

1 **Topo-edaphic environment and forest plantation disturbance explain patterns of**
2 **grassland species richness, composition, and structure in an agro-ecological landscape,**
3 **Maputaland, South Africa**

4
5 Starke A.P ^{1*}, O'Connor T.G ², Everson C.S ^{3,4}
6

7 ¹ Post Graduate Forestry Programme, Department of Plant and Soil Science, University of
8 Pretoria

9 ² South African Environmental Observation Network (SAEON), PO Box 2600, Pretoria,0001

10 ³Centre for Water Resources Research, University of KwaZulu-Natal, South Africa

11 ⁴Department of Plant and Soil Sciences, University of Pretoria
12
13

14 *Author Correspondence: Box 166, Umdloti Beach, 4350, South Africa; Tel: +27

15 761456896; Email: allister.starke@gmail.com
16

17 Keywords: sub-tropical grassland, hygrophilous grassland, geoxylic suffrutex, grassland
18 afforestation, secondary grassland
19
20
21
22
23
24
25
26
27
28
29

Abstract

Grasslands of the Maputaland coastal plain are biologically diverse and provide a variety of ecosystems services. Yet grasslands in this region are vulnerable to continuing development by plantation forestry which provide economic benefits to local communities. In order to provide a framework for land use that maintains grassland heterogeneity in complex agro-ecological systems, this paper characterises the main relations between grassland species composition with the physical environment and forestry plantation disturbance. Grassland species composition corresponded with landscape position and soil organic carbon. Grasslands occurring in infertile, elevated landscape positions were the most diverse having a greater richness of tufted graminoids, herbaceous forbs, and geoxylic suffrutices than grassland occurring in low-lying dystrophic sites, which were dominated by rhizomatous and stoloniferous graminoids. Previously afforested grasslands (i.e. secondary grassland) were species poor, lacked keystone grasses such as *Themeda triandra*, were dominated by a few species of rhizomatous or stoloniferous grasses, and had been colonised by pioneer or ruderal forbs. Grassland species composition affects the provision of ecosystem services so to maintain a full complement of these attributes, grassland landscapes in Maputaland should comprise intact grasslands which cover both elevated and low-lying topographic positions.

Introduction

Sub-tropical grasslands of South Africa's Indian Ocean Coastal Belt Biome (IOCB) have been extensively transformed through plantation agriculture and urbanisation resulting in altered ecosystem functioning and biodiversity loss (Mucina et al. 2006). However, the short-term economic benefits of grassland transformation are offset by a loss of ecosystem services such as hydrological regulation (Everson et al. 2011), supply of livestock forage, and a loss of non-forage grassland resources, such as plants used for medicinal, spiritual or nutritional purposes (Dzerefos and Witkowski 2001; Bengtsson et al. 2019). In order to optimise the provision of

61 ecosystem services from a landscape, study of the relationship between species composition
62 and environmental conditions is required because the provision of ecosystem services from
63 natural vegetation may vary considerably in heterogeneous and diverse ecosystems. Dzerefos
64 and Witkowski (2001), for example, highlight a variety of medicinal resources offered by
65 species-rich highveld grasslands that occur across a range of local habitat types, documenting
66 120 medicinal species which include contributions from trees, shrubs, geoxyllic suffrutices,
67 graminoids, bulbs, and herbaceous dicotyledons. Differences of botanical and structural
68 heterogeneity also affect how grasslands should be managed (Tilman 1987; O'Connor et al.
69 2010), indicating that different types of IOCB grassland would fulfil different functions in an
70 agro-ecological landscape.

71 A key management objective in agro-ecological systems is to maintain delivery of ecosystem
72 services from natural vegetation while pursuing competing production activities (Joubert et al.
73 2016). Forestry plantations require fire-protection (Joubert et al. 2016), sustainable cropping
74 requires fertile soils (Jury 2008), and livestock production is best undertaken in grasslands
75 offering forage of high quality that is available throughout the year (O'Connor et al. 2010).
76 Non-forage grassland resources (e.g. medicinal plants) require habitat for forb and woody plant
77 species. Hence, in a system of interest, understanding the dominant patterns of vegetation
78 heterogeneity is a precondition to deciding which areas of land should be considered for
79 production activities.

80 Topo-edaphic influences are a primary determinant of landscape-level variation in vegetation
81 composition and structure of southern African savannas (Rutherford et al. 2006; Clegg and
82 O'Connor 2012). For example, on the Maputaland coastal plain, there is a clear distinction in
83 vegetation composition occurring on 'fine textured' soils located in low-lying interdunal
84 landscape positions compared with vegetation growing in sandy elevated positions (Matthews
85 et al. 1999; Pretorius et al. 2016). Grasslands species richness is generally highest in nutrient
86 poor (Tilman 1987) or undisturbed sites (O'Connor 2005). The expectation for IOCB
87 grasslands is, therefore, that undisturbed, nutrient-poor grasslands will be more diverse and
88 supply a greater variety of non-forage ecosystem services than nutrient-rich but less diverse
89 grasslands, which should provide superior forage resources.

90 The composition and structure of secondary grassland after annual crop abandonment differs
91 considerably from its undisturbed 'old-growth' counterpart (Roux 1969) but this tends to
92 reflect the type of disturbance (O'Connor 2005; Buisson et al 2018). Factor affecting the

93 composition of regenerating grassland include competition from pioneer grasses in fertile post-
94 agricultural soils (Tilman 1987; Lindsay and Cunningham 2011), propagule constraints that
95 are influenced by the proximity to patches of untransformed grassland (Mentis 2006), and that
96 the majority of grassland forb species (especially re-sprouting bulbs) resemble K- rather than
97 r-selected species, as plants are usually long-lived post-establishment and their reproductive
98 output is low (Bond and Midgley 2003; Zaloumis and Bond 2016). Afforestation affects
99 grassland composition through shading and soil disturbance which typically results in the
100 return of a mono-dominant grass sward with poor forb richness, even after decades of
101 regeneration (Zaloumis and Bond 2016).

102 A challenge encountered during agro-ecological planning is developing acceptable approaches
103 to mitigate the negative effects associated with vegetation disturbance and fragmentation
104 (Joubert et al. 2016). Commercial forestry landscapes develop ecological networks that aim to
105 protect wetlands from the adverse effects of plantation trees and to provide functional grassland
106 habitat matrices (Joubert et al. 2016). However, in communal landscapes (i.e. those
107 characterised by a mixture of settlement, small-holder agriculture and rangeland) the objectives
108 for grassland management should reflect a greater diversity of needs, such as to include grazing
109 and non-forage resources, for example plant medicines (Dzerefos and Witkowski 2001;
110 O'Connor 2005). This study is a component of a programme intended to develop a land use
111 model for the IOCB that aims to support production enterprises as well as to optimise provision
112 of grassland ecosystem services. The aim was to describe the main grassland types in terms of
113 botanical composition, structure, and environmental determinants, as a basis for decision-
114 making concerning appropriate land use for specific grassland types.

115 The expected pattern of floristic and structural variation was that grassland composition would
116 relate to differences in landscape topography and soil conditions. Specifically, that low-lying
117 grasslands would contain sufficient clay, soil organic carbon and moisture to maintain
118 rhizomatous and stoloniferous lawn-grass communities, whereas a more complex composition
119 of tufted grasses, woody plants and forbs would occur in nutrient poor, elevated topographic
120 positions. It was further expected that previously afforested, regenerated grassland would be
121 floristically less diverse than communal elevated or low-lying grasslands. An analysis of the
122 forage and non-forage ecosystem services provided by the grassland types identified in this
123 study are reported in a companion paper (Starke et al. 2020).

