Topo-edaphic environment and forestry plantation disturbance affect the distribution of grassland forage and non-forage resources, Maputaland, South Africa

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Keywords: Grassland ecosystem services, non-forage grassland resources, hygrophilous grassland, secondary grassland

Abstract

Grasslands are integral to rural livelihoods in southern Africa because they provide hydrological regulation services and a variety of plant resources including livestock fodder, medicines, and food products. To ensure ongoing provision of these resources in rapidly developing rural landscapes, an understanding of the relations between grassland species composition and ecosystem services is required. This study examines the provision of grassland forage and non-forage resources across five grassland types in relation to environmental determinants of site topography, soil conditions, and plantation-forestry disturbance. Grasslands characteristic of low-lying and fertile landscape positions were dominated by nutritious lawn grasses and therefore tended to complement rangeland practices, whereas grasslands associated with elevated areas or infertile conditions were diverse in species composition and consequently provided the majority of plant medicines, spiritual resources, fruit-

beverage resources, oils, and craft materials. Secondary grassland, resulting from forestry plantation abandonment, had moderate forage potential and limited non-forage resources. Our results provide a simple framework for approaching grassland resource classification, grassland conservation and land use management on the Maputaland coastal plain.

Introduction

Grasslands are among the most diverse vegetation types in South Africa, averaging about 82 species per 1000 m^2 (Cowling et al. 1989). Plant types present in grasslands include herbaceous dicotyledons, non-graminoid monocotyledons, geophytes (collectively termed forbs), grasses, sedges, and woody tree or shrub species. Grasslands provide different ecosystem products and services (Bengtsson et al. 2019). For example, over four million ha of grassland in KwaZulu-Natal has the potential to supply forage for about 700 000 Large Stock Units (LSU) (Avenant 2008), while grassland-adapted forb and woody species provide browse and non-forage products such as medicine, food or building materials (Dzerefos and Witkowski 2001; Shackleton et al. 2018). If managed sustainably, livestock production on natural grassland has considerably less impact on the biological integrity and ecosystem functioning of grasslands by comparison with land uses such as cropping or plantation agriculture (O'Connor and Kuyler 2009). However, despite these positive ecological attributes, old-growth natural grasslands around the world are consistently faced with conversion to other land uses, especially in rapidly developing rural landscapes (Jewitt et al. 2015; Buisson et al. 2018).

The value of grassland resources to rural communities is derived from forage and non-forage plant species but these values are likely to vary spatially in relation to changes of plant composition according to the local environment. Decisions about land use should, therefore, strive to ensure that all grassland components in a landscape are available as community resources (Sigwela et al. 2017). For example, the composition of grassland on the Maputaland coastal plain corresponds with soil organic carbon (SOC) and clay in the soil A-horizon (Matthews et al. 1999; Starke et al. 2020). Grasslands occurring in low-lying topography on organic soils are characterised by dominance of prostrate and tufted-rhizomatous grass species, while a heterogeneous mix of grasses, forbs, and woody plants occur upon elevated dune-ridges in nutrient-poor soils (Starke et al. 2020). Prostrate grasses tend to supply sustainable quality forage because they can tolerate ongoing defoliation as they regenerate due to intercalary growth and escape complete defoliation due to the grazing height of large herbivores (Hempson et al. 2015). Tufted and ligneous grass species provide quality grazing after burning and a balance of fibrous roughage during winter or summer months (Morris 2002). Forb and woody species diversity in grasslands is also likely to correspond with increasing potential for grasslands to supply non-forage grassland products such as medicinal plants (Dzerefos and Witkowski 2001).

Communal rangelands differ from commercial livestock operations in that they adopt continuous stocking systems where, depending on the seasonal availability of forage resources, livestock are unfenced and selectively consume preferred grass or browse species within a proximate distance to corrals (Moyo et al. 2012). A weakness of this approach is that selective grazing limits the growth and reproduction of palatable grasses leading to dominance by less-palatable species (Tainton 1999). This decreases stocking capacity and the perceived value of grasslands to rural communities which may increase the risk of grassland transformation to croplands or plantations (Sigwela et al. 2017). In such circumstances, a prerequisite for successful grassland management is understanding the spatial and temporal relations of grassland resources across the landscape, as this can assist with prioritising compartments of land to ensure a long-term provision of grassland ecosystem services. For example, veld condition assessments provide meaningful insight into grasslands that are vulnerable to degradation and can track changes in grassland composition across time (Tainton 1999).

Rural districts in coastal Maputaland face an unenviable choice between transforming their communal rangelands to other forms of land use or preserving grassland ecosystem services. An understanding, therefore, of the resources supplied by different grassland types could provide guidelines whereby a community can select the appropriate land uses for different development needs. This study quantifies the value of forage and non-forage resources across five grassland types, enabling the following questions to be addressed: (i) How do relationships among environmental conditions, species composition and the resource value of grassland species affect how grasslands could be managed? (ii) What effect does afforestation have to grassland resources? (iii) How do differences in grassland resources effect the competing nature of different land uses in a developing agro-ecological landscape?

In a companion study, Starke et al. (2020), found that grasslands located in low-lying landscape positions on soils with high SOC contained mostly palatable rhizomatous and stoloniferous prostrate grasses, while elevated grasslands contained a diverse composition of tufted graminoids, forbs and woody plant species. The expectation was, therefore, that forage variables indicating good grazing would correspond with the grassland composition of low-lying landscape positions in nutrient rich soils, and that non-forage resources and poor grazing would correspond with a different species composition found on elevated nutrient-poor grasslands. We also predicted that impoverished forb diversity in disturbed sites would mean that secondary grassland would supply the least variety of non-forage resources.

Study site and methods

Study site

The study was conducted in a sub-tropical ecosystem consisting of a forest-grassland-wetland mosaic in eastern South Africa (Figure 1a,b,c). The region is humid, with a mean annual temperature of 21°C and mean annual precipitation of 964 mm (Mucina et al. 2006). The coastal region of Maputaland is characterised by distinct elevated and low-lying topographic features that provide different soil and moisture conditions for vegetation (Matthews et al. 1999; Starke et al. 2020). Elevated areas comprise dune-ridges (±45-65 m amsl) that are comparably more prominent in the landscape than interdune hummocks or smaller ridges which are embedded within lower-lying floodplains (±35-45 m amsl) (Figure 1c; Starke et al. 2020). Elevated areas are composed of dystric regosols, meaning that soil conditions are unconsolidated, sandy, with low amounts of clay and SOC. By contrast, lower-lying interdune plains are humic gleysols composed of sands containing a high SOC (Starke et al. 2020). Embedded within low-lying interdune areas are wetland-depressions comprising sour organic histosols and peat deposits (Pretorius et al. 2016; Starke et al. 2020).

