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# 1 WHAT DRIVES PATCHINESS IN PALMIET WETLANDS?

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13  
14 **Keywords:** fen, alternate stable states, succession, ecosystem engineer, competition,  
15 wetlands in drylands

16  
17 Wetland communities are shaped by high levels of stress, disturbance and competition.  
18 Using South African palmiet wetlands as a case study (*Prionium serratum* dominated  
19 valley-bottom wetlands), we explore whether autogenic or allogenic succession is the  
20 dominant process driving community dynamics in valley-bottom wetlands in drylands.  
21 Several wetland rehabilitation programmes in South Africa use the dominant wetland  
22 species Palmiet (*Prionium serratum*) as a pioneer to facilitate recolonization. However  
23 research is needed on palmiet wetland dynamics and formation to guide these  
24 restoration efforts. We explore vegetation patterns by analyzing which environmental

25 parameters drive dominance of Palmiet, resulting in the characteristic patchiness of  
26 palmiet wetlands, and which plant functional traits account for this. In 20 plots from three  
27 palmiet wetlands distributed across the Cape Floristic Region of South Africa, key soil,  
28 groundwater and vegetation parameters, as well as community composition were  
29 measured. Twenty-two dominant species were selected and 13 functional traits  
30 measured. Soil pH and relative groundwater depth were the main environmental  
31 parameters driving community assembly in palmiet wetlands. Palmiet-dominated  
32 communities were characterized by greater stem diameter, leaf length-width ratio, leaf  
33 area and cellulose and lignin concentration compared to fynbos communities. These  
34 traits suggest adaptations to disturbances such as fires (thicker stems) and floods (long,  
35 thin leaves, flexible shoots and thicker stems). We propose three hypotheses of palmiet  
36 wetland development which shed light on palmiet wetland restoration and highlight gaps  
37 for future research.

38

## 39 1 INTRODUCTION

40 Wetlands are dynamic ecosystems subjected to high levels of stress (e.g. water  
41 inundation), disturbance (e.g. floods or fires) as well as competition (Clement and Proctor  
42 2009; Mitsch and Gosselink 2015; Moor et al. 2017). Wetland landscape patterns are  
43 thought to be the combination of varying interactions between abiotic (climate,  
44 topography, hydrology, geomorphology) and biotic (productivity, competition,  
45 herbivory, peat accumulation) processes (Tooth and McCarthy 2007; Mitsch and  
46 Gosselink 2015). However, water level has been proposed to be the single most important  
47 determinant for wetland vegetation community dynamics (Clement and Proctor 2009).  
48 Extremes are also thought to have more impact on vegetation development in wetlands  
49 than average conditions (Clement and Proctor 2009). Indeed, vegetation has been shown  
50 to be most sensitive to the mean highest groundwater level, especially during the growing  
51 season (Wierda et al. 1997). Others propose that biotic processes can be of great  
52 importance, such as in the case of ecosystem engineers: species that significantly modify  
53 their environment in their favour, inhibiting return to a previous state (Clement and  
54 Proctor 2009).

55 Due to their transitional nature in both space and time, wetlands are at the center of a  
56 debate about the relative roles of autogenic versus allogenic succession (Mitsch and  
57 Gosselink 2015). Autogenic succession is the classical ecological theory which suggests  
58 that species are organised in recognisable communities, that the community changes  
59 through time due to mainly biotic effects, and that these changes are linear and directed  
60 towards a stable, mature, climax ecosystem (Odum 1969; Mitsch and Gosselink 2015).  
61 Allogenic succession is an individualistic hypothesis (continuum concept) which  
62 proposes that the distribution of each species is governed by its response to the

63 environment (abiotic factors), that each species responds differently, no two species  
64 occupy the exact same niche and that the observed replacement or invasion sequence is  
65 influenced to a large degree by chance (Gleason 1917).