124

125 **Study site and Methods**

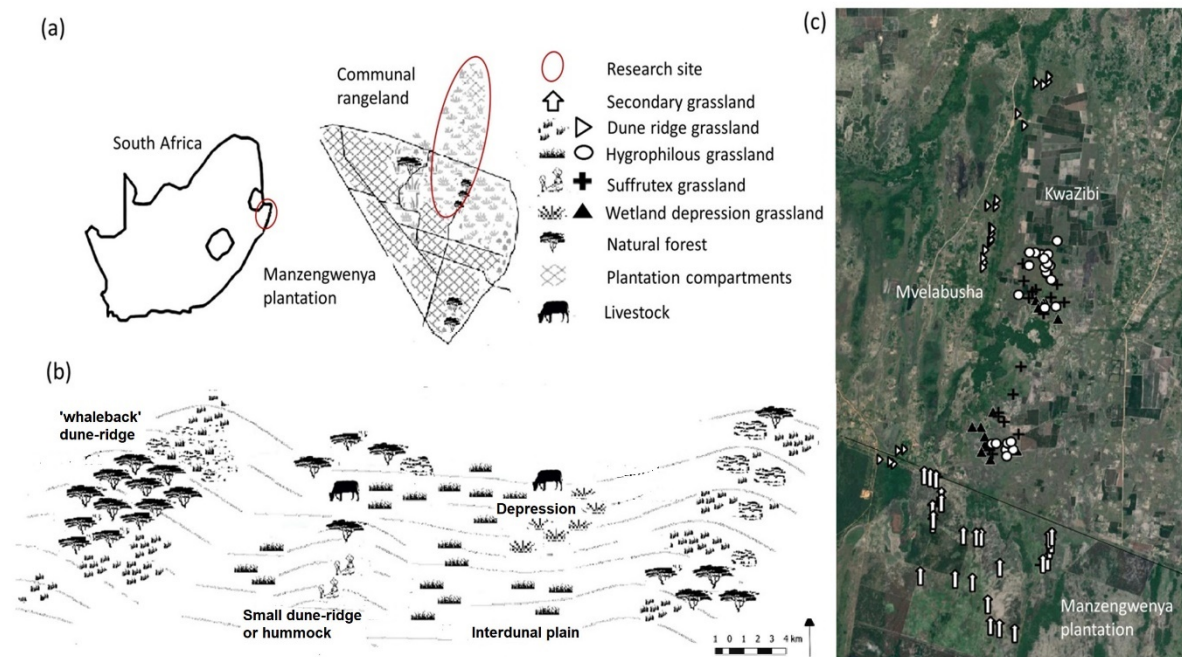
126 *Location, topography, and vegetation type*

127 The study was conducted in a mosaic of forests, grasslands, wetlands, timber plantations and
128 rural settlements on the Maputaland coastal plain, north-east South Africa (Figure 1a, b). The
129 region is humid with a mean annual temperature of 21°C and a mean annual precipitation of
130 964 mm (Mucina et al. 2006). Most precipitation falls in summer between October to March,
131 but up to 40% may occur between April to August. Fire occurs naturally and typically occurs
132 during cooler, drier months between May and October (Mucina et al. 2006).

133

134 The topography of the coastal plain is undulating, with paleo-dune elements that are
135 characterised by large ‘whaleback’ dune-ridges, smaller less-pronounced dune-ridges,
136 hummocky dunes, interdunal flats, floodplains, and wetland-depressions. Dune-ridges and
137 hummocks are composed of nutrient-poor dystic regosols that are unconsolidated, sandy and
138 drain well (Figure 1b) (Matthews et al. 1999; Botha and Porat 2007). Consequently, they
139 contain minimal amounts of clay and soil organic carbon (SOC). Low-lying interdunal plains
140 vary in width and form the basis of a network of pan-systems. They are composed of humic
141 gleysols (i.e. acidic sands containing a high amount of SOC) but are less mesic than wetland-
142 depressions which are closest to the water table. Wetland-depressions contain sour organic
143 histosols with a rich organic A horizon and peat deposits (Matthews et al. 1999; Pretorius et al.
144 2016). These topographic features are underlain by a sedimentary sequence of unconsolidated
145 sandy-clay horizons, termed the Port Durnford formation, followed by Tertiary derived white
146 sandy limestone, and then a Cretaceous clay horizon, all of which slope in an easterly direction
147 (Botha and Porat 2007). Underlying stratifications direct a network of complex subsoil
148 aquifers, which permeate upper soil horizons in low-lying areas during periods of high
149 precipitation (Everson et al. 2019).

150



151
 152 Figure 1 (a) Geographic location of the study area, showing the extent of the Manzengwenya
 153 plantation and adjacent communal rangeland. (b) Conceptual topographic and ecological
 154 framework of vegetation in the study area. (c) An aerial image of the study site showing plot
 155 locations of stratified grassland types.

156
 157 The IOCB grasslands on the Maputaland coastal plain comprise a mosaic of forest-grassland
 158 vegetation which is sub-tropical in character. Grassland within the districts of Mvelabusha
 159 and KwaZibi (Figure 1c) contain regionally recognised grassland types, such as coastal belt
 160 grassland that support elements of dry-grassland, palm veld, and thicket groups (Mucina et al.
 161 2006), hygrophilous grassland (van Wyk et al. 1991), and a specialised wooded grassland
 162 community characterised by geoxylic suffrutex species (Maurin et al. 2014). Geoxylic
 163 suffrutices are an unusual group of pyrogenic low-growing woody-plants that have large
 164 underground stems called geoxyles. They occur in SA's coastal grasslands forming so-called
 165 'underground' forests (Maurin et al. 2014). Grasslands were utilised by livestock as
 166 communal rangeland, with stocking rates estimated to vary between 0.2 and 1 LSU ha⁻¹.
 167 Secondary grasslands occurred in Manzengwenya plantation on previously afforested sites
 168 that had been abandoned for between 10-15 years (Figure 1c). Two *Pinus elliotii* rotations
 169 had been completed in the plantation which was afforested in the late 1950s. Secondary
 170 grassland had been grazed by livestock and had been burned at a return interval of three to
 171 six years since 2000 (Starke et al. 2019).

172

173 *Sampling approach*

174 Four potential grassland types, representing a topographic gradient from low-lying to elevated
175 areas, were stratified *a priori* to sampling by using high-resolution aerial imagery (differences
176 in green hue-value separated types) in combination with a 5 m digital elevation model at a
177 resolution 30 m 1 arc second in ArcGIS (Figure 1c). Indicator species (van Wyk et al. 1991;
178 Matthews et al. 1999; Pretorius et al. 2016) in the field were used to assess whether
179 stratification was correct. In each of these grassland units, plot locations were chosen using the
180 sampling design tool in ArcGIS (ESRI ArcGIS 2011). Stratified plots (Figure 1c) of (i) dune-
181 ridge grassland (n = 23) occurred on dune crests and slopes; (ii) geoxylic-suffrutex grassland
182 (n = 22) was confined to lower ridges or hummocks embedded within interdune plains; (iii)
183 hygrophilous grassland (n = 26) covered flat interdunal plains; (iv) and, wetland-depression
184 grassland (n = 14) were located within depressed or seasonally wet grassland areas. Secondary
185 grassland was stratified as regenerated grassland in the north of Manzengwenya plantation
186 resulting in sampling plots (n = 24) towards the south of the study area. This was not of concern
187 because climate gradients, at this spatial scale, extend from east to west with no clear effect
188 along the north-south gradient. Permanently saturated wetlands were not part of this study.

189

190 If GIS plot positions were unsuitable for sampling, a new position within 100 m of the original
191 GIS point was randomly selected in the field. The botanical composition of each 100 m²
192 circular plot was measured using a modified Braun-Blanquet approach, whereby the mid-point
193 cover range of each species in a plot was estimated after Wikum and Shanholtzer (1978) and
194 then modified according to van der Maarel (2007) using a scale of : a single plant = 1.2; < 5%
195 = 2.5; 5-25% = 10; 25-50% = 40; 50-75 = 80; 75-100% = 160. The approach provides a scaled
196 increase in cover percentage for abundant species (which are often underestimated) and suits
197 ordinal data used in multivariate analysis (van der Maarel 2007). Plant nomenclature follows
198 the African Plant Database (2020).

199

200 Measures of botanical diversity were species richness and forb richness within a plot. Grassland
201 structure was represented by physiognomic variables that were derived from sampled data.
202 Structural variables were summarised by percentage cover of the variable of concern per plot,
203 and were: (i) all woody species; (ii) geoxylic-suffrutex species; (iii) sedges; (iv) all grasses; (v)

204 tufted-only grasses; (vi) tufted grasses having either stolons or rhizomes; (vii) herbaceous
205 dicotyledon forbs; (viii) and herbaceous monocotyledon forbs.

206

207 A soil sample was collected from the top 10 cm in the centre of each plot. Samples were
208 analysed for texture and chemical composition at Analytical Services, KwaZulu-Natal
209 Department of Agriculture and Rural Development (Manson et al. 2020). Variables analysed
210 were percent soil organic carbon (SOC), percent clay, percent nitrogen (N), phosphorus (P, mg
211 L⁻¹), potassium (K, mg L⁻¹), calcium (Ca, mg L⁻¹), magnesium (Mg, mg L⁻¹), pH, exchange
212 acidity and reserve acidity (in cmol L⁻¹).

213

214 Hydrological variables (depth and head) for each plot were derived from contours of the main
215 groundwater aquifer modelled for the year 2016 using MODFLOW 2005 (Everson et al. 2019).
216 For each plot, the depth to the water table represented the difference in vertical distance from
217 the ground surface elevation (derived from the Shuttle Radar Topography Mission DEM raster
218 interpolated using 5 m surveyed contours, at a 30 x 30 m resolution) to the MODFLOW
219 modelled water table elevation. The head was derived as the distance of the water table to the
220 mean sea-level. The landscape position of a plot was assigned a binomial value, indicated as
221 Elevated (1) or Low-lying (2).