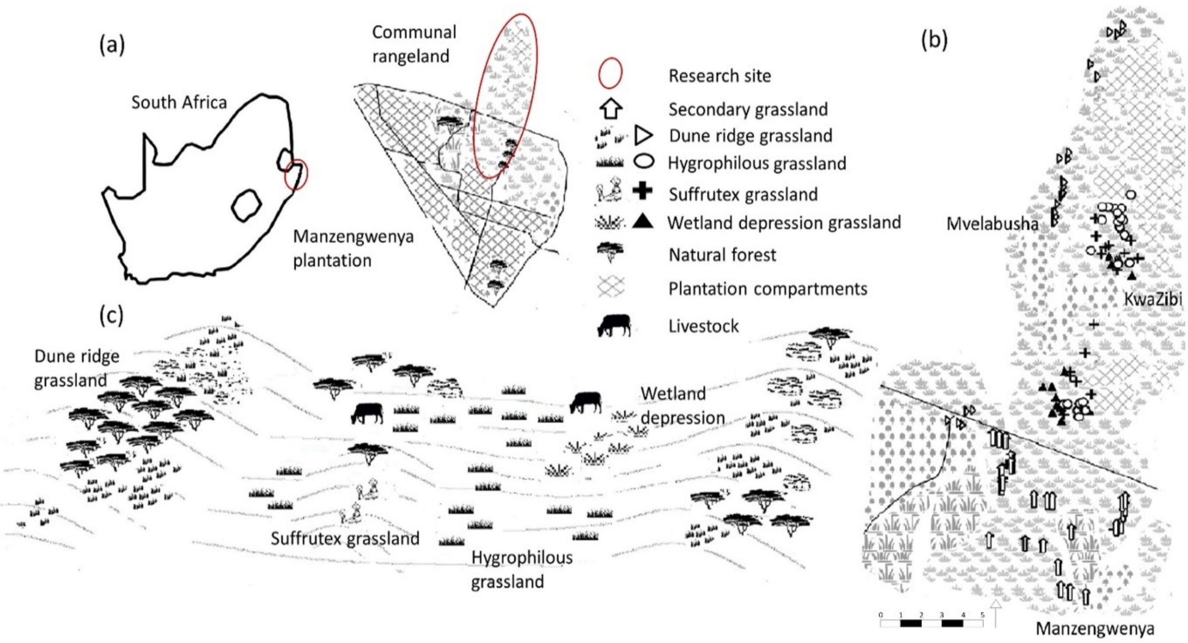

Figure 1 (a) Geographic location of the study area, showing the extent of Manzengwenya plantation and adjacent communal rangeland. (b) The study site showing plot locations in relation to grassland types in

Manzengwenya plantations and communal grasslands. (c) Conceptual topographic and grassland community framework of the study area (adapted from Starke et al. 2020).

Vegetation description

Grasslands are a central component of forest-grassland-wetland mosaic ecosystems of the Indian Ocean Coastal Belt Biome (IOCB). They account for most non-wooded natural vegetation in the study area, functioning as rangeland for livestock among a matrix of different land uses such as homesteads, horticultural gardens, natural forest, permanently saturated wetlands, and forestry woodlots (von Roeder 2014; Everson et al. 2019). Communally managed grasslands were considered old-growth grassland, which is grassland that had not been subject to rigorous exogenous transformation *sensu* Buisson et al. (2018). In a companion study, Starke et al. (2020) recognise two elevated (dune-ridge and suffrutex) and two low-lying (hygrophilous and wetland-depression) grassland types in community-managed rangeland, and a secondary grassland which had regenerated within clear-felled and then abandoned afforested compartments in Manzengwenya plantation (Figure 1b). The species composition of elevated and low-lying grassland types correspond with landscape topography (Figure 1c), the soil environment, and forestry plantation disturbance. In elevated sites, dune-ridge grassland is characterised by tufted graminoids, including *Hyperthelia dissoluta* and *Andropogon schirensis*, and is forb rich. On small-scale interdune-ridges or hummocks, geoxylic suffrutex grassland is indicated by an abundance of geoxylic-suffrutex species such as *Parinari capensis* or *Syzygium cordatum*, and a richness of forbs and grasses. In lower-lying areas, hygrophilous grasslands support a mix of tufted grasses and lawn grasses. Well-watered wetland-depression grasslands on carbon-rich soils or peat are largely composed of prostrate lawn grasses. Livestock density in communal rangelands is estimated to be 0.2 – 1 LSU ha^{-1}. Secondary grassland, in abandoned *Pinus elliotii* forestry compartments (Figure 1b), is composed of pioneer lawn grasses, pioneer tufted grasses and ruderal forb species. Secondary grassland has been subject to livestock grazing and fire that would have constrained the development of woody vegetation. Fires occur as a natural disturbance in the landscape between May and October when fuel is dry, having occurred at intervals of 3-6 years between 1990 – 2016 (Starke et al. 2019).

Floristic and soil sampling

A detailed description of sampling is given in Starke et al. (2020). In brief, grassland sampling (109 plots) was conducted in community managed grasslands across an environmental gradient from elevated to low-lying topographic positions and in a secondary grassland within Manzengwenya plantation (Figure 1b,c). Floristic composition was determined by estimating the cover-abundance of species within 100 m^2 circular plots according to a modified Braun-Blanquet cover-abundance scale (Starke et al. 2020). Indicator Species Analysis provides a combined value of species abundance and fidelity, termed 'indicator value' (IV) (McCune and Mefford 2018). IVs of selected species were reported from the analysis conducted by Starke et al. 2020. Estimates of SOC of the A-horizon in each floristic plot was determined using near-infrared spectroscopy. Plant nomenclature follows the African Plant Database (2020).