66 For wetlands that are subjected to severe disturbance that exceeds the capacity of an  
67 ecosystem for resilience, the concept of alternative stable states applies. Beyond a certain  
68 threshold, typical succession processes will not restore the original state (Suding et al.  
69 2004). It is argued that traditional successional concepts are of limited use in wetlands  
70 since community dynamics may not be directional or orderly, or predictable in the long-  
71 term (Niering 1989). The alternative concept of progression towards maturity may  
72 rather apply (Mitsch and Gosselink 2015). In structuring these communities, the role of  
73 chance (competitive lottery; Sale 1977), coincidence and abiotic (allogenic) factors and  
74 as well as catastrophic events (floods and droughts) have been suggested to be of more  
75 importance (Mitsch and Gosselink 2015).

76 The exposure of wetland ecosystems to water stress, both in terms of periodic drying and  
77 flooding, has led to the evolution of characteristic plant functional traits in wetland  
78 species (Mitsch and Gosselink 2015; Moor et al. 2017; Sieben et al. 2017a). A trade-off  
79 between competitive ability and stress tolerance limits has been proposed (Wisheu and  
80 Keddy 1992). Two trait categories in wetlands are proposed: regenerative or juvenile  
81 traits (seed characteristics, dispersal, seedling establishment) and morphological,  
82 physiological and phenological adult traits (Clement and Proctor 2009). The juvenile  
83 traits are related to success at colonising gaps, whereas adult traits are related to ability  
84 to survive stress or compete. There is no evidence that these trait subsets are coupled  
85 (Shipley et al. 1989), implying good colonizers may not necessarily be strong competitors.

86 Soil saturation, resulting in temporary or permanent anoxia in the root zone, and water-  
87 table fluctuations, resulting in submergence as well as mechanical disturbance are key  
88 challenges to wetland species (Moor et al. 2017). Traits associated with soil saturation  
89 include anaerobic respiration in the root zone, development of aerenchyma, higher leaf  
90 dry matter content, and lower specific leaf area and leaf nitrogen content (Mitsch and  
91 Gosselink 2015; Moor et al. 2017). Traits associated with adaptations to water-table  
92 fluctuations and flooding include: high root biomass allocation, extensive rhizomes, high  
93 stem flexibility, narrow leaves, and sclerophylly (Colmer and Voeselek 2009; Catford and  
94 Jansson 2014; Moor et al. 2017). Leaf mass area was found to be correlated with three  
95 components of leaf mechanical resistance, which could have implications for flood  
96 resistance: work-to-shear, force-to-punch and force-to-tear (Onoda et al. 2011).

97 South African valley-bottom palmiet wetlands are small, narrow peatlands which are  
98 subject to extreme water stress: soil saturation, water table fluctuations, floods as well as  
99 droughts and fires (Rebelo 2012; Job 2014). Palmiet wetland vegetation is composed of  
100 patches dominated by a single species, *Prionium serratum*, or Palmiet (hereafter palmiet  
101 communities), and patches of other plant communities (hereafter fynbos communities).  
102 Fynbos is a fire-adapted shrubland that characterizes the Cape Floristic Region, South  
103 Africa. Palmiet is a unique competitor and has even been suggested to be an ecosystem  
104 engineer (Sieben 2012; Sieben et al. 2017a). Palmiet wetland development is not well  
105 understood, though it is suggested that these wetlands have formed in valley-bottoms  
106 characterized by repeated cut-and-fill cycles over geological timescales resulting in valley  
107 floor-planing (Pulley et al. 2018; Grenfell et al. 2020). It is important to understand  
108 palmiet wetland formation and community dynamics, as this could inform restoration  
109 and rehabilitation practice (Grenfell et al. 2020). Currently several restoration and  
110 rehabilitation programmes are using Palmiet as a pioneer species to facilitate

111 recolonization of degraded river and wetland ecosystems. However there is little to no  
112 research supporting this work, justifying greater research efforts into understanding  
113 palmiet wetland dynamics and formation, with the goal of guiding rehabilitation  
114 practices. We aim to compare homogeneous, species-poor palmiet communities with  
115 more functionally diverse fynbos communities in palmiet wetlands. We explore  
116 vegetation patterns by analysing which environmental parameters drive dominance of  
117 Palmiet (allogenic vs autogenic succession), resulting in the characteristic patchiness of  
118 palmiet wetlands, and which plant functional traits account for its super-dominance.  
119 Using these data as a departure point, we hypothesize on the development of palmiet  
120 wetlands, and whether Palmiet-dominated communities represent climax ecosystems  
121 (succession) or whether both communities are 'mature' end-stage communities.