222

223 *Statistical procedures*

224 Grassland classification was performed using Euclidean space based on Ward's Minimum
225 Distance and constrained by the number (five) of originally stratified grassland types. Ward's
226 minimum distance is an agglomerative hierarchal technique resulting in the smallest within-
227 group variation at each cluster (McCune and Mefford 2018). Preparation of data for
228 classification involved removal of species with less than two occurrences, conversion of Braun-
229 Blanquet cover-abundance to modified mid-point values (van der Maarel 2007), and log
230 transformation. A post-classification assessment to assess within-group homogeneity was
231 conducted using a multi-response permutation procedure (MRPP) based on Bray-Curtis
232 distance. For MRPP, the test statistic A is a descriptor of within-group agreement. If plots are
233 identical within groups, then $A = 1$, if heterogeneity within groups equals expectation by
234 chance, then $A = 0$, if variation within groups is highly heterogeneous and less than expected
235 by chance, then $A > 0$. Heterogeneity commonly encountered in community ecology is often
236 below 0.1, a result of $A = > 0.3$ is considered relatively high (McCune and Mefford 2018).

237 Indicator species analysis (ISA), a species ranking system derived from a function of
238 abundance and the fidelity of a species to a particular group was calculated for each classified
239 grassland type and reported as the species variable Indicator Value (IV) (Dufrene and Legendre
240 1997).

241

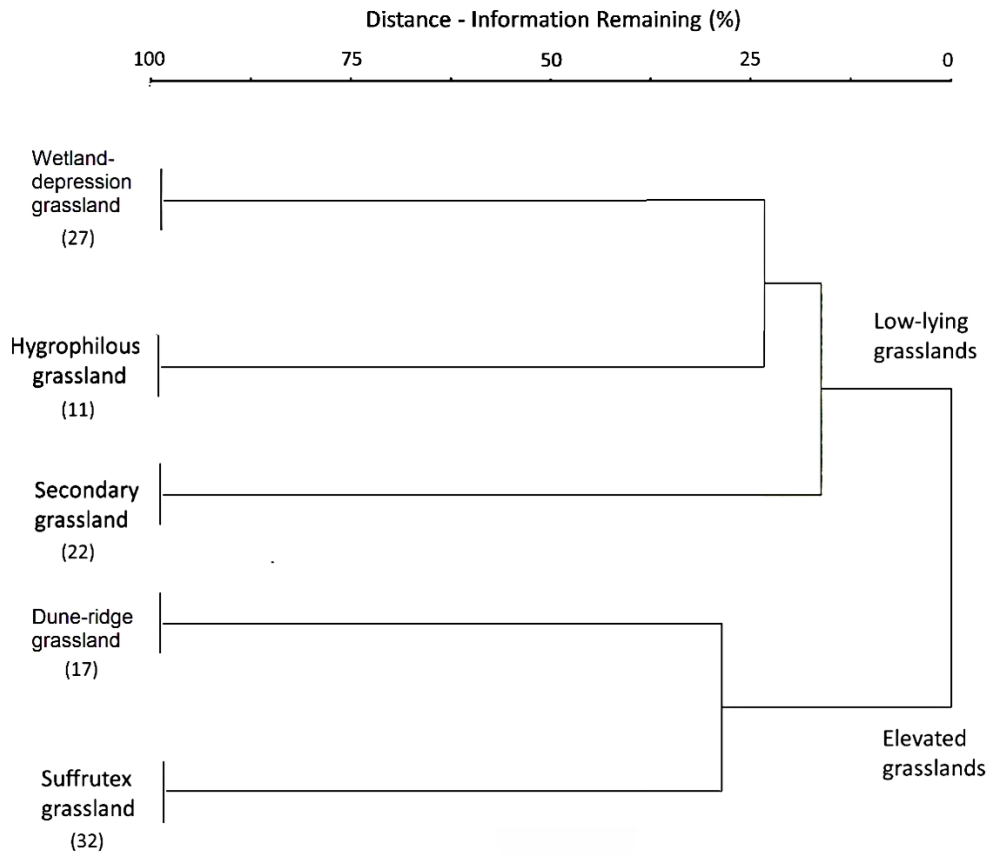
242 Differences in the means of botanical, physiognomic and environmental variables were
243 compared across grassland types using Welch's ANOVA, with group means compared using
244 Tukey's test. Comparisons were undertaken using the Real Statistics package (Zaiontz 2016).
245 Topographic, edaphic, and hydrological variables were subjected to correlation-type Principal
246 Component Analysis (PCA) in order to understand relations among environmental variables,
247 to identify redundant variables, and to identify topo-edaphic gradients. Convex hulls (i.e. the
248 smallest convex set of polygons that contains all points in a given set) were plotted in the PCA
249 ordination to show relations between soil variables and the floristic composition of grassland
250 types. Non-metric multidimensional scaling (NMS), an indirect gradient analysis technique,
251 was then used to relate dominant gradients of floristic composition with grassland structural
252 and topo-edaphic co-variables. NMS maximises rank-order correlation, so few assumptions
253 about the distribution of data are required (McCune and Mefford 2018). NMS was conducted
254 using Bray-Curtis distance, and 250 iterations were used. The PCA and NMS were conducted
255 using the software PCord ver. 7 (McCune and Mefford 2018).

256 **Results**

257 *Grassland Classification*

258 Accounting for approximately 72% of variation in the data, Wards Minimum Distance
259 successfully classified the five grassland types (Figure 2). Percentage chaining was low (1%)
260 meaning that few sample units joined with more than one group at a time. MRPP indicated
261 groups were distinct ($p < 0.001$) and that in-group heterogeneity was slightly greater than
262 expected by chance ($A = 0.2$). The structure of the classification ~~was distinct in~~ showed that
263 grassland composition corresponded with either elevated or low-lying topographic positions.
264 The number of significant ($p < 0.05$) indicator species in dune-ridge ($n = 39$) and suffrutex
265 grassland ($n = 35$) were greater than wetland-depressions ($n = 14$), hygrophilous grassland (n
266 $= 12$), or secondary grassland ($n = 11$) (Table 1, and Appendix C).

267



268

269

270

271 Figure 2. Hierarchical dendrogram (scaled by Ward's objective function) showing the
 272 primary structure in species composition. Main groupings distinguished elevated from low-
 273 lying grasslands, with secondary grassland forming an independent unit within the low-lying
 274 grassland group.

275

276

277

278

279

280

281

282 Table 1. Indicator species values (IV) across grassland types

Elevated grasslands				Low-lying grasslands					
Dune-ridge grassland	IV	Suffrutex grassland	IV	Hygrophilous grassland	IV	Wetland depression grassland	IV	Secondary grassland	IV
<i>Hyperthelia dissoluta</i>	79.7	<i>Tristachya leucothrix</i>	71.9	<i>Eragrostis lappula</i>	85.5	<i>Leersia hexandra</i>	43.6	<i>Digitaria diversinervis</i>	93.2
<i>Andropogon schirensis</i>	74.5	<i>Cymbopogon caesius</i>	66.5	<i>Themeda triandra</i>	78.8	<i>Acroceras macrum</i>	43.4	<i>Cynodon dactylon</i>	39.1
<i>Imperata cylindrica</i>	68.6	<i>Helichrysum cymosum</i>	63.6	<i>Restio zuluensis</i>	44.6	<i>Brachiaria arrecta</i>	35.8	<i>Dactyloctenium germinatum</i>	24.1
<i>Hilliardiella aristata</i>	60.0	<i>Parinari capensis</i>	60.2	<i>Eragrostis inamoena</i>	42.2	<i>Centella asiatica</i>	32.1	<i>Pinus elliotii</i>	18.2
<i>Acalypha villicaulis</i>	51.1	<i>Salacia kraussiana</i>	45.0	<i>Hemarthria altissima</i>	39.2	<i>Lobelia coronopifolia</i>	28.6	<i>Sacciolepis curvata</i>	13.6
<i>Indigofera tristis</i>	51.0	<i>Digitaria natalensis</i>	44.1	<i>Richardia brasiliensis</i>	31.8	<i>Andropogon eucomus</i>	25.0	<i>Desmodium dregeanum</i>	11.3
<i>Diheteropogon filifolius</i>	49.2	<i>Ancylobothrys pumilis</i>	42.1	<i>Hypoxis rigidula</i> var. <i>rigidula</i>	23.3	<i>Panicum repens</i>	24.4	<i>Digitaria didactyla</i>	10.1
<i>Andropogon gayanus</i>	45.5	<i>Ochna natalensis</i>	37.7	<i>Cyperus obtusifolius</i>	21.5	<i>Ischaemum polystachyum</i>	23.3	<i>Senecio madagascariensis</i>	9.4
<i>Trachyandra asperata</i>	37.7	<i>Aristida stipitata</i>	36.3	<i>Gazania krebsiana</i>	16.7	<i>Cyperus sphaerocephalus</i>	21.9	<i>Digitaria debilis</i>	9.1
<i>Ozoroa obovata</i>	36.4	<i>Elephantorrhiza elephantina</i>	36.1	<i>Edrastima cephalotes</i>	16.6	<i>Kyllinga melanosperma</i>	20.0	<i>Eucalyptus grandis</i>	9.1

* Species order ranked by Indicator Value (IV). Significance for an indicator species was $p < 0.05$. The remainder of significant indicator species are in Appendix C.