Forage sampling

Grassland forage composition was estimated by sampling the three most dominant plant species in 20 x 1 m^2 quadrats along 109 transects using the dry-weight-rank method ('t Mannetjie and Haydock 1963). The mid-point of forage transects bisected the centre of the floristic plots. To obtain an estimate of dry-weight, the mass of each quadrant was scored using weighted multipliers relative to each grassland type. Multipliers were obtained prior to sampling using preselected reference quadrats which were continually checked to ensure consistency (Haydock and Shaw 1975).

Dominant grasses from each grassland type, defined as those species contributing > 75% of phytomass, were sampled for leaf Nitrogen (N) and Acid Detergent Fibre (ADF). Leaf sampling occurred in mid-summer and was replicated during mid-winter. Samples were oven-dried at 60°C for 48 hours, then ground and sieved through 1 mm mesh. Nitrogen concentration was determined using method 990.03 of the Association of Official Analytical Chemists (1997) and using a LECO, FP2000, nitrogen analyser (Basha et al. 2012). ADF of samples was determined using the methods of Van Soest et al. (1991). N and ADF for each transect were expressed by percent and were the mean value of pooled summer and winter samples relative to the total biomass of a transect. A composite value for N and ADF of non-measured grass species was derived as the mean value of all measured species within a specific grassland type. Due to winter rainfall in May 2017 there was little variability of N and ADF in samples between seasons.

The grazing value (GV) of a transect was the percentage composition of each species multiplied by the appropriate forage score. Forage scores were collated from veld condition assessments previously conducted in Maputaland; scores ranged from 1 for non-palatable to 10 for very palatable (Potgieter 2008; Trollope et al. 2011).

Non-forage resources

Use-classes relating to grassland non-forage resources were collated from classes used in ethnobotanical literature (Cunningham 1985; Phillips and Gentry 1993) and from agroforestry databases (Orwa et al. 2009; Heuzé et al. 2013). Non-forage use-classes were: Medicinal, Spiritual, Integrated Pest Management (IPM)-Ethnoveterinary, Crafts-Dye-Fibre, Fruit-Beverage, Leaf-Tuber consumption, Building-Thatching, Oils, and Fuel. The review consulted the following search engines and databases: Google Scholar, FAO AGRIS (Celli et al. 2015), Bielefeld Academic Search Engine – BASE (Bäcker et al. 2017), ICRAFs Agroforestree database (Orwa et al. 2009), Feedipedia (Heuzé et al. 2013), and Plant Resources of Tropical Africa - PROTA (Lemmens et al. 2012). No unpublished literature was consulted, and priority was given to peer-reviewed articles from the closest possible geographic location to the study area.

A species-use matrix was compiled from the floristic data sampled by Starke et al. (2020) and the following variables were calculated. The non-forage use-value (UV) of a species was the number of individual non-forage use-classes applicable to a given species (Phillips and Gentry 1993). This method does not distinguish between the relative degree of importance of different uses, but the approach suits data collated through review (Hoffman and Gallaher 2007). Individual plot resource-value (RV) was the number of individual use-classes available from a floristic plot, while the 'use-class' RV was the number of species related to a given use-class in a plot. For example, the fruit-beverage RV of a plot was the number of species cited to supply fruit or beverage resources. Medicinal plant species were further classified by medicinal or spiritual treatment type. This followed classes set out by Hutchings et al. (1996) which are love, infertility, venereal disease, gynaecology, children, gastrointestinal, renal, debility, toothache, respiratory, febrile, headache, cardiac, nervous, pain, swelling, skin, and ears.

Statistical procedures

The overall RV, use-class RV and grazing indices (GV, N and ADF) were compared across the five grassland types ~~classified by Starke et al. (2020)~~, using Welch's ANOVA with individual differences in means compared using Tukey's test. An analysis of medicinal use-classes (summarised as the number of species per ailment in a plot) between elevated (dune-ridge and suffrutex) and low-lying (hygrophilous and wetland-depression) grasslands was conducted using a Kruskal-Wallis test because this technique suits smaller sample sizes (Zaiontz 2016).

Non-metric dimensional scaling (NMS), using the Bray-Curtis dissimilarity index, was conducted to assess relationships between the primary gradient of change in grassland species composition with forage variables (GV, N, and ADF), use-class RV and SOC. Correlation strength was reported by Kendall's correlation coefficient. Further gradients of resource distribution were examined using a 3D surface contour overlay (McCune and Mefford 2018).

Results

Comparison of grassland resources

Woody plants (78 uses from 36 species) and forbs (76 uses from 80 species) accounted for majority of the 178 total uses found in the review. At least 60% of plant species had one cited use. The average UV of a species was 1.7. Species with the most individual uses (UV = 5) were woody plants. The most frequently encountered use-class was medicinal, which applied to about 50% of forbs and 30% of woody species. *Cymbopogon caesius* was one of the few grasses that had medicinal uses. About 20% of non-graminoid species had spiritual applications, the most common as love charms. Less common uses were fruit-beverage (15%), craft-dye-fibre (10%), oils (6%) and leaf-tuber consumption (3%).

Dune-ridge grassland had the greatest total RV but plot averages did not differ from suffrutex grassland, meaning that both types of elevated grassland had a similar richness ~~composition~~ of non-forage resource richness. Dune-ridge and suffrutex grasslands had higher total RV (by a factor of five) than hygrophilous, wetland-depression, or secondary grassland (Table 1, Figure 2). The use-classes most responsible for these differences were medicinal, spiritual, fruit-beverage, building-thatching, oils, and IPM-ethnoveterinary. Crafts-dye-fibre, leaf-tuber, and fuel did not differ as strongly across grassland types.