## 122 **2 METHODS**

### 123 *Study region & wetlands*

124 The Cape Floristic Region has a Mediterranean-type climate characterised by summer  
125 drought and winter rainfall resulting from the passage of cold fronts (Midgley et al. 2003).  
126 The soils of the Cape Floristic Region are mainly nutrient poor, highly leached dystrophic  
127 lithosols associated with the sandstone mountains of the Cape Supergroup (Midgley et al.  
128 2003). Vegetation of this region is predominantly fynbos, which is a biodiverse, fire-  
129 adapted shrubland composed of three elements: restioids, ericoids and proteoids (Low  
130 and Rebelo 1996). Dominant growth forms are shrubs and graminoids with few true  
131 trees. For a floristic description and classification of different wetland vegetation  
132 communities for the fynbos and other nutrient-poor sandstone and quartzite substrates  
133 across South Africa, see Sieben et al. (2017c).

134 Three palmiet wetlands were selected as study sites within the Cape Floristic Region: the  
 135 Theewaterskloof and Goukou wetlands (Western Cape) and the Kromme wetland  
 136 (Eastern Cape) (**Table 1**). Despite being situated as much as 470 km apart, these  
 137 wetlands are remarkably similar in vegetation composition. They tend to occur at  
 138 altitudes of around 400 m; mean annual precipitation is highly variable, highest in the  
 139 Theewaterskloof catchment and lowest in the Goukou catchment and the global aridity  
 140 index follows the same trend. Mean annual runoff is also highest in the Theewaterskloof  
 141 catchment but lowest in the Kromme catchment. In the case of the Kromme and Goukou,  
 142 most of this runoff occurs over short periods, during flood events (Job 2014; Rebelo et al.  
 143 2015). All three wetlands have accumulated peat layers that are between 0.5 and 10 m  
 144 deep (**Table 1**).

145 **Table 1.** Site information for the three study wetlands. MAP: mean annual precipitation, MAR: mean annual  
 146 runoff in millions of cubic meters (Mm<sup>3</sup>) (Nsor 2007; Middleton and Bailey 2008; Sieben 2012; Job 2014;  
 147 Kotze 2015). The global aridity index is reported as a mean for the quaternary catchments shown in Figure  
 148 1 (Trabucco and Zomer 2018). Peat depth is from the literature (Rebelo et al. 2019)

Catchment	Theewaterskloof	Goukou	Kromme
Co-ordinates	33°57'40.32"S, 19°10'10.00"E	34° 0'30.46"S, 21°24'59.97"E	33°52'24.69"S, 24° 2'24.13"E
Altitude (m)	362.4	180.7	353.6
MAP (mm)	1241	645	745
Winter 2014 (mm)	644	316	197
Summer 2015 (mm)	107	351	148
MAR (Mm <sup>3</sup> )	149.8	52.3	25.4
Rainfall Region/Pattern	winter	winter	bimodal
Peat Depth (m)	0.5-2	3-10	0.5-2.8
Mean Aridity Index	4857.9	2580.2	4377.5

149

150

151 *Study design*

152 To capture seasonal variation in wetland properties and processes each wetland was  
153 sampled twice: once in September 2014, just after winter, and once in March/April 2015,  
154 just after summer. Rainfall for the six months preceding the first fieldtrip was average for  
155 all sites (approximating 50% of the MAP); however, rainfall for the six months preceding  
156 the second fieldtrip was far lower for Theewaterskloof and the Kromme (**Table 1**).  
157 Therefore, for Theewaterskloof and the Kromme, the second campaign represents a drier  
158 season, whereas there is little difference for the Goukou wetland. At each of the three  
159 wetland sites, least disturbed stretches of wetland were sampled. It should be noted that  
160 all wetlands are transformed to some degree, with channelization occurring upstream or  
161 downstream of selected fragments. At each site, cross-sectional transects (100-200 m)  
162 were made across the wetland, with six plots (3x3 m) placed between 20-50 m apart,  
163 yielding 18 plots (**Fig. 1**). Transects and plots were chosen in the field to ensure adequate  
164 representation of the two plant communities, which we term: palmiet and fynbos,  
165 yielding a final sum of 20 plots. Plots were defined as palmiet communities when the  
166 percentage cover of palmiet was over 60% (**Table A1**), and as fynbos communities when  
167 the presence of palmiet was less than 60%, yielding sample sizes of 10 and 10 for palmiet  
168 and fynbos communities respectively. Piezometers (3 m, PVC) were placed adjacent to  
169 every second plot, yielding a total of 12 piezometers (**Fig. 1**).

