<td>2</td>
<td>1</td>
<td>1.00</td>
</tr>
<tr>
<td>Gardenia volkensii K.Schum.</td>
<td>0</td>
<td>2</td>
<td>0.48</td>
</tr>
<tr>
<td>Grewia bicolor Juss.</td>
<td>8</td>
<td>8</td>
<td>1.00</td>
</tr>
<tr>
<td>Grewia flavescens Juss.</td>
<td>1</td>
<td>2</td>
<td>1.00</td>
</tr>
<tr>
<td>Grewia monticola Sond.</td>
<td>6</td>
<td>5</td>
<td>1.00</td>
</tr>
<tr>
<td>Grewia villosa Willd.</td>
<td>1</td>
<td>1</td>
<td>1.00</td>
</tr>
<tr>
<td>Gymnosporia sp.</td>
<td>2</td>
<td>0</td>
<td>0.48</td>
</tr>
<tr>
<td>Lannea schweinfurthii (Engl.) Engl.</td>
<td>2</td>
<td>2</td>
<td>1.00</td>
</tr>
<tr>
<td>Ormocarpum trichocarpum (Taub.) Engl.</td>
<td>1</td>
<td>1</td>
<td>1.00</td>
</tr>
<tr>
<td>Phileanoptera violacea (Klotzsch) Schirr.</td>
<td>2</td>
<td>2</td>
<td>1.00</td>
</tr>
<tr>
<td>Sclerocarya birrea (A.Rich.) Hochst.</td>
<td>10</td>
<td>6</td>
<td>0.27</td>
</tr>
<tr>
<td>Ziziphus mucronata Willd.</td>
<td>2</td>
<td>2</td>
<td>1.00</td>
</tr>
<tr>
<td>Herbaceous species with highest canopy cover</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aristida adsensionis L.</td>
<td>15</td>
<td>14</td>
<td>1.00</td>
</tr>
<tr>
<td>Brachiaria deflexa (Mez) Clayton</td>
<td>15</td>
<td>15</td>
<td>1.00</td>
</tr>
<tr>
<td>Chamaecrista absus (L.) H.S.Irwin &amp; Barneby</td>
<td>13</td>
<td>13</td>
<td>1.00</td>
</tr>
<tr>
<td>Lineum viscosum (J.Gay) Fenzi</td>
<td>10</td>
<td>13</td>
<td>0.39</td>
</tr>
<tr>
<td>Melinis repens (Willd.) Zizka</td>
<td>12</td>
<td>8</td>
<td>0.25</td>
</tr>
<tr>
<td>Tragus berteronianus Schult.</td>
<td>13</td>
<td>15</td>
<td>0.48</td>
</tr>
</tbody>
</table>

* Significantly different at $P < 0.05$. SE: Standard error

* Woody species with mean canopy cover greater than 0.2% recorded in plots on either LU or HU.
commonly *B. bicolor*. A few weak physical crusts were observed on HU. The surface-growing lycophyte, *Selaginella dregei* (C.Presl) Hieron., was not assessed as one of the vascular plants and occurred sporadically on LU and HU.

**Discussion**

The lack of a decline in plant species richness found with heavy land utilization is in agreement with that in the Bushbuckridge region of lowveld savanna in Mpumalanga where plant species richness in heavily utilized communal land was about 11% higher than that in adjacent conservation areas (Shackleton 2000). Recent studies have also shown no decline in plant species richness with heavy communal utilization of certain grassland sites elsewhere in South Africa (Rutherford and Powrie 2011, Rutherford et al. 2011). It follows that if the significant decline in plant cover found with heavy utilization of the communal savanna is regarded as land degradation, the results do not support the notion that such intensity of land use is the cause of net biodiversity loss in these savannas. However, it remains an open question whether the loss of plant cover would adequately comply with the current definitions of degradation as a persistent loss in ecosystem productivity (Scholes and Biggs 2005) or services (Vogt et al. 2011).

The parity found in plant species richness on LU and HU may reflect their possible positions at the two extremes of the Intermediate Disturbance Hypothesis (Grime 1973) and would therefore indicate that there was no elevated plant species richness on either side of the contrast. Thus, competitive exclusion would cap species numbers on LU whereas ongoing disturbance would limit species number on HU. Alternatively, the relatively low species turnover may point to the tolerance of most of these savanna species to disturbance through long adaptation to utilization (Rutherford et al. 2006a). This would be reflected in the modified form of the Intermediate Disturbance Hypothesis where a relatively flat trajectory or steady gentle decline in diversity with grazing intensity is indicated for semi-arid systems with a long evolutionary history of grazing (see Cingolani et al. 2005). Minor losses of species on HU could be offset and balanced by colonization, possibly through disturbance-induced microhabitat differentiation and resource partitioning (see Guo 1998, Chesson 2000). Although it might be argued that the relatively small change in plant species composition with heavy land utilization, as reflected by low beta diversity and Sorenson's Dissimilarity Index, involves mainly minor species, some of these may nevertheless be indicators of concern for conservation management.