Table 1. Differences in mean plot values of non-forage and forage variables

Landscape class	**Elevated**				**Low-lying**				**Forestry plantation**		**Welch's Anova**
Grassland type	Dune-Ridge (n = 17)		Suffrutex (n = 32)		Hygrophilous (n = 11)		Wetland-Depression (n = 27)		Secondary (n = 22)		
	x̄	SD	x̄	SD	x̄	SD	x̄	SD	x̄	SD	
Non-forage variables											
RV (Resource value)	31.7_b	8.74	28.7_b	8.42	4.4_a	2.40	6.0_a	5.94	4.0_a	2.93	**81.4**
Medicinal	11.5_b	3.88	11.4_b	3.45	1.7_a	1.10	2.7_a	2.47	1.7_a	1.06	**67.7**
Spiritual	3.8_b	2.22	3.6_b	1.65	0.8_a	0.72	0.9_a	1.08	0.3_a	0.64	**28.1**
IPM-Ethnoveterinary	2.2_a	1.0	1.2_b	1.06	-	-	0.2_c	0.73	0.4_c	0.67	**14.9**
Crafts-Dye-Fibre	$1.0_{a,b}$	0.94	1.2_a	1.01	$0.7_{b,c}$	0.68	0.3_c	0.57	0.4_c	0.73	**5.2**
Fruit-Beverage	5.3_b	1.61	4.2_b	1.31	0.3_a	0.46	0.6_a	0.93	0.6_a	0.59	**70.3**
Leaf-Tuber	0.5_a	0.54	0.4_a	0.51	0.05_b	0.241	$0.3_{a,b}$	0.46	$0.1_{a,b}$	0.35	**4.5**
Building-Thatching	4.4_b	1.7	3.8_b	1.3	0.7_a	0.71	0.5_a	0.77	0.3_a	0.61	**53.7**
Oils	2.4_a	0.78	1.7_a	0.70	0.11_b	0.332	0.12_a	0.448	0.14_b	0.147	**58.8**
Fuel	0.6_a	0.80	1.2_a	0.78	0.11_b	0.332	0.20_b	0.414	0.09_b	0.301	**10.3**
Forage variables											
GV (Grazing value)	0.32_b	0.076	0.29_b	0.119	0.46_a	0.145	0.41_a	0.110	0.33_b	0.067	**6.4**
Nitrogen	0.81_c	0.101	1.06_b	0.104	1.05_b	0.102	1.16_a	0.164	1.02_b	0.167	**12.8**
ADF	43_a	3.1	35_b	4.6	30_c	4.1	37_b	3.1	35_b	3.3	**23.7**

[1] Significant difference ($p < 0.05$) of variables across grasslands indicated by bold F-stat.
[2] Tukey's post-hoc test, different subscripts indicate significant differences in mean values of row variables across columns ($p < 0.05$)

Most fruit-beverage resources were associated with trees or shrubs, which included species such as *Strychnos spinosa* or *Sclerocarya birrea.* However, fruiting geoxylic suffrutex species (e.g. *Salacia kraussii*, *Parinari capensis* and *Syzygium cordatum* and forbs (e.g. *Ancylobothrys capensis*) also contributed to the fruit-beverage resources offered by dune-ridge and suffrutex grassland. Building resources such as polls (e.g. *Hymenocardia ulmoides*) and thatching grass species (e.g. *Hyperthelia dissoluta*) were largely restricted to elevated dune-ridge or suffrutex grasslands, whereas the occurrences of sedge species used for fibre (e.g. *Cyperus natalensis*) were relatively common in low-lying grassland positions. Leafy vegetable species locally known as *imfino* (e.g. *Vigna vexillata* and *Asystasia gangetica*) tended to be less abundant in low-lying grasslands.

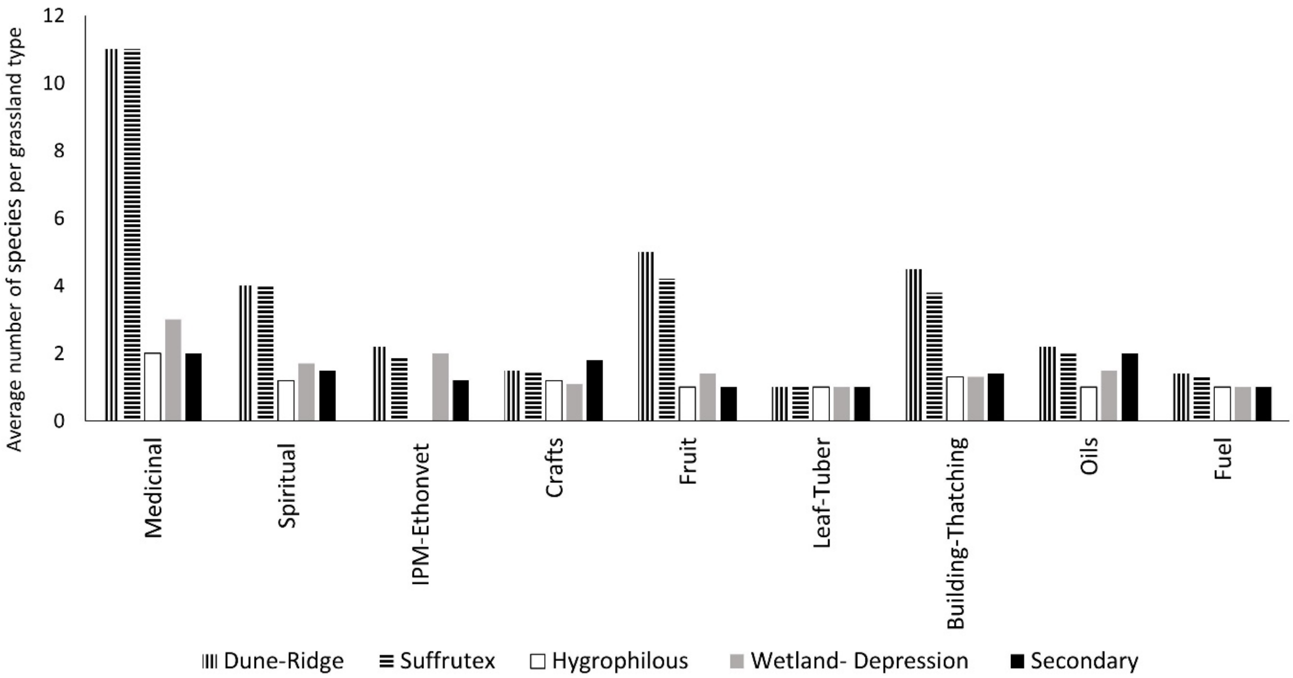

Figure 2. The average number of species per plot across use-classes and grassland types.