170 *#Figure 1 approximately here#*

171 *Sampling*

172 a) *Plant community composition and vegetation analysis*

173 In each plot, all plants were identified to species level where possible and percentage  
174 cover was estimated for each species using the Braun-Blanquet Scale (Mueller-Dombois  
175 and Ellenberg 1974). Vegetation (above-ground biomass) was sampled from three  
176 randomly selected subplots of 0.28x0.28 m within each plot. This above-ground biomass  
177 was dried for 48 hours at 70°C, weighed and then ground and homogenised using a mill.  
178 Plant total nitrogen and total phosphorus were determined using acid digestion and were  
179 measured with a continuous -flow analyzer (CFA) (SKALAR: SAN++) (Walinga et al.  
180 1989). Potassium, calcium, and magnesium were analyzed by Inductively Coupled  
181 Plasma-emission spectrometry (ICP-OES) (Walinga et al. 1989) after acid digestion of  
182 approximately 0.3 g of dried and finely ground vegetation with H<sub>2</sub>SO<sub>4</sub>-Se-salicylic acid.  
183 Thirteen plant functional traits were collected for 22 dominant wetland species. All  
184 methods were based on the standardised protocol of Pérez-Harguindeguy et al. (2013),  
185 see **Table A2** for details.

186 *b) Soil sampling and chemical analyses*

187 One composite soil sample was taken from 10 points throughout each plot at a depth of  
188 1-10 cm using a hand-held auger of 1 cm in diameter. Soil pH-H<sub>2</sub>O was measured after  
189 adding distilled water to a 10 g soil sample and shaking it for an hour. In each plot one  
190 additional undisturbed soil sample was taken of the topsoil using a 100 cm<sup>3</sup> metal  
191 Kopecky ring to measure bulk density. Samples were weighed after oven drying for 48  
192 hours at 70°C and values expressed as g/cm<sup>3</sup>. Soil water content was calculated  
193 gravimetrically by weighing approximately 20 g of fresh soil before and after drying for  
194 24 hours at 105°C. Soil organic matter content was determined by loss on ignition (4h at  
195 550°C). Total phosphorus and nitrogen were analyzed on a CFA. Soft extractions were  
196 done on fresh soil to determine NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup>. Samples were extracted and

197 preserved for later analysis on a CFA using AA-EDTA (ammonium acetate –  
198 ethylenediaminetetraacetic acid) for  $\text{PO}_4^{3-}$  and AA-KCl (ammonium acetate - potassium  
199 chloride) for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  respectively (Houba et al. 1989). Nutrient pools were  
200 calculated by multiplying nutrient concentrations by bulk density measurements.

201 Cation exchange capacity was determined using the method of Brown (1943) by weighing  
202 approximately 8 g of soil before and after air drying in an incubator at 40°C for 48 hours.  
203 Samples were then sieved through a 2 mm sieve, 25 ml ammonium acetate solution (1M)  
204 was added to 2.5 g of soil and samples were shaken for one hour. Soil pH was measured  
205 and samples were filtered through a 0.45  $\mu\text{m}$  filter before being analyzed for H, Ca, K, Mg,  
206 Na, Al, Fe, Mn ions on an ICP-OES. Potassium, calcium, and magnesium were analyzed on  
207 the ICP-OES after acid digestion of approximately 0.3 g of dried and finely ground soil  
208 with  $\text{H}_2\text{SO}_4$ -Se-salicylic acid (Walinga et al. 1989). Soil microbial biomass carbon was  
209 measured as a proxy for microbial activity in the soil at each site. We used the chloroform  
210 fumigation direct extraction protocol for microbial biomass carbon (Martens 1995; Beck  
211 et al. 1997).