283

284 *Edaphic and hydrological variation*

285 SOC and N were roughly five-fold greater in low-lying than in elevated grasslands,
 286 demonstrating that measures of soil fertility corresponded with landscape position and species
 287 composition (Table 2). SOC ranged from about 15% in wetland-depression grassland plots to
 288 less than 0.3% in some dune-ridge and suffrutex plots. Suffrutex grassland had the least clay,
 289 but clays in dune-ridge grassland were moderately high (about 5%). Phosphorus was
 290 considerably less in hygrophilous than in wetland-depression or secondary grassland.
 291 Potassium did not differ across grassland types. Soil pH was low (acidic) across all grassland
 292 types, but exchange acidity was considerably greater in lower-lying than elevated grassland
 293 areas. Depth to the water table was furthest from the soil surface in dune-ridge grasslands
 294 which differed considerably with hygrophilous, depression and secondary grassland.

295

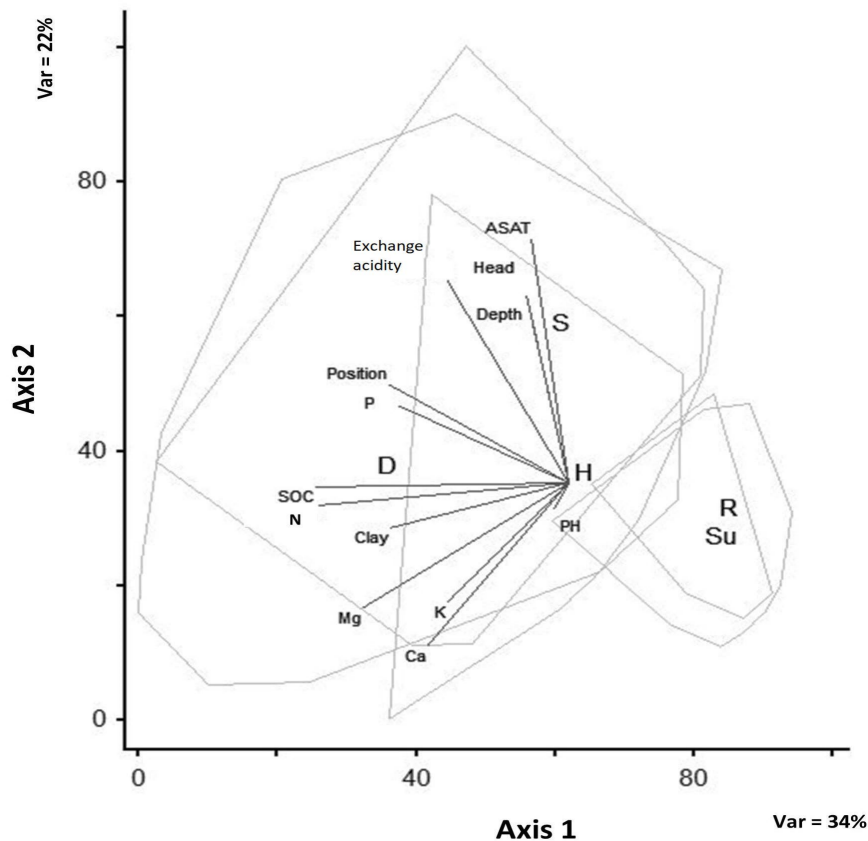
296 Table 2. Summary of environmental variables across vegetation types

Variable	Elevated grassland				Low-lying grassland						Welchs Anova
	Dune-ridge (n = 17)		Suffrutex (n = 32)		Hygrophilous (n = 11)		Wetland-depression (n = 27)		Secondary grassland (n = 22)		
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	
Carbon %	0.7 _a	0.36	0.7 _a	0.41	4.0 _b	2.20	9.0 _c	4.90	4.3 _b	3.82	F = 28.7
Clay %	5.0 _{a,b}	2.20	1.3 _b	2.07	3.4 _b	1.83	7.2 _a	5.97	3.4 _b	5.31	F = 10.5
Nitrogen %	0.05 _a	0.025	0.08 _a	0.021	0.3 _a	0.13	0.6 _b	0.37	0.3 _a	0.25	F = 28.2
Phosphorus Mg ^{-L}	7.0 _a	3.30	9.0 _a	3.70	10.0 _a	4.30	20.0 _b	13.00	18.0 _b	11.30	F = 8.9
Potassium Mg ^{-L}	35.0	15.40	38.0	25.10	49.0	24.10	53.0	32.10	38.0	34.30	F = 0.26
pH	4.9 _a	0.38	4.6 _a	0.42	4.4 _b	0.33	4.3 _b	0.39	3.9 _c	0.43	F = 14.7
Exchange acidity	0.09 _a	0.023	0.1 _a	0.03	0.5 _b	0.51	0.5 _b	0.45	0.7 _b	0.59	F = 13.8
Depth to water table (m)	13.0 _a	3.40	9.8 _{b,c}	3.44	8.5 _{c,d}	0.75	9.0 _{c,d}	2.79	7.6 _d	1.77	F = 8.6
Head (m above mean sea level)	29.0 _a	8.10	32.0 _a	9.10	31.0 _a	5.80	35.0 _a	6.10	41.0 _b	5.90	F = 9.7
<p>* Tukey's post-hoc test, different subscripts indicate significant differences in mean values among variables in rows ($p < 0.05$)</p> <p>* Significant differences between grasslands were $p < 0.05$, bold F values show rows values that were significantly different across grassland types</p>											

297

298 Principal component analysis captured 56% of environmental variance on the first two axes
 299 (Figure 3). The first axis expressed changes in landscape position, SOC and clay, which
 300 correlated positively with soil chemical properties of N, Mg, K and P. The second axis
 301 expressed changes in the water table (depth, head) and, to a lesser extent, landscape position,
 302 which correlated positively with acid saturation, residual acidity, and weakly negatively with
 303 Ca. The transition from low-lying topographic positions containing high SOC and clay to
 304 nutrient-poor elevated landscape positions did not correlate with water table depth; this was
 305 possibly due to the complexity of low-lying (but locally elevated) suffrutex grassland and that
 306 some dune-ridge grassland plots contained moderate amounts of clay. Other non-measured
 307 variables such as long-term fluctuation of the primary aquifer and perched aquifers would also
 308 have affected this result.

309



310
311

312 Figure 3. The first two axis of a correlation-type PCA of the topo-edpahic variables
 313 (eigenvalues: Axis 1 = 4.46; Axis 2 = 3.18; culminative eigenvalue = 13.99). See Appendix A
 314 for correlation values. **Key to variables:** ASAT = Acid saturation, Clay = Clay, Ca =
 315 Calcium, Depth = Depth to water table, Exchange acidity = Exchange acidity in cmol L^{-1} ,
 316 Head = Distance of aquifer to sea level, K = Potassium, Mg = Magnesium, N = Nitrogen, P
 317 = Phosphorus, Ph = Potential hydrogen, Position = Topographic position, SOC = Soil organic
 318 carbon. **Key to vegetation centroids:** R= Dune-ridge, Su = Suffrutex, H = Hygrophilous, D
 319 = Wetland-depression, S = Secondary. Convex hulls show the extent of grassland types.

320

321 *Description of vegetation units*

322 A total of 178 plant species were sampled, which included 49 graminoids, 69 herbaceous
 323 dicotyledons, 17 herbaceous monocotyledons, 25 woody trees or shrubs, ten sedges, and eight
 324 geoxylic suffrutex species. The species richness in dune-ridge and suffrutex grasslands was
 325 approximately twice that of hygrophilous, wetland-depression or secondary grasslands (Table
 326 3). Graminoids accounted for 74% and herbaceous forbs accounted for 12% of plot cover.

327

328 Grassland structural composition (i.e. summarised physiognomic variables) corresponded
329 strongly with site topography. Elevated grasslands had a greater woody component, suffrutex
330 component, and more diverse composition of tufted-only grasses and forbs than low-lying
331 grasslands, which were largely composed of prostrate or upright rhizomatous or stoloniferous
332 grasses (Table 3). Secondary grassland was comparable with both hygrophilous and wetland-
333 depression grassland in terms of species composition and structure, evident by having a mix of
334 tufted and lawn grasses. Sedge cover did not differ across grassland types.