Species in grasslands occurring in elevated areas (dune-ridge and suffrutex) and low-lying (hygrophilous and wetland-depression) topographic areas covered all medicinal use-classes. However, elevated grasslands contained more species related to the treatment of gastro-intestinal (df =13, $p < 0.05$), gynaecology (df = 6, $p < 0.05$), respiratory (df = 4, $p < 0.05$), febrile (df = 4, $p < 0.05$) and skin (df = 4, $p < 0.05$) than low-lying grasslands (Figure 3). By contrast, hygrophilous and wetland-depression grasslands were important habitat for uncommon but moisture-dependent medicinal plant species such as *Chironia purpurascens*, *Lobelia coronopifolia* and *Cephalaria oblongifolia*. Secondary grassland accounted for 13 of the 17 medicinal use-classes, meaning that plantation forestry disturbance had decreased the capacity of grasslands to provide medicinal plant resources used for treating infertility, venereal, renal and cardiac ailments (Figure 3).

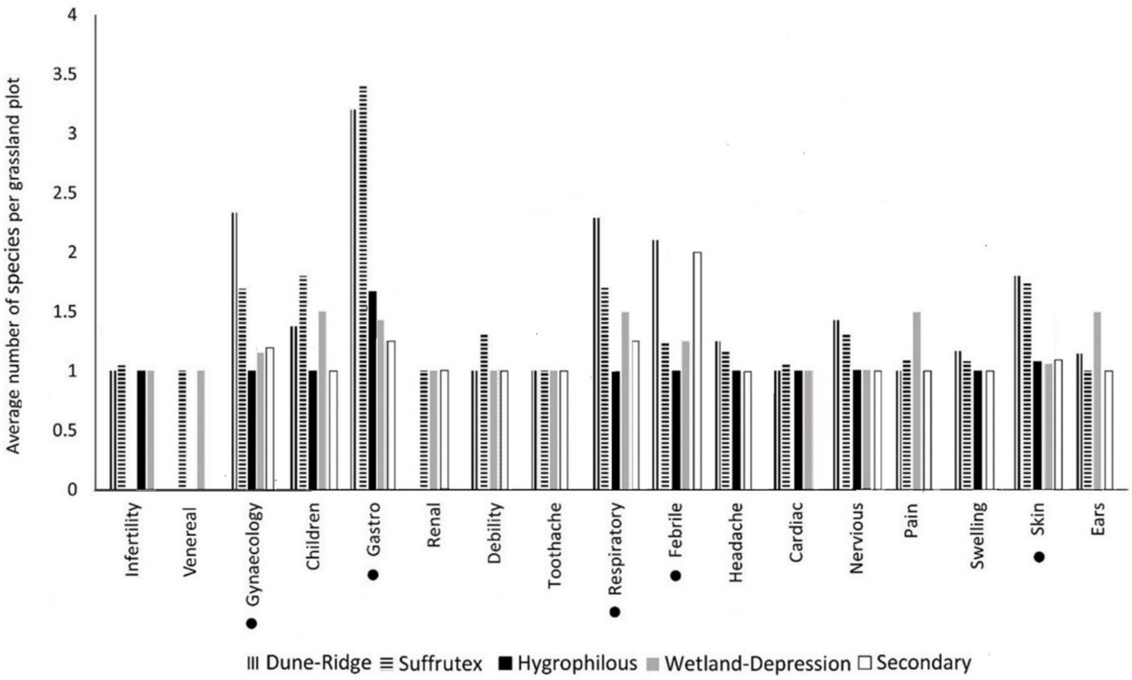

Figure 3. The average number of species per plot across medicinal use-classes and grassland type. Dark circles (below use-classes) indicate a significant ($p < 0.05$) difference between elevated and low-lying grasslands.

Hygrophilous and wetland-depression grasslands had the best combination of variables for livestock forage. GV per plot was greatest in hygrophilous grassland, wetland-depression grassland had on average the highest leaf N, while dune-ridge grassland had the highest ADF (Table 1). Low GV and N, coupled with high ADF in elevated grasslands indicated that dune-ridge and suffrutex grasslands were least suited to supply high-quality forage resources. Based on the statistical significance, the indices of GV and N in secondary grassland were equal to or greater than those of dune-ridge and suffrutex grasslands.

Grasses responsible for high forage scores in wetland-depression grassland were *Acroceras macrum* and *Urochloa arrecta,* and *Themeda triandra* for hygrophilous grassland (Table 2). Species contributing to high percent ADF in dune-ridge grassland were fibrous grasses such as *Hyperthelia dissoluta* and also *Andropogon schirensis*. The leaf N of woody-suffrutex species was relatively high and comparable with palatable grass species. Pioneer lawn grasses *Cynodon dactylon* and *Digitaria diversinervis* were major contributors to the forage value of secondary grassland.

Table 2. N and ADF values, GV and indicator value (IV) scores of dominant species across grassland types.

Landscape class	**Grassland type**	**Species**	**Growth Form**	**ADF**	**N**	**GV**	**IV**
Elevated	Dune-ridge	*Andropogon schirensis*	Densely tufted grass	45	0.6	4	60
		Andropogon gayanus	Robust tufted grass	40	0.8	7	45
		Hyperthelia dissoluta	Robust tufted grass	58	0.6	4	76
		Trachypogon spicatus	Rhizomatous and tufted grass	40	0.5	1	29
		Urelytrum agropyroides	Coarse tufted grass	40	1.2	1	32
	Suffrutex	*Cymbopogon caesius*	Densely tufted grass	45	1.0	2	63
		Digitaria natalensis	Tufted and rhizomatous grass	38	0.8	6	41
		Parinari capensis	Geoxylic suffrutex	42	1.0	1	44
		Syzygium cordatum	Geoxylic suffrutex	16	1.5	1	24
		Tristachya leucothrix	Tufted grass	45	0.6	6	72
Low-lying	Hygrophilous	*Themeda triandra*	Caespitose rhizomatous grass	27	1.1	8	56
		Eragrostis lappula	Upright rhizomatous and tufted grass	32	0.8	2	67
	Wetland-depression	*Acroceras macrum*	Prostrate, rhizomatous and tufted grass	33	1.5	7	39
		Urochloa arrecta	Prostrate, hygrophyte, stoloniferous and tufted grass	36	1.0	7	26
		Centella asiatica	Prostrate, cosmopolitan herbaceous dicotyledon	33	1.5	1	28
		Leersia hexandra	Hydrophyte and rhizomatous grass	39	1.8	4	48
Forestry plantation	Secondary	*Cynodon dactylon*	Rhizomatous and stoloniferous	28	0.9	3	33
		Digitaria diversinervis	Rhizomatous and stoloniferous	36	1.0	4	77

* Indicator value (IV) as given by Starke et al. (2020).