### 212 *c) Groundwater sampling and chemical analyses*

213 Depth to the water table was measured in each piezometer using a sounding device, and  
214 standing water emptied using a bailer. Once fresh water had refilled the piezometer, a  
215 sample was taken for a pH, and conductivity reading. Six water samples were taken and  
216 filtered (0.45  $\mu\text{m}$ ) to test for water quality parameters. The concentration of phosphate  
217 ( $\text{PO}_4^{3-}$ -P), ammonium ( $\text{NH}_4^+$ -N), total phosphorus (P-tot), and total Kjeldahl nitrogen  
218 were measured on a CFA. Concentrations of sodium, magnesium and calcium were  
219 measured on the ICP-OES.

220

221 *Data analysis*

222 We performed an analysis of similarity (ANOSIM) to determine whether palmiet and  
223 fynbos vegetation were in fact distinct, using the Bray–Curtis dissimilarity index. Next,  
224 we performed a similarity percentage analysis (SIMPER) to determine which species  
225 characterised palmiet and fynbos communities. We used the ‘Vegan’ package for  
226 community ecology in R for these two analyses (Warton et al. 2012) as well as to calculate  
227 functional diversity indices & community weighted means.

228 To test the relationship between plant community, wetland (Theewaterskloof, Goukou,  
229 Kromme) and soil, groundwater, vegetation tissue chemistry and functional diversity  
230 parameters, we fitted linear mixed models taking season into account (winter 2014,  
231 summer 2015). Plots were entered as a random effect to account for the dependence  
232 between observations from within the same plot. Wetland, plant community, season and  
233 the interaction between wetland and plant community were entered as fixed effects.  
234 First, the significance of the interaction was tested by comparing the fit of this model to a  
235 reduced model with only the three main effects. Where the interaction term was  
236 significant, we split the dataset by wetland and tested for the effect of plant community  
237 in all three wetlands separately. Where the interaction term was not significant, we  
238 excluded it from the model and tested the significance of the main effect: plant  
239 community. Significance was tested using an F-test with Kenward-Roger correction for  
240 degrees of freedom, as implemented in the “pbKRtest” package of R. All variables, besides  
241 pH and ratios, were  $\log(x+1)$  transformed prior to analysis to satisfy the assumptions of  
242 normality and homoscedasticity of the linear mixed models.

243 Lastly a Detrended Correspondence Analysis (DCA) was performed on species abundance  
244 data, using the “vegan” package in R. Each season was analyzed separately (2014, 2015).

245 Soil and vegetation parameters that differed significantly between palmiet and fynbos  
246 communities were correlated to the first and second axes, and overlain on the plot.

### 247 **3 RESULTS**

#### 248 *Abiotic parameters driving palmiet and fynbos communities*

249 The only measured soil property that differed between fynbos and palmiet communities  
250 was pH, where it was marginally higher in fynbos communities (**Table 3**). Nutrients,  
251 nutrient pools and soil buffering capacities showed no significant differences or  
252 interesting trends. Relative groundwater depth was significantly different between the  
253 two communities, tending to be closer to the surface but more variable for fynbos  
254 communities, and deeper below the ground for palmiet communities (**Table 4**). There  
255 was significantly higher Kjeldahl nitrogen in the groundwater of palmiet compared to  
256 fynbos communities in the Goukou wetland, however these trends were not observed for  
257 other wetlands.

258

259 **Table 3.** The difference in soil parameters between fynbos and palmiet communities of three South African palmiet wetlands. The significance of the difference between  
 260 fynbos and palmiet communities within each wetland is displayed using letters ( $p < 0.05$ ). CEC stands for cation exchange capacity. For all parameters the effect of wetland  
 261 was non-significant.