335

336 **Dune-ridge grassland**

337 Dune-ridge grassland occurred on nutrient poor, sandy soils in elevated positions at an average
338 height of 13 m above the water table, and was characterised by a mix of large thatching grasses
339 (e.g. *Hyperthelia dissoluta*, *Andropogon gayanus*), smaller tufted grasses (e.g. *Andropogon*
340 *schirensis*, *Diheteropogon filiformis*), and mixed tufted-rhizomatous or stoloniferous grass
341 species (e.g. *Imperata cylindrica*). Of these grasses, *Imperata cylindrica* is often associated
342 with disturbance. Woody tree or shrubs comprised about 10% of cover, common species were
343 *Ozoroa obovata*, *Strychnos madagascariensis*, *Vangueria infausta* and *Combretum molle*.
344 Suffrutex woody species such as *Parinari capensis* and *Salacia kraussiana* comprised < 5%
345 cover. Forbs accounted for 13% of plot cover and were the most diverse plant group (29
346 species). Common forbs were *Hilliardiella aristata*, *Acalypha villicaulis*, *Indigofera tristis*,
347 *Trachyandra asperata* and *Zornia capensis* subsp. *capensis* (Table 1 and Appendix C).

348

349 **Suffrutex grassland**

350 Suffrutex grassland occurred in relatively elevated positions in proximity to low-lying plains,
351 and had low amounts of clay, SOC and N. Grass cover included medium sized tufted species
352 (e.g. *Cymbopogon caesius*, *Urelytrum agropyroides*), smaller tufted grasses (e.g. *Tristachya*
353 *leucothrix*, *Aristida stipitata*), and tufted-rhizomatous grasses such as *Digitaria natalensis*.
354 Woody shrub and suffrutex species averaged 25% of cover but reached up to 80% in some
355 plots (Table 3). Typical woody shrubs were *Ochna natalitia*, while geoxylic suffrutex species
356 were *Parinari capensis*, *Salacia kraussii*, *Syzygium cordatum*, *Elephantorrhiza elegantissima*,
357 *Gymnosporia markwardii*, *Eugenia albanensis*, and *Ozoroa* sp. nov. Semi-herbaceous shrubs
358 or creepers (e.g. *Jasminum multipartitum*) accounted for 13% of plot cover, while herbaceous
359 dicotyledon forbs (e.g. *Helichrysum cymosum*) and monocotyledon forbs (e.g. *Ledebouria*

360 *revoluta*) accounted for roughly 20% and 5% percent of plot cover, respectively (Table 1, and
361 Appendix C).

362

363 **Hygrophilous grassland**

364 Hygrophilous grasslands, located in acidic hydromorphic soils containing about 5% SOC and
365 5% clay, were a mosaic of caespitose but rhizomatous graminoids (e.g. *Eragrostis lappula*,
366 *Themeda triandra*, *Eragrostis inamoena*), tufted only grasses (e.g. *Sporobolus subtilis*) and
367 stoloniferous or rhizomatous prostrate grasses (e.g. *Hemarthria altissima*). *Dactyloctenium*
368 *germinatum*, a disturbance-associated graminoid, was common but not abundant. A fast-
369 growing annual grass species, *Sorghastrum stipoides*, was not encountered during sampling
370 but was noted to occur during late summer in hygrophilous grassland areas. Most forbs were
371 prostrate or decumbent herbaceous dicotyledons; *Richardia brasiliensis* (an alien species)
372 indicated disturbance, while other typical forbs were *Gazania krebsiana*, *Berkheya rhapontica*,
373 and *Edrastrima cephalotes*. Common monocotyledon forbs were *Hypoxis rigidula* subsp.
374 *rigidula* and *Hypoxis filiformis*. Hygrophilous grassland contained two regional endemics,
375 namely *Restio zuluensis* and *Helichrysopsis septentrionale* (Table 1, and Appendix C). The
376 woody component in hygrophilous grassland averaged less than 1% of cover (Table 3).

377

378 **Wetland-depression grassland**

379 Wetland-depressions were the most hydrophytic grassland type, occurring in the lowest
380 topographic positions on soils with high (5-15%) SOC. Dominant grasses included prostrate
381 species *Acroceras macrum* and *Digitaria diversinervis* but also hygrophytes such as *Leersia*
382 *hexandra* and *Urochloa arrecta*. The most common tufted graminoid was *Andropogon*
383 *eucomus*, while common tufted-rhizomatous grasses were *Ischaemum fasciculatum* and
384 *Panicum repens* (Table 1). *Centella asiatica* was ubiquitous but not necessarily dominant.
385 Monocotyledon forbs were represented by the orchid *Satyrium sphaerocarpaceum* which occurred
386 in about 15% of plots. Typical sedges were *Cyperus sphaerocephalus*, *Kyllinga melanosperma*
387 and *Juncus lomatoxyllus*. The woody component of wetland-depression grassland averaged
388 about 2% of cover.

389

390 **Secondary grassland**

391 Secondary grasslands occurred in low-lying topographic positions at an average of 8 m above
392 the water table (Table 2), and reflected disturbance across all grassland structural components.
393 In the woody component, alien invasive *Pinus elliotii* and *Eucalyptus grandis* saplings

394 accounted for less than 5% of cover, while herbaceous dicotyledons were competitive species
 395 such as *Pteridium aquilinum* (bracken fern), *Senecio madagascariensis* and *Desmodium*
 396 *dregeanum*. Common disturbance-associated graminoids were *Dactyloctenium germinatum*
 397 (occurring in 65% of plots), stoloniferous *Cynodon dactylon*, and, to a lesser extent, tufted-
 398 only grasses such as *Melinis repens*. Common prostrate lawn grasses were *Digitaria*
 399 *diversinervis* (occurring in 100% of plots), *Acroceras macrum* (occurring in 35% of plots),
 400 *Urochloa brizantha*, *Digitaria didactyla*, *Sacciolepis curvata*, and *Ischaemum polystachyum*
 401 (Table 1, and Appendix C). Common annual or short-lived perennial grasses were *Digitaria*
 402 *debilis* and *Perotis patens*. Regeneration, or persistence, of a native woody species in secondary
 403 grassland was indicated by sparsely occurring *Parinari capensis*, *Diospyros lycioides*,
 404 *Sclerocroton integerrimus* and *Vangueria infausta*.

405

406 Table 3. Summary of diversity and grassland physiognomy across vegetation types

Variable	Elevated grassland				Low-lying grassland						Welch's Anova
	Dune-ridge (n = 17)		Suffrutex (n = 32)		Hygrophilous (n = 11)		Depression (n = 27)		Secondary (n = 22)		
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	
Total species richness	90		133		58		95		77	-	-
Mean richness per plot	28 _a	5	29 _a	4.6	12 _b	3.5	12 _b	4.6	12 _b	3.3	F = 86.2
Total forb richness	41	-	61	-	30	-	36	-	31	-	-
Mean forb richness per plot	10 _a	3.3	10 _a	2.6	4 _b	2.1	4 _b	2.8	3 _b	2.3	F = 33.1
Total dicot richness	30		46	-	23		28	-	27	-	-
Mean dicot forb richness per plot	9 _a	3.1	7 _a	2	3 _b	2.2	4 _b	2.3	3 _b	2	F = 19.6
Monocot forb richness	11	-	15	-	7	-	8	-	4	-	-
Mean monocot forbs per plot	1.3 _{a,b}	1.20	2 _a	1.5	0.8 _b	0.85	0.7 _b	0.71	0.1 _c	0.35	F = 14.4
Woody cover	11 _b	6.1	32 _a	26.3	0.6 _c	2.41	2 _c	7.6	3 _c	8.5	F = 18.6
Suffrutex cover	5 _b	2.9	22 _a	23.1	0.1 _c	0.29	0.6 _c	2.36	0.1 _c	0.35	F = 11.4
Grass cover	62 _a	17.4	31 _b	18.1	63 _a	24.3	71 _a	34.3	81 _a	29.1	F = 18.3
Tufted grasses cover	43 _a	2.1	14 _b	15.2	0.5 _c	86	9 _c	19.3	2.4 _c	2.77	F = 34.1
Rhizome and stolon cover	18 _a	4.1	15 _a	11.7	63 _b	24.8	63 _b	38.3	79 _b	29.1	F = 37.7
Sedge cover	1.7	1.41	2	1.7	2	1.2	2	1.4	1.3	1.4	F= 1.3
Total forb cover	13	20.1	21	19.1	12	3.9	10	19.1	23	32.9	F= 1.7
Dicotyledon forb cover	13	20.6	19	19.6	11	3.7	9	19.1	20	34.3	F= 1.8
Monocotyledon forb cover	2 _{a,b}	1.2	3 _a	1.5	1 _{b,c}	0.85	0.9 _{b,c}	0.71	0.1 _c	0.35	F = 15.6
<p>* Tukey's post-hoc test, different in subscripts indicate significant differences in mean values among variables ($p < 0.05$)</p> <p>* Significant differences between grasslands were $p < 0.05$, bold F values show rows values that were significantly different across grassland types</p>											