Multivariate analysis of grassland resources

A three-dimensional NMS solution revealed the least stress in the data (stress = 13.2, $p < 0.001$). The first ordination axis (explaining 52% of variation and correlating with SOC) accounted for the primary difference in species composition in grasslands which occurred across a gradient between elevated and low-lying grassland types (Figure 4). The second and third axes accounted for 14% and 12% of variation in the ordination, respectively. Non-forage use-classes of fruit-beverage ($r^2 = 0.74$), medicine ($r^2 = 0.71$) and building-thatching ($r^2 = 0.73$) correlated positively with the first ordination axis (Appendix B), meaning that a gradual change in species composition from low-lying grassland to elevated grasslands resulted in increasing complexity of non-forage grassland resources. Forage variables GV and N correlated weakly ($r^2 < 0.2$) with wetland-depression grassland and, to a lesser extent, hygrophilous grassland.

The primary gradient of species composition and edaphic environment, therefore, represented an inverse relationship between forage and non-forage resources, however, variation described by the second and third axes implied that additional (non-topographic) factors also affected the distribution of grassland resources. For example, forestry disturbance had constrained the species composition of secondary grassland and consequently its forage value. Although not shown by ANOVA (Table 1), contour models (Appendix A) indicated that geo-suffrutex grassland provided a slightly greater variety of medicinal plant species than dune-ridge grassland.

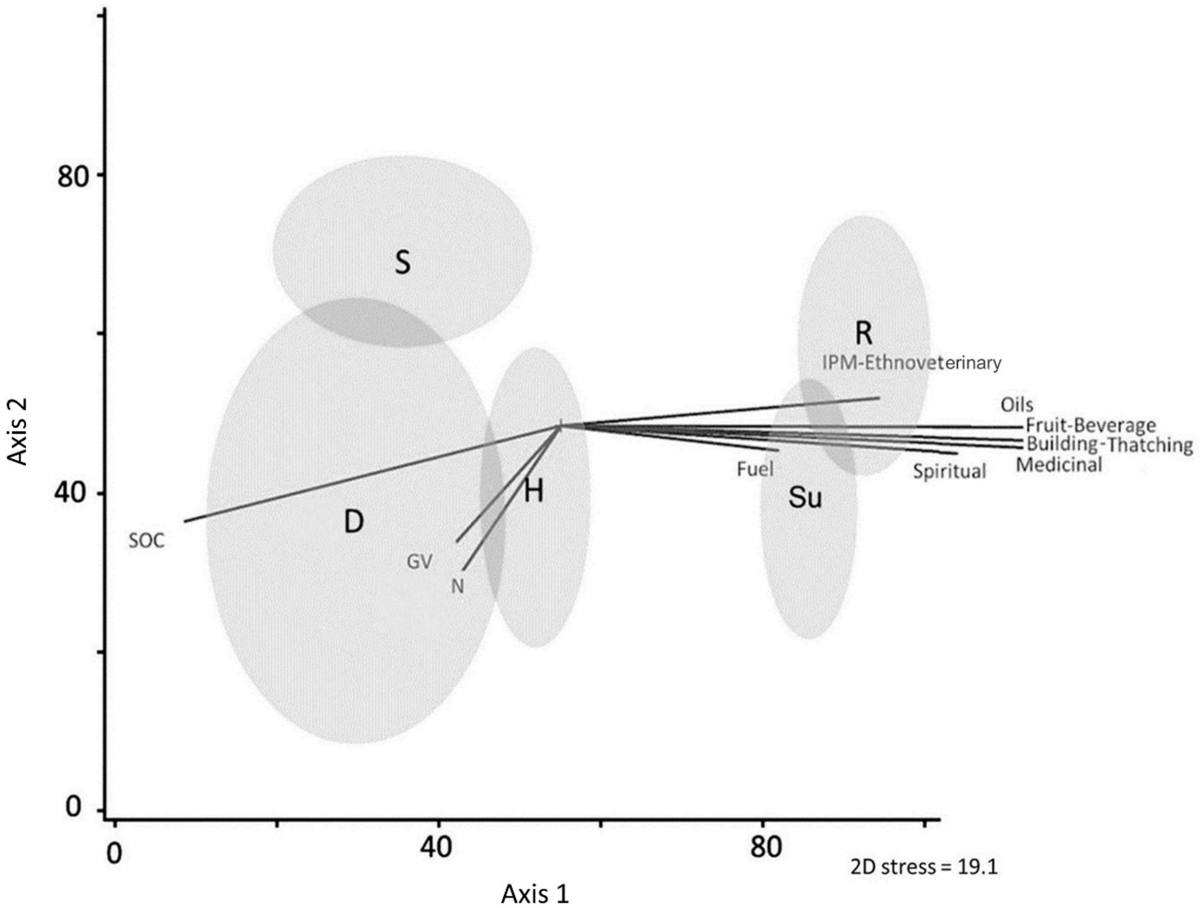

Figure 4. NMS ordination of species composition across grassland types, and a biplot representing forage and use-variables. SOC (a proxy for soil fertility) was plotted to show the topo-edaphic gradient along the first axis. Grassland types (**R** = Dune-ridge, **Su** = Suffrutex, **H** = Hygrophilous**, D** = Wetland-depression and **S** = Secondary) are represented by centroids, with ellipses showing the standard deviation along the first and second axis. Variable codes: **SOC** = Soil organic carbon, **GV** = grazing value, **N** = percent nitrogen of grasses in a plot. Use-classes (refer to the number of species of a use-class in a plot): **Fuel** = cooking or other fuel purposes, **IPM-Ethnoveterinary** = pest and ethnoveterinary purposes, **Oils** = species with oil resources, **Fruit-Beverage** = species consumed for fruit or beverage purposes, **Spiritual** = species used for spiritual purposes, **Building-Thatching** = species used for construction purposes, **Medicinal** = medicinal plant species.