Forb species were particularly well represented comprising about half of the plant species both on LU and on HU. Some forb species increased and some decreased on HU although few of these changes were significant (Table 2). These data suggest that forb species are important natural components of *C. mopane* vegetation and are not necessarily associated with land degradation. The suggestion that forb species are absent in areas that are 'well-managed' or 'undegraded' in the lowveld and only start to appear under degraded conditions, and peak under severely degraded conditions (Steenekamp and Bosch 1995) appears unsupported by this study. The high proportion of forbs may result from a natural cycle of prolonged, below-average rainfall that preceded this study (see O'Connor 1998). Forbs and annual grass species persisted as dominants for at least four decades following a drought of several years in typical mopane vegetation in the Limpopo Province of South Africa (Jordaan et al. 2004).

The mean plant species richness found on both LU and HU appears markedly higher than that found on a range of sites in nine regions in *C. mopane* savanna across southern Africa (Siebert et al. 2003). The average richness for these regions was 27 species per 200 m² plot which is less than a third the richness of about 97 per 200 m² that was derived from rarefaction curves in the current study (Figure 3). Even the Musina region with the highest richness of 45 remains below half that indicated in this study. It might be argued that the higher plant species richness may be due to the close proximity of land-use types in this study where dispersal exchange across the fence may have raised the plant species richness on both

![Figure 4: Unsaturated hydraulic conductance of soils on LU and HU at selected tensions. LU: low utilization. HU: high utilization. Bars indicate standard error.](image-url)
sides. However the relatively low beta diversity across the fence line suggests an insufficiently sized pool of species to account for the magnitude of the difference in plant species richness with the other studies. It is also possible that the high proportion of sometimes cryptic forb species may have not been fully recorded in broad-scale surveys, but this has not been substantiated. It has been contended that plant species richness in *C. mopane* savanna peaks temporarily, largely due to annuals, after initial recovery from a period of disturbance such as prolonged drought (Siebert et al. 2003).

Mean plant canopy cover and heights of herbaceous and woody layers diminished with heavy utilization as has been reflected in a number of studies. The significant reduction in woody plant height on HU corresponds to a decline found in a communal area compared to conservation areas in Maputaland (Gauquis and Van Rooyen 2010), and in areas with greater disturbance within communal land of the lowveld (Shackleton et al. 1994) and in *C. mopane* savanna in northern Namibia (Strohbach 2000a). LiDAR data has confirmed a decrease in mean height of woody vegetation on the communal lands adjacent to the southern Kruger National Park (Fisher et al. 2009).

The trend for reduction in woody plant cover on HU is consistent with the decline reported for communal areas adjacent to the southern Kruger National Park (Mathieu et al. 2009). However, the decline in woody plant cover was the net result of individual species either increasing or decreasing in cover. Despite a strong coppicing ability (O’Connor et al. 2007.), *C. mopane* decreases significantly on HU as does *C. ternatum*, both of which have also been shown to decline along an increasing degradation gradient in northern Namibia (Strohbach 2000a,b). The decline in cover of *C. mollis* on HU may relate to its ineffectiveness at resprouting (O’Connor et al. 2007). These decreases in woody plant cover on HU were partly compensated for by the significant increase in cover of *D. cinerea*, a species that Shackleton et al., (1994) reported as being facultatively tolerant of disturbance rather than increasing with disturbance in the lowveld. The apparent insensitivity of *S. birrea* to utilization may be misleading given its status as a protected species in South Africa and its favored retention where other indigenous species have been cleared near homesteads or in arable plots (Shackleton et al. 2005).

The modest decline in cover of herbaceous species on HU was the net result of decreases of mainly *A. adscensionis* and the palatable *B. deflexa* that was partly offset by the expected increase in cover of ‘weedy’ species such as *T. berteronianus* (Snyman et al. 1990). The usual increase in cover of annual plants under heavy utilization was also counterbalanced by the decline in mainly the palatable annual *B. deflexa*. To what extent the structural change effectively from woodland to shrubland might have been indirectly responsible for certain changes in herbaceous species (see Treydte et al. 2009) is unknown.