407

408

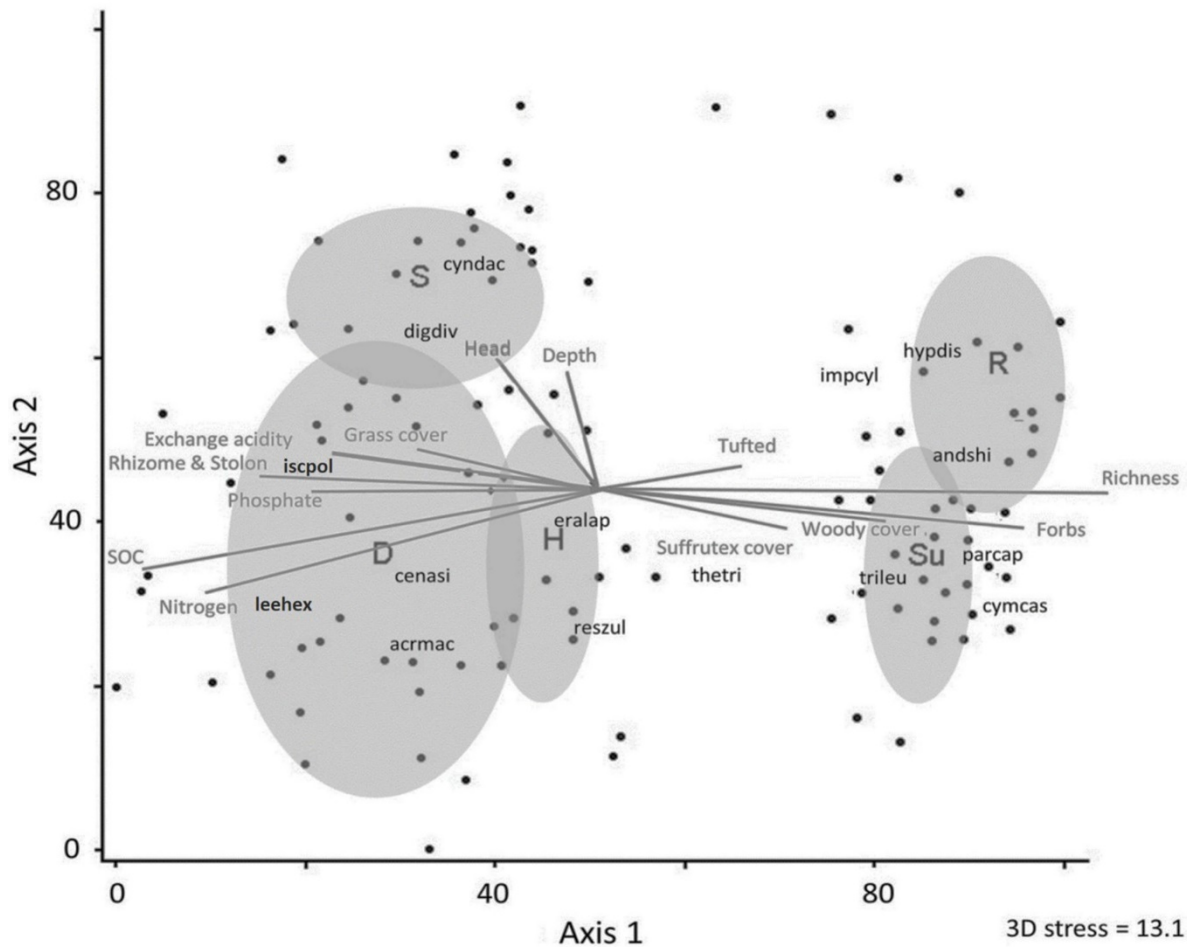
410 *Correspondence of grassland composition with physiognomic and environmental variables*

411 A three-dimensional NMS solution revealed the least stress in the data (stress = 13.1, $p <$
412 0.001). The first axis explained 51% of variation, while the second and third axes accounted
413 for 16% and 12% of variation, respectively. A strong pattern of increasing diversity, as
414 indicated by species and forb richness, corresponded with a topographic change from low-lying
415 to elevated grassland (Figure 4). Total grass cover and the cover of stoloniferous plus
416 rhizomatous grasses increased with increasing SOC, N, P and exchange acidity (Figure 4). The
417 size of ellipses in the ordination indicated that wetland-depression grassland had a broad range
418 of species composition, whereas hygrophilous grassland (centrally located in ordination) was
419 a strong floristic link between low-lying and elevated grasslands.

420

421 Clay did not correspond well with the primary change of vegetation composition, probably
422 because comparable amount were recorded in dune-ridge and hygrophilous grassland soils
423 (Table 2). Hydrological variables of water table depth and head did not relate with the
424 composition of vegetation explained by the first NMS axis, and only weakly with the second
425 NMS axis. Therefore, contrary to expectation, depth to the water table did not correlate with
426 the primary gradient of vegetation composition or edaphic variables indicating soil fertility
427 (such as SOC or N). Hence, the primary gradient of change in vegetation composition and
428 structure related to the soil environment but not to modelled water table depth of the primary
429 aquifer.

430



431

432 Figure 4. NMS ordination and biplot for grasslands at Manzengwenya (see Appendix B for
 433 biplot correlation values). **Key to vegetation centroids:** R= Dune-ridge, Su = Suffrutex, H =
 434 Hygrophilous, D = Wetland-depression, S = Secondary. **Key to species:** acrmac = *Acroceras*
 435 *macrum*, andshi = *Andropogon schirensis*, cymcae = *Cymbopogon caesius*, cenasi = *Centella*
 436 *asiatica*, cyndac = *Cynodon dactylon*, digdiv = *Digitaria diversinervis*, eralap = *Eragrostis*
 437 *lappula*, hypdis = *Hyperthelia dissoluta*, impcyl = *Imperata cylindrica*, iscpol = *Ischaemum*
 438 *polystachyum*, leehex = *Leersia hexandra*, parcap = *Parinari capensis*; reszul = *Restio*
 439 *zuluensis*, thetri = *Themeda triandra*, trileu = *Tristachya leucothrix*. **Key to diversity**
 440 **variables:** Forbs = Forb richness, Richness = Species richness. **Key to physiognomic**
 441 **variables:** Grass cover = cover of grass species, Rhizome and stolon = cover of grasses with
 442 rhizomes or stolons, Suffrutex cover = cover of geoxylic-suffrutex species, Tufted = cover of
 443 tufted only grasses; Woody cover = cover of woody species; Monocots = cover of herbaceous
 444 monocotyledons. **Key to edaphic variables:** SOC = % soil organic carbon; Nitrogen = %
 445 nitrogen; Exchange acidity = Exchange acidity in cmol/L; Phosphate = Phosphorus in mg/L.
 446 **Key to hydrological variables:** Depth = mean distance from ground surface elevation to
 447 water table elevation; Head = distance to mean sea-level.

448 Discussion

449 *Patterns of floristic composition and structure in relation to dune topography*

450 The primary gradient of change in grassland richness, composition and structure shifted from
451 dominance by prostrate and rhizomatous lawn grasses in low-lying fertile landscape positions,
452 to a heterogeneous mixture of grasses, forbs and woody species in nutrient-poor, elevated areas.
453 Judging by the first division of the classification, species turnover between low and elevated
454 grasslands was in the order of 70% (Figure 2), meaning that about a third of species occurred
455 across both elevated and low-lying topo-edaphic environments. These co-occurring species
456 were largely represented by ruderals or disturbance specialists, for example, *Centella asiatica*
457 (Scott-Shaw and Morris 2016), *Perotis patens* and *Imperata cylindrica* (Gibbs Russell et al.
458 1990). However, non-ruderal species, for example *Themeda triandra*, also occurred across
459 topo-edaphic conditions such as in mesic hygrophilous grassland, on sandy dune ridges and in
460 suffrutex grassland. Elevated grasslands contained a distinctly richer and more complex
461 composition of tufted-only grasses, monocotyledon and dicotyledon forbs, trees, shrubs,
462 creepers and geoxylic suffrutices than low-lying grasslands. In contrast to elevated grasslands,
463 low-lying grasslands were less diverse in terms of forbs and woody plants but contained a
464 distinct composition of prostrate rhizomatous and stoloniferous grasses. These findings are
465 consistent with the theory that grassland species-richness is greatest in nutrient-poor sites
466 (Tilman 1987).