Discussion

The effect of topo-edaphic conditions on grassland resources

Many of the remaining unprotected IOCB ecosystems in Maputaland are rapidly developing into an agro-ecological landscape composed of natural vegetation inter-mixed with land uses such as homesteads, horticultural gardens, and forestry plantations (von Roeder 2014; Jewitt et al. 2015). The role of grasslands within such a matrix is uncertain, raising questions about the future provision of grassland ecosystem services and the products they provide. A principal ecological pattern of IOCB coastal grasslands is that floristic composition tends to follow a topographic gradient from relatively simple communities in fertile low-lying sites to more complex grassland communities in elevated and unfertile areas (Starke et al. 2020). Important findings were therefore that differences of grassland floristic composition corresponded with differences in the supply of grassland ecosystem services, and that low-lying areas provided a different set of ecosystems services to elevated grasslands. Specifically, that forage resources in low-lying hydrophytic grasslands were superior to drier elevated grasslands and that species rich elevated grasslands had a greater diversity of non-forage grassland resources such as of medicinal plants, fruit-beverage, oils and building material.

Non-forage grassland resources

Arguably the most valuable non-forage grassland resources occurring in elevated grasslands were medicinal plant species because of the central role plant medicines have in primary South African health care (Hutchings et al. 1996; Mander et al. 2007) of which the most common use-classes were for gynaecology, gastrointestinal, respiratory, and febrile conditions, and skin treatment (Figure 3). Other culturally valuable non-forage grassland resources were related to spiritual use, for example, *Helichrysum* species (or *imphepho*), which induces trances and invokes ancestor spirits (Sobiecki 2006).

The grassland woody component, which provided a substantial variety of non-forage resources, occurred mostly in elevated grassland. For example, tree or shrub species that have evolved to survive in fire-exposed grassland conditions such as *Annona senegalensis* or *Sclerocarya birrea,* and geoxylic suffrutex species such as *Salacia kraussii* and *Parinari capensis,* provide fruit, beverage and oil resources (Cunningham 1985). Tree species used for timber or craft applications (e.g. *Combretum molle*) occurred solely in dune-ridge grassland, while leafy vegetables (*imfinos*) such as *Asystasia* *gangetica* also indicated a preference for growing in elevated grasslands. Graminoids did not provide as diverse an array of non-forage resources as woody or forb species; however, useful graminoids were *Cymbopogon caesius* (used medicinally for oils), thatching grasses such as *Hyperthelia dissoluta,* and craftwork grasses such as *Digitaria eriantha* (Cunningham 1985).

Forage resources

We showed that low-lying grasslands had greater forage value (GV and N) than elevated and secondary grasslands. This was an effect of topographic position because low-lying grasslands were wetter and more fertile than elevated grassland (Starke et al. 2020). Wetland-depression grassland was largely composed of palatable lawn-grasses (e.g. *Acroceras macrum*), whereas hygrophilous grassland was characterised by a heterogenous composition of lawn and caespitose-rhizomatous species, some of which were more nutritious (e.g. *Themeda triandra*) than others (e.g. *Eragrostis lappula*). Various grazing management systems are conceivably appropriate for hygrophilous and wetland-depression grasslands, but any option employed should ensure an appropriate pattern of grazing to maintain species composition and prevent competition from taller, less palatable species (Morris 2002; Hempson et al. 2015). The duration and intensity of grazing in hygrophilous and wetland-depression grasslands should differ from elevated grasslands because prostrate lawn grasses avoid comprehensive defoliation by livestock (Roux 1969; Hempson et al. 2015), while the forage value of grazing lawns is further improved because lawn-grass structure is appropriate for cattle to maintain a high intake (Illius et al. 1995). The composition of elevated grassland was dominated by tufted grass species which would have progressively become more fibrous as the growing season developed and therefore less nutritious (Morris 2002). However, tufted fibrous grasses are valuable in rangeland systems because they provide a mixed dietary intake for livestock, which require a balance of high protein and fibrous forage, and they provide intermittent high-quality leafy forage after seasonal burns (Morris 2002).

Seasonal forage resources are a key component of any grazing system because access to quality forage at the height of the dry-season ~~is a key~~ strongly influences herbivore population dynamics (Illius and O'Connor 2000). In this context, low-lying and elevated grasslands would provide different forms of dry-season winter forage, hygrophilous and wetland-depression grassland would supply a high protein forage, while tufted grasses in elevated grasslands would provide a low-quality but a relatively large absolute amount of forage. In an ideal agro-ecological landscape these differences, that is the ratio of grazing lawns to high biomass tall grassland over space and time, would ensure that a robust set of forage resources are available for meeting livestock needs across seasons. The diet of cattle is composed of significant amounts of browse during the dry season (Skinner et al 1984) so, in addition to tall-grass forage, the woody component of elevated grasslands will provide supplementary fodder resources through various browse species (Kunene et al. 2009).

Secondary grassland

The soil conditions and floristic elements, such as lawn grass dominance, of secondary grassland was comparable with low-lying communal grasslands (Starke et al. 2020). This was a consequence of secondary grassland being located in mesic sites and sharing lawn grasses such as *Cynodon dactylon, Digitata diversinervis, Ischaemum polystachyum* and *Acroceras macrum.*-However, after a decade of regeneration the resources provided by secondary grassland were fewer than in their environmental analogue of low-lying communal grasslands. For example, secondary grassland had notably lower forage value than wetland-depression and hygrophilous grasslands, and also did not contain the same variety of non-forage resources, specifically, hygrophilous medicinal plant species (Figure 3). Additionally, *Themeda triandra*, a keystone fodder graminoid (Snyman et al. 2013), was not recorded in secondary grassland and is a good example of a valuable native forage grass that can be extirpated from a landscape due to land use change (Roux 1969).

The lack of old-growth grassland recovery in secondary grasslands has been reported elsewhere on the Maputaland coastal plain (Zaloumis and Bond 2016) and is a typical consequence of forestry plantation disturbance (Buisson et al. 2018). This has implications for the supply of ecosystem services because short-term ambition to convert grassland to alternate land uses can lead to decadal-long consequences for the ecosystem services supplied by that system. Furthermore, active restoration of sub-tropical grassland species is challenging and costly (Buisson et al. 2018) with a consequence that large-scale restoration of grassland biodiversity is not a practical option for most rural communities. In the context of grassland recovery after the abandonment of forestry plantations, hydrological services would return relatively quickly (Scott and Lesch 1997) while forage resources would partially return but would not match their pre-disturbance value without assisted regeneration. Many cultural ecosystem services provided by grasslands are likely to be lost during grassland transformation, specifically medicinal geophytes which are particularly vulnerable to disturbance (Roux 1969).