As with the present study, a study of termites in savanna of northern Botswana (Schuurman 2006), that also used toilet roll baits, found an overwhelming dominance of fungus-growing termites that belonged to the same four fungus-growing genera as reported here. That study confirmed the importance of sampling in the rainy season for *Alldontermes* and *Microtermes* since species of these genera virtually disappear in the dry season. It should be noted that toilet roll and other baits may not have sampled soil feeders and species feeding on well-humified litter.

The lack of significant difference found in the incidence of termites between low and high utilization areas has been mirrored elsewhere in south-central Africa, for example, in arid *C. mopane*-dominated vegetation in Namibia (Zeidler et al. 2004). Although occurrence of *Alldontermes* species was not significantly different between LU and HU, the limitation of this genus to only four baits on LU may relate to their preference to feed mainly on wood and leaf-litter (Uys 2002), the latter of which was far more abundant on LU. Although it is possible that termite movement across the fence may have contributed to not finding significant differences between the two sides, available information indicates that sampling at 60 m from the fence should be beyond the normal termite foraging radius (Ferrar 1982).

The greatly reduced biological soil capping with heavy utilization was probably due to trampling by the higher stock numbers and also possibly people on HU. The significantly reduced canopy cover on HU would also increase soil exposure to direct sunlight and raise evaporation. This would further explain why the bryophytes were limited to the shady areas under shrubs and their complete absence from six HU plots. The increased unsaturated hydraulic conductance on HU may be due to this reduced surface capping. The increased conductance is consistent with another preliminary study of water infiltration in the Giyani area about 80 km further north where the exclusion of cattle for a number of years resulted in no significant difference in infiltration.
rates over time, compared to increasing infiltration in adjacent heavily grazed communal areas (A. Swemmer, Personal communication).

The apparent stability in many physical and chemical soil properties with high land utilization may possibly suggest that the system is relatively resilient although the long-term sustainability of heavy utilization remains to be assessed. Continued heavy grazing in communal areas can, in the long-term, be clearly influenced by multiple factors, including some that are extraneous to the grazing system (Vetter and Bond 2010).

Benchmark sites against which to gauge change may not remain constant. In a study in the lowlands of northern KwaZulu-Natal the stark contrast between low woody plant cover on communal land and high cover on adjacent conservation land has been attributed not only to long-term woody plant utilization in the communal areas but also to bush encroachment over many decades in the conservation area (Wigley et al. 2009). The current study has tacitly assumed LU as the benchmark site. Although its herbaceous layer cover was relatively sparse and mainly annual, this sparse understorey with relatively little perennial grass is typical of many areas of C. mopane savanna (Werger and Coetzee 1978, Klintenberg and Verlinden 2008). However, there appears to be much variation (Siebert et al. 2003, Poilecot and Gaidet 2010) where perennial herbaceous species are often replaced by annuals following drought (O’Connor 1998, Buitenwerf et al., 2011). The drought conditions in the few years preceding this study may have contributed to the relatively high proportion of annual plants on LU although the drought conditions appeared to not have been broken at the time of sampling of vegetation.

The equitable levels of plant species richness found across the major land-use contrast of the current study depend strongly on the behavior of the ephemeral plants. There is a need for comprehensive sampling over multiple seasons and years to better evaluate the effects of climatic variation and land-use on the incidence of the ephemeral plant group in C. mopane savanna. There is also a need to investigate a wider range of potential benchmark sites bearing in mind that game farms are not necessarily ideal for this purpose (see Parsons et al. 1997). Game farms involve balancing multiple objectives which can complicate their use as benchmarks (Sutherland and Peel 2010). Benchmark setting for biodiversity indication purposes remains a relatively neglected issue (Feld et al. 2010). Further research on the effects of rangeland land-use intensity and patterns on the diversity of the potentially important termite assemblages appears much needed, not only in mopane savanna.

From this study we conclude that a possible future spread of more intensive communal use of C. mopane savanna rangelands would be less likely to impact on plant species richness and diversity than having a more marked effect in changing the relative abundance of individual species and in effecting a structural transformation from woodland to predominantly shrubland physiognomy. Although compositional changes may be important conservation and agricultural concerns, the effects of any large-scale reduction in canopy size and architecture could also extend beyond the regional paradigm and affect broader-scale ecosystem services such as climate regulation (De Bello et al. 2010).

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References


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Peel MJS, Kruger JM, Zacharias PJK. 2005. Environmental and management determinants of vegetation state on protected areas in the


Steenekamp SJ, Bosch OJH. 1995. Construction and evaluation of condition assessment and grazing capacity models for use in grazing management in the eastern mixed bushveld of...