467

468 Contrary to expectation, plant composition corresponded poorly with the modelled water table
469 depth of the primary aquifer (Figure 4). This may have been an artefact of topographic
470 resolution (only 5 m elevation contours were available for the region); however, water-table
471 depth, resulting from regional 18-20 year wet-dry climatic cycles (Kelbe et al. 1983) may also
472 have affected soil composition. Evidence of vegetation adaption to dynamic moisture cycles
473 was reflected by graminoids occurring in low-lying grasslands (such as *Urochloa arrecta* and
474 *Leersia hexandra*) which can endure aerated and flooded anoxic soil conditions (Gibbs Russel
475 et al. 1990). Forb richness in low-lying grasslands was generally poor, but dystrophic areas
476 provided habitat for endemic hydrophytes such as *Helichrysopsis septentrionalis* and *Restio*
477 *zuluensis* (Table 1). Hygrophilous and wetland depression grassland are a valuable source of
478 livestock forage because they offer a high concentration of palatable leaf material per unit of
479 ground cover, suit continuous grazing management, and can provide quality forage during dry

480 periods when surrounding elevated grasslands are not productive (O'Connor et al. 2010;
481 Hempson et al. 2015).

482

483 Geoxylic suffrutex grasslands are a unique grassland type in Maputaland and are thought to
484 have evolved under conditions of excessive fire and moisture (Maurin et al. 2014). Occurring
485 upon slightly raised dune-ridges, slopes or hummocks, their dominant structural components
486 were woody geoxylic suffrutex species, but they also contained a diverse composition of
487 herbaceous forbs including monocotyledon and dicotyledon re-sprouting bulbs, legumes,
488 tufted grasses, and non-suffrutex woody trees or shrubs. Suffrutex grassland lacked the SOC
489 and clay of surrounding low-lying grasslands, indicating they were not frequently flooded for
490 extended periods and had persisted because they were above the 'high-water' flood-line. The
491 species composition of suffrutex grasslands differed slightly with that of dune-ridge grasslands,
492 and their greater forb richness suggested they were the least disturbed elevated grassland. By
493 contrast, ruderal grasses such as *Imperata cylindrica*, *Urochloa maxima* and *Perotis patens*
494 (Gibbs Russel et al. 1990) indicated that dune-ridge grassland had been affected by
495 anthropogenic processes such as small-scale agriculture, livestock corrals or settlement.

496

497 *Differences between communal and secondary grassland*

498 The composition of naturally regenerated grasslands (i.e. secondary grassland) are expected to
499 differ substantially from their untransformed old-growth counterparts (O'Connor 2005;
500 Zaloumis and Bond 2016). However, in a heterogenous topo-edaphic landscape, patterns of
501 species composition of secondary grassland are also likely to follow environmental co-
502 variables such as the effects of topography. That secondary grassland shared a considerable
503 portion of species with communal low-lying grasslands (Figure 2; Figure 4) was, in part, due
504 to sampling predominantly 'low-lying' sites at Manzengwenya plantation but was also likely a
505 consequence of regenerated residual 'old-growth' grassland species and colonisation by
506 common ruderal species. The result suggests that a secondary grassland 'analogue' of elevated
507 grasslands would be expected to occur in previously afforested sandy dune-ridge positions.

508

509 Dominant patterns of floristic regeneration in 'low-lying' secondary grassland were therefore
510 monotypic dominance of prostrate rhizomatous or stoloniferous grass species, the occurrence
511 of ruderal or competitive dicotyledon forbs, poor monocotyledon forb diversity, and a failure
512 of keystone species to recolonise after forestry plantation disturbance. Typical keystone

513 graminoides, such as *Themeda triandra*, were not found in secondary grassland and were
514 presumably unable to persist in a forestry environment and recolonise cleared areas after trees
515 had been removed. Conversely, those species co-occurring in secondary and low-lying
516 communal grasslands were adapted to persist within a forestry plantation environment (e.g.
517 *Digitaria diversinervis*) or were able to regenerate naturally after plantation abandonment.
518 These species would likely have persisted in plantations among unshaded grassland refuges
519 such as wetland edges, roadways, or other uncultivated environments during active forestry
520 cycles.

521

522 *Implications for future land use*

523

524 The template of grassland classification used this study has served well in terms of considering
525 the provision of grassland ecosystems services, which is fully developed in Starke et al. (2020).
526 However, forestry plantations provide economic incentives for small-holder growers in
527 northern Maputaland, and a sharp increase in recent decades (200 to 6800 ha between 1990
528 and 2012) has inevitably come at a cost to grassland ecosystems and to water security (Kelbe
529 et al. 2014; von Roeder 2014). Decentralised management of communal grasslands is also
530 likely to have contributed to extreme variation in the topographic location of plantations. Our
531 analysis suggests that poor condition hygrophilous grassland, i.e. those sites dominated by
532 disturbance-associated species such as *Centella asiatica*, would incur the least biodiversity loss
533 with the best chance of recovery after de-afforestation. However, for hydrological reasons,
534 afforestation of hygrophilous grassland is not tolerable (Everson et al. 2011; Kelbe et al. 2014;
535 Everson et al. 2019) and agricultural cultivation of low-lying areas would rather suit water
536 conservative horticultural crops that require fertile, acidic soils (Jury et al. 2008).

537

538 The most appropriate sites for forestry plantations would be in already disturbed dune-ridges
539 as indicated by low forb richness and dominance by disturbance-associated species. Here,
540 plantations would be furthest from the water table and possibly better protected from fire than
541 low-lying plains which are directly exposed to prevailing northerly and southerly winds
542 (Geldenhuys 1994; Starke et al. 2019). The most fitting ecological land use for wetland-
543 depression and hygrophilous grassland would be for livestock production through the supply
544 of quality forage resources; supplementary forage and medical resources could be supplied by
545 elevated grasslands. Intact suffrutex grasslands should be preserved at all cost because as they

546 are a regionally endemic grassland type (Mucina et al. 2006; Maurin et al. 2014) that contain a
547 diversity of medicinal and spiritual plant species (Starke et al. 2020).

548

549 The cost of transforming grasslands to forestry plantations incurs a loss of grassland ecosystem
550 services that may affect communities who rely on the environment for their livelihoods, and
551 also urban populations who utilise native plants that are sourced from rural areas. In a
552 companion study (Starke et al. 2020), we quantified the forage and non-forage resources
553 supplied by these five grassland types, finding 180 individual plant uses. Low-lying grasslands
554 had the best quality of forage, while elevated grasslands contained about 50 medicinal plant
555 species and a majority of the commercially prospective woody species (e.g. *Sclerocarya birrea*,
556 *Strychnos spinosa*). Small-holder farmers aiming to establish forestry plantations on their land
557 should be aware that grassland transformation can severely diminish the range of plant
558 resources available to their communities, and that it may take decades for species to return
559 following plantation abandonment. Consequently, in forest-grassland mosaic ecosystems,
560 farmers might consider exploring approaches to land use that involve less structural
561 transformation to native vegetation, for example, by considering agro-forestry practices such
562 as silvopasture (Starke et al. 2019).

563 **Conclusion**

564 Plantation forestry offers one of the few production opportunities available in Maputaland and
565 transformation of IOCB grasslands is likely to continue in the coming decades. However, the
566 consequences of forestry expansion into grassland ecosystems will include ongoing water-
567 insecurity (Kelbe et al. 2014; Everson et al. 2019), reduced supply of livestock forage, and
568 degradation of non-forage grassland resources such as plant-medicines or other products
569 supplied by grasslands species. These ‘trade-offs’ could be mitigated through effective land
570 use planning, whereby low-lying grassland sites are recognised as areas with potential for
571 income-generating rural livestock production (Musemwa et al. 2008), whereas elevated
572 grasslands would serve to maximise grassland heterogeneity and supply non-forage resources.
573 Transformation of primary grassland ecosystems is a serious action and given that primary
574 grasslands do not recover their species composition (Zaloumis and Bond 2016; Buisson et al.
575 2018) after ploughing or afforestation, these actions will negatively impact the provision of
576 grassland ecosystems services for decades into the future.