		Theewaterskloof		Goukou		Kromme
		Palmiet	Fynbos	Palmiet	Fynbos	Palmiet
Physical properties	pH	4.5±0.12 <sup>a</sup>	4.6±0.50 <sup>b</sup>	4.0±0.09 <sup>a</sup>	4.9±0.35 <sup>b</sup>	5.3±0.18
	Bulk Density (g/cm <sup>3</sup> )	0.3±0.15	0.3±0.11	0.2±0.04	0.3±0.10	0.3±0.12
	Soil Water Content (%)	42.2±22.79	50.8±17.76	58.7±3.66	62.0±5.28	70.6±6.06
	Soil Organic Matter (%)	24.0±14.43	23.0±11.67	34.6±4.46	30.1±6.49	18.3±3.60
Nutrients	N/P Ratio	12.8±3.47	15.9±5.49	15.9±0.62	16.3±1.69	12.1±2.38
	P <sub>tot</sub> (mg/kg)	363.0±192.95	313.7±147.34	436.3±67.12	472.3±124.47	242.1±61.27
	PO <sub>4</sub> -P (mg/kg)	5.0±2.58	5.1±3.58	7.0±3.51	4.0±1.97	2.3±1.10
	N <sub>tot</sub> (mg/kg)	4920.2±3143.93	4777.3±2379.75	6919.0±851.32	7681.7±2042.59	3008.4±953.82
	NH <sub>4</sub> -N (mg/kg)	2.9±2.07	5.2±5.98	4.8±2.33	6.3±2.77	11.0±21.30
	NO <sub>3</sub> -N (mg/kg)	0.7±0.58	0.6±0.55	0.1±0.06	0.9±0.77	0.5±0.66
Nutrient pools	P pool (mg/L)	99.6±26.25	100.9±63.80	105.0±28.71	140.9±56.19	64.0±23.54
	PO <sub>4</sub> Pool (mg/L)	1.5±0.94	1.7±1.49	1.7±0.91	1.3±1.17	0.6±0.41
	N pool (mg/L)	1309.9±535.51	1442.2±779.41	1658.3±409.94	2270.7±806.22	764.6±278.91
	NH <sub>4</sub> Pool (mg/L)	0.8±0.41	1.8±2.15	1.1±0.39	1.8±0.72	2.5±4.40
	NO <sub>3</sub> Pool (mg/L)	0.2±0.19	0.2±0.17	0.0±0.01	0.3±0.24	0.1±0.15
Buffering capacity	CEC (meq/100g)	14.7±8.44	17.5±5.31	25.4±3.41	24.9±2.14	21.5±3.10
	Base Saturation (%)	10.2±4.12	9.1±3.72	12.1±1.41	15.8±3.91	29.2±3.52
	Na (meq/100g)	0.2±0.06	0.2±0.17	0.5±0.18	0.6±0.14	0.8±0.19
	Ca (mg/kg)	434.3±468.30	308.8±171.88	434.8±61.15	442.1±129.08	758.6±215.45
	Mg (mg/kg)	552.2±347.30	527.0±261.28	928.0±147.85	1864.1±589.98	1216.3±165.98
	K (mg/kg)	4220.2±2936.51	4243.8±2246.99	3933.3±527.58	5555.9±1503.44	3186.2±487.17
Biological	Microbial Biomass	0.3±0.15	0.4±0.36	1.5±0.61	0.8±0.27	0.5±0.22

\* Statistics for pH:  $F=5.16$ ,  $ndf=1$ ,  $ddf=12$ ,  $p=0.04$ .

262  
263

264 **Table 4.** The difference in groundwater parameters between fynbos and palmiet communities in South African palmiet wetlands. Significance is displayed using letters  
 265 ( $p < 0.05$ ). Parameters in bold are those where the effect was the same regardless of location (wetland effect not significant).