The role of grasslands in agro-ecological landscapes

Transformation of IOCB vegetation on the Maputaland coastal plain towards an agro-ecological matrix of land uses will have long-term consequences for most of its grassland environments. The risks involved include localised species extinction, specifically forbs (Zaloumis and Bond 2016) but also grass species (Starke et al. 2020), and further risks to water security because afforestation of hygrophilous or wetland-depression grasslands reduces the resilience and functioning of wetland systems (Everson et al. 2019). Grassland fire regimes are susceptible to landscape fragmentation and even a relatively small area of fire-protected forestry plantation will affect the composition of surrounding grassland. There are no straight-forward options for the sustainable use of grasslands in the context of developing rural production landscapes (O'Connor 2005; Starke et al. 2020). However, grasslands in the coastal Maputaland region are relatively productive and wetland depression or hygrophilous grasslands provide good quality year-round forage. If utilised for forage in conjunction with commercialising local livestock products (Mapiye et al. 2007), then a more secure future for grassland ecosystems might be realised. For example, by maintaining a balanced ratio of short lawn grasses and tufted fibrous grasses across rangeland, communities would optimise forage resources, while also ensure habitat for medicinal plants or other potentially commercial non-forage resources such as palm fibre (Cunningham 1985). In elevated grasslands, a variety of opportunities are available for the development of silvopastoral systems which include livestock-derived income (Mapiye et al. 2007; Musemwa et al. 2008), commercialising woody grassland species such as *Sclerocarya birrea* (Shackleton et al. 2018) or medicinal plant production (Mander et al. 2007). In secondary grasslands, a silvopasture land use system might also focus on commercial nut crops (e.g. *Macadamia integrifolia* or *Anacardium occidentale*) planted at low-densities (50-150 trees ha^{-1}) so that trees provide enough light for native forage grasses such as *Urochloa brizantha* or *Urochloa maxima* for livestock production.

Conclusion

Grasslands in Maputaland provide productive grazing lawns and habitat for a variety of plants that supply non-forage resources. The spatial differences of forage and non-forage grassland resources were related to topographic position, soil conditions, and human disturbances. These differences would assist in meeting a key challenge in natural resource management, which is to analyse objectively the trade-offs between agricultural production and maintaining natural environments (Neke and Du Plessis 2004). If these trade-offs are not conducted correctly, grassland resources such as the supply of medicinal and other non-forage resources will diminish considerably over time. Grasslands are tolerant of a variety of grazing and browsing practices so livestock products are a reasonable option that could ensure ecological and resource sustainability of grassland ecosystems. In Maputaland, one focus could be towards developing novel land use types that integrate grassland products with newly-emerging African consumer markets.

Acknowledgements

This research was funded by the Water Research Commission (WRC) of South Africa, project no: K5/2554, with co-funding and support provided by the Department of Economic Development, Tourism and Environmental Affairs (EDTEA). We thank the TMM Trust and the Department of Agriculture, Forestry and Fisheries (DAFF) for access to Manzengwenya plantation. The izinduna of KwaZibi district, Mr. M.E Tembe and MvelaBusha district, Mr. J.M Tembe, including field assistants X. Ngubane, and B. Mdhluli of the Isibusiso-Esihle Science Discovery Centre provided essential support during the project.

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Appendices

APPENDIX A

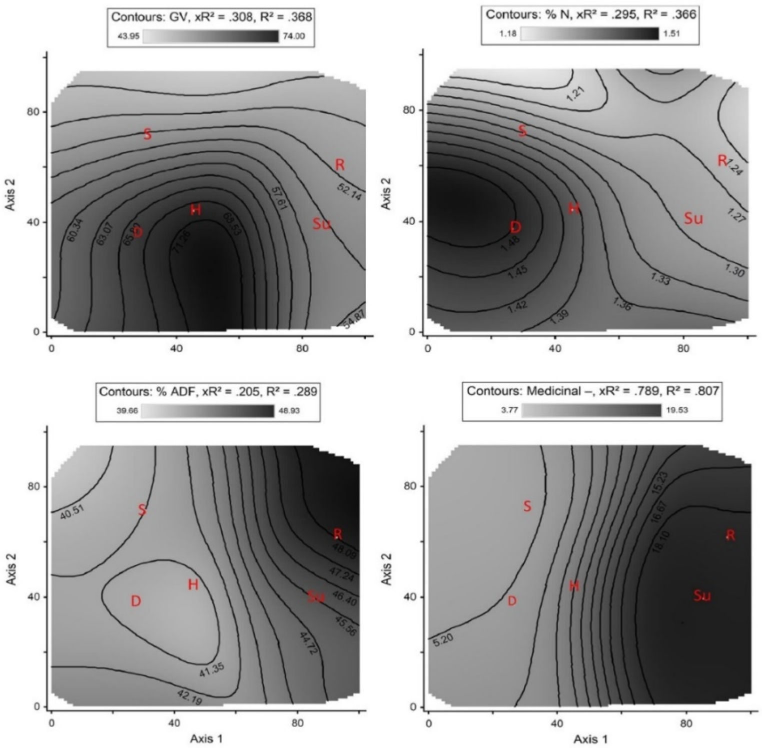

Figure A. NMS contour model showing how species composition affected the distribution of forage resources and medicinal plant species across grasslands

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APPENDIX B

Table B. Pearson's correlation coefficient (presented in r^2 values) of forage and use-classes variables with the first three ordination axes

Variable	Axis-1	Axis-2	Axis-3
Acid Detergent Fibre	0.06	0.01	0.04
Grazing value	0.16	0.11	0.05
Nitrogen	0.12	0.19	0.05
Medicinal	0.71	0.03	0.04
Spiritual	0.54	0.03	0.01
IPM - Ethnoveterinary	0.42	0.04	0.01

Crafts-Dye-Fibre	0.18	0.01	0.01
Fruit-Beverage	0.74	0.01	0.04
Leaf - Tuber	0.11	0.02	0.02
Building-Thatching	0.73	0.02	0.02
Oils	0.66	0.01	0.03
Fuel	0.29	0.03	0.05
Soil organic carbon	0.52	0.11	0.06