577 **Acknowledgements**

578 **References**

- 579 African Plant Database (version 3.4.0). 2020. Conservatoire et Jardin botaniques de la Ville de
580 Genève and South African National Biodiversity Institute, Pretoria. [http://www.ville-](http://www.ville-ge.ch/musinfo/bd/cjb/africa)
581 [ge.ch/musinfo/bd/cjb/africa](http://www.ville-ge.ch/musinfo/bd/cjb/africa).
- 582 Bengtsson J, Bullock JM, Egoh B, Everson CE, Everson T, O'Connor TG, O'Farrell PJ, Smith
583 HG, Lindborg R, 2019. Grasslands—more important for ecosystem services than you
584 might think. *Ecosphere* 10: e02582.
- 585 Bond WJ, Midgley JJ, 2003. The evolutionary ecology of sprouting in woody plants.
586 *International Journal of Plant Sciences* 164: S103–S114.
- 587 Botha G, Porat N. 2007. Soil chronosequence development in dunes on the southeast African
588 coastal plain, Maputaland, South Africa. *Quaternary International* 162: 111–132.
- 589 Buisson E, Le Stradic S, Silveira FAO, Durigan G, Overbeck GE, Fidelis A, Fernandes GW,
590 Bond WJ, Hermann J, Mahy G, Alvarado ST, Zaloumis, NP, Veldman JW. 2018.
591 Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy
592 woodlands. *Biological Reviews* 94: 590-609.
- 593 Clegg BW, O'Connor TG. 2012. The vegetation of Malilangwe Wildlife Reserve, south-eastern
594 Zimbabwe. *African Journal of Range and Forage Science* 29: 109-131.
- 595 Dzerefos CM, Witkowski ETF. 2001. Density and potential utilisation of medicinal grassland
596 plants from Abe Bailey Nature Reserve, South Africa. *Biodiversity and Conservation*
597 10: 1875–1896
- 598 Dufrière M, Legendre P. 1997. Species assemblages and indicator species: the need for a
599 flexible asymmetrical approach. *Ecological Monographs* 6: 345–366.
- 600 ESRI ArcGIS. 2011. Redlands, CA: Environmental Systems Research Institute.
- 601 Everson CS, Dye PJ, Gush MB, Everson TM. 2011. Water use of grasslands, agroforestry
602 systems and indigenous forests. *Water SA* 37: 781–788.
- 603 Everson CS, Scott-Shaw BC, Kelbe BE, Starke AP, Pearton T, Geldenhuys CJ, Vather T,
604 Maguire M. 2019. *Water-efficient production methods and systems in Agroforestry,*

605 *Woodland and Forestry Plantations*. WRC Report No. TT 781/18. Pretoria: Water
606 Research Commission.

607 Gibbs Russell GG, Watson L, Koekemoer M, Smook L, Barker NP, Anderson HM. and
608 Dallwitz, MJ (eds) 1990. *Grasses of southern Africa*. Pretoria: Memoirs of the botanical
609 survey of South Africa.

610 Geldenhuis CJ. 1994. Bergwind Fires determine the location pattern of forest patches in the
611 Southern Cape landscape, South Africa. *South African Journal of Biogeography* 21:
612 49–62.

613 Hempson GP, Archibald S, Bond WJ, Ellis RP, Grant CC, Kruger FJ, Kruger LM, Moxley C,
614 Owen-smith N, Peel MJS, Smit IPJ, Vickers KJ. 2015. Ecology of grazing lawns in
615 Africa. *Biological Revisions* 90: 979–994.

616 Jury MR, Nyathikazi N, Bulfoni E, 2008. Sustainable agricultural for a community in a nature
617 reserve on the Maputaland coast of South Africa. *Scientific Research and Essays* 3:
618 376–382.

619 Joubert L, Pryke JS, Samways MJ. 2016. Past and present disturbances influence biodiversity
620 value of subtropical grassland ecological networks. *Biodiversity Conservation* 25: 725–
621 737.

622 Kelbe BE, Scott K, Thambu D, Escott B, Blackmore A, Grundling P, Grundling,A, James B,
623 Fox C. 2014. *The impacts of proposed stream flow reduction activities in the W70 and*
624 *W32 catchments*. Pretoria: Department of Water Affairs.

625 Kelbe BE, Garstang M, Brier G. 1983. Analysis of rainfall variability in the north eastern region
626 of South Africa. *Archives for meteorology, geophysics, and bioclimatology*. 32: 231-
627 252.

628 Lindsay EA, Cunningham SA. 2011. Native grass establishment in grassy woodlands with
629 nutrient enriched soil and exotic grass invasion. *Restoration Ecology* 19: 131–140.

630 Manson AD, Bainbridge SH, Thibaud GR. 2020. Methods used for analysis of soils and plant
631 material by Analytical Services at Cedara. KwaZulu-Natal Department of Agriculture
632 and Rural Development, South Africa.

633 Mentis MT. 2006. Restoring native grassland on land disturbed by coal mining on the Eastern
634 Highveld of South Africa. *South African Journal of Science* 102: 193-197.

- 635 Matthews WS, Van Wyk AE, Van Rooyen N. 1999. Vegetation of the Sileza Nature Reserve
636 and neighbouring areas, South Africa, and its importance in conserving the woody
637 grasslands of the Maputaland Centre of Endemism. *Bothalia* 29: 151–167.
- 638 Maurin O, Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya AM, van der Bank M,
639 Bond, WJ. 2014. Savanna fire and the origins of the “underground forests” of Africa.
640 *New Phytologists* 204: 201–14.
- 641 McCune B, Mefford MJ. 2018. PC-ORD. Multivariate analysis of ecological data. Gleneden
642 Beach OR: MjM Software design.
- 643 Mucina L, Scott-Shaw R, Rutherford M, Camp KG, Matthews W, Powrie L, Hoare D. 2006.
644 Indian Ocean Coastal Belt. In: Mucina, L, Rutherford MC. (eds.). *The Vegetation of*
645 *South Africa, Lesotho and Swaziland*. Pretoria: SANBI. pp. 569–583.
- 646 Musemwa L, Mushunje A, Chimonyo M, Fraser G, Mapiye C, Muchenje V. 2008. Nguni cattle
647 marketing constraints and opportunities in the communal areas of South Africa. *African*
648 *Journal of Agricultural Research* 3: 239–245.
- 649 O'Connor TG. 2005. Influence of land use on plant community composition and diversity in
650 Highland Sourveld grassland in the southern Drakensberg, South Africa. *Journal of*
651 *Applied Ecology* 42: 975–988.
- 652 O'Connor TG, Kuyler P, Kirkman KP, Corcoran B. 2010. Which grazing management
653 practices are most appropriate for maintaining biodiversity in South African grassland?
654 *African Journal of Range & Forage Science* 27: 67-76.
- 655 Pretorius L, Brown LR, Bredenkamp GJ, van Huyssteen CW. 2016. The ecology and
656 classification of wetland vegetation in the Maputaland Coastal Plain, South Africa.
657 *Phytocoenologia* 46: 125–139.
- 658 Roux E. 1969. *Grass: A Story of Frankenwald*. Cape Town: Oxford University Press.
- 659 Rutherford MC, Mucina L, Lötter MC, Bredenkamp GJ, Smit JHL, Scott-Shaw CR, Hoare DB,
660 Goodman PS, Bezuidenhout H, Scott L, Ellis F, Powrie L, Siebert F, Mostert TH,
661 Henning BJ, Ventner CE, Camp KGT, Siebert S, Matthews WS, Hurter P. 2006. The
662 Savanna Biome. In: Mucina L, Rutherford MC. (eds.). *The Vegetation of South Africa,*
663 *Lesotho and Swaziland*. Pretoria. SANBI. pp. 439 – 536.

- 664 Scott-Shaw R, Morris CD, 2016. Grazing depletes forb species diversity in the mesic
665 grasslands of KwaZulu-Natal, South Africa. *African Journal of Range and Forage*
666 *Science* 23: 21-31.
- 667 Starke AP, Geldenhuys CJ, O'Connor TG, Everson CE. 2019. Forest and woodland expansion
668 into forestry plantations informs screening for native agroforestry species, Maputaland
669 South Africa. *Forest, Trees and Livelihoods* 29. 1-15.
- 670 Starke AP, O'Connor TG, Everson CE. 2020. Topo-edaphic environment and forestry
671 plantation disturbance affect the distribution of grassland forage and non-forage
672 resources, Maputaland – South Africa. *African Journal of Range and Forage Science*.
673 In press.
- 674 Tilman D. 1987. Secondary succession and the pattern of plant dominance along experimental
675 nitrogen gradients. *Ecological Monographs* 57: 189–214.
- 676 van der Maarel E. 2007. Transformation of cover-abundance values for appropriate numerical
677 treatment-Alternatives to the proposals by Podani. *Journal of Vegetation Science* 18:
678 767–770.
- 679 van Wyk G.F. 1991. *Classification of the grassland communities of the Nyalazi State Forest*.
680 CSIR Project Report No. 91513 (1990-1991). Pretoria: Council for Scientific and
681 Industrial Research.
- 682 von Roeder MA. 2014. *The impact of Eucalyptus plantations on the ecology of Maputaland*
683 *with special reference to wetlands*. MSc Thesis, Technische Universitat Munchen,
684 Munchen.
- 685 Wikum DA, Shanholtzer GF. 1978. Application of the Braun-Blanquet cover-abundance scale
686 for vegetation analysis in land development studies. *Environmental Management* 2:
687 323–329.
- 688 Zaiontz C. 2016. Real Statistics Resource Pack software. www.real-statistics.com.
- 689 Zaloumis NP, Bond WJ. 2016. Reforestation or conservation? The attributes of old growth
690 grasslands in South Africa. *Philosophical transactions of the royal society* 371:
691 20150310.