		Theewaterskloof		Goukou		Kromme
		Palmiet	Fynbos	Palmiet	Fynbos	Palmiet
Physical	<b>pH</b>	<b>5.3±0.44</b>	<b>5.8±0.73</b>	<b>5.6±0.33</b>	<b>5.7±0.23</b>	5.8±0.33
	<b>Conductivity (uS/cm)</b>	<b>44.5±10.61</b>	<b>76.3±16.74</b>	<b>128.0±53.25</b>	<b>134.5±13.55</b>	149.4±34.17
	<b>Relative Groundwater Depth (m)</b>	<b>0.7±0.01<sup>a</sup></b>	<b>0.7±0.98<sup>b</sup></b>	<b>1.5±1.10<sup>a</sup></b>	<b>0.2±0.37<sup>b</sup></b>	1.0±1.14
Nutrients	Kjeldahl Nitrogen (mg/l)	1.1±0.33	2.6±1.23	4.1±2.85	1.0±0.13	3.6±5.14
	<b>NH<sub>4</sub>-N (mg/l)</b>	<b>0.0±0.04</b>	<b>0.3±0.32</b>	<b>0.1±0.08</b>	<b>0.1±0.07</b>	0.1±0.06
	<b>P<sub>tot</sub> (mg/l)</b>	<b>0.1±0.10</b>	<b>0.2±0.09</b>	<b>0.2±0.18</b>	<b>0.1±0.07</b>	0.3±0.38
	<b>PO<sub>4</sub>-P (mg/l)</b>	<b>0.0±0.02</b>	<b>0.0±0.02</b>	<b>0.0±0.02</b>	<b>0.0±0.02</b>	0.0±0.02
Ions	<b>Na (mg/l)</b>	<b>2.8±0.57</b>	<b>4.9±0.23</b>	<b>14.2±5.62</b>	<b>13.4±0.84</b>	17.6±2.05
	<b>Ca (mg/l)</b>	<b>0.4±0.01</b>	<b>1.7±1.67</b>	<b>5.2±1.55</b>	<b>4.8±3.17</b>	4.2±2.76
	<b>Mg (mg/l)</b>	<b>0.4±0.09</b>	<b>0.8±0.23</b>	<b>1.4±1.09</b>	<b>1.8±0.12</b>	2.6±0.41

\* Statistics for RGD:  $F=0.68$ ,  $ndf=1$ ,  $ddf=6$ ,  $p=0.02$ ; KjN:  $F=16.59$ ,  $ndf=1$ ,  $ddf=4$ ,  $p=0.02$ .

266  
 267  
 268

269 *Biotic factors driving palmiet and fynbos communities*

270 Although there was no significant difference in soil or groundwater K and Mg, there was  
271 a significantly higher concentration of these cations in palmiet vegetation compared to  
272 that of the fynbos vegetation (**Table 5**). Nutrient concentrations in plant tissues did not  
273 differ significantly between communities. There was no significant difference in the  
274 number of functional types for the two communities (**Table 6**). Diversity indices did not  
275 differ significantly between communities, however various community weighted means  
276 did vary. Stem diameter, leaf length-width ratio, leaf area as well as cellulose and lignin  
277 concentration in the leaves were significantly higher in palmiet communities relative to  
278 fynbos communities. Conversely, the community weighted mean for percentage of plant  
279 silicon concentration was higher in fynbos than palmiet communities.

280

281 **Table 5.** The difference in vegetation parameters between fynbos and palmiet communities in three South African palmiet wetlands. The significance of the difference  
 282 between fynbos and palmiet wetland communities is displayed using letters ( $p < 0.01$ ). For all parameters the effect of wetland was non-significant.

	Theewaterskloof		Goukou		Kromme
	Palmiet	Fynbos	Palmiet	Fynbos	Palmiet
N/P ratio	18.7±2.15	24.3±10.28	17.9±3.7	30.6±10.59	22.3±5.65
Ptot (mg/kg)	366.7±121.58	359.5±271.63	408.9±129.8	217.3±90.02	378.5±254.16
Ntot (mg/kg)	6836.7±2364.66	6741.8±2026.69	7079.6±1467.41	6013±1357.84	7478.9±4245.99
K (mg/kg)	5406.8±2790.54 <sup>a</sup>	3015.8±1662.88 <sup>b</sup>	6887±3390.71 <sup>a</sup>	3312.4±1432.24 <sup>b</sup>	10070.9±4701.28
Ca (mg/kg)	2965.3±1758.7	1427±591.15	2375.8±864.54	2021.6±1173.54	2643.8±1200.94
Mg (mg/kg)	1715±398.18 <sup>a</sup>	996.9±254.89 <sup>b</sup>	1469.8±497.69 <sup>a</sup>	1008.5±302.37 <sup>b</sup>	1483.1±377.77

\* Statistics for K:  $F=10.00$ ,  $ndf=1$ ,  $ddf=12$ ,  $p=0.008$ ; Mg:  $F=12.07$ ,  $ndf=1$ ,  $ddf=12$ ,  $p=0.004$ .

283  
284

285 **Table 6.** Composition of fynbos and palmiet communities in three South African palmiet wetlands, including functional diversity indices and community weighted means.  
 286 The significance of the difference between fynbos and palmiet communities is displayed: \* p<0.05, \*\* p<0.01, \*\*\* p<0.001; F and p values are given in **Table A3**. Parameters  
 287 in bold are those where the effect was the same regardless of location (wetland effect not significant).

		Theewaterskloof		Goukou		Kromme
		Palmiet	Fynbos	Palmiet	Fynbos	Palmiet
General	Number of species	5.7±1.37	8.0±1.26	3.0±0.00	8.4±2.28	*** 4.3±1.06
	<b>Number of functional types</b>	<b>4.2±1.17</b>	<b>4.2±0.75</b>	<b>3.0±0.00</b>	<b>3.9±1.17</b>	<b>2.4±0.84</b>
	<b>% Cover by dominant</b>	<b>85.0±9.49</b>	<b>59.2±22.00</b>	<b>80.0±17.80</b>	<b>64.6±18.96</b>	<b>97.5±3.54</b>
Diversity Indices	<b>Functional richness</b>	<b>6.9±2.71</b>	<b>7.3±2.64</b>	<b>1.3±0.25</b>	-	-
	<b>Functional evenness</b>	<b>0.7±0.24</b>	<b>0.6±0.20</b>	<b>0.9±0.11</b>	-	-
	<b>Functional diversity</b>	<b>0.9±0.06</b>	<b>0.8±0.06</b>	<b>0.8±0.08</b>	-	-
	<b>Functional dispersion</b>	<b>3.4±0.53</b>	<b>3.7±1.03</b>	<b>4.2±0.26</b>	<b>3.2±1.28</b>	<b>2.0±1.51</b>
	<b>Rao's entropy</b>	<b>14.1±2.36</b>	<b>16.3±5.04</b>	<b>19.0±2.22</b>	<b>13.6±6.74</b>	<b>8.0±5.88</b>
Community Weighted Means	<b>Shoot length (mm)</b>	<b>1662.2±72.40</b>	<b>1295.8±537.18</b>	<b>1471.6±90.58</b>	<b>1319.1±213.99</b>	<b>1450.8±307.91</b>
	<b>Stem diameter (mm)</b>	<b>55.1±6.65</b>	<b>28.5±16.70</b>	** 49.9±3.16	<b>19.3±16.37</b>	** 70.9±10.69
	<b>Total biomass (g)</b>	<b>896.5±134.39</b>	<b>443.5±273.06</b>	* 5199.0±2215.49	<b>709.3±1545.10</b>	* 1151.7±269.82
	<b>Leaf length-width ratio</b>	<b>19.9±2.56</b>	<b>9.9±5.99</b>	* 19.2±1.25	<b>6.4±6.48</b>	* 23.1±4.31
	<b>Leaf mass (mg)</b>	<b>10358.7±1938.03</b>	<b>8705.7±4546.80</b>	<b>6064.6±448.05</b>	<b>10626.4±5336.56</b>	<b>8306.8±1691.15</b>
	<b>Leaf area (mm<sup>2</sup>)</b>	<b>11884.4±1969.51</b>	<b>6463.8±3676.64</b>	* 9202.4±675.86	<b>4355.3±3021.99</b>	* 12680.7±2510.67
	<b>Specific leaf area (mm<sup>2</sup>/mg)</b>	<b>1.5±0.27</b>	<b>1.4±0.47</b>	<b>1.7±0.23.00</b>	<b>3.7±3.10</b>	<b>3.7±1.84</b>
	<b>Si concentration (%)</b>	<b>833.2±355.77</b>	<b>4842.7±5179.11</b>	* 734.3±23.80	<b>5270.6±3679.17</b>	* 844.4±321.60
	<b>Cellulose per leaf (mg)</b>	<b>2958.2±397.18</b>	<b>1435.8±872.81</b>	* 2440.4±181.16	<b>625.0±954.89</b>	* 3352.1±683.38
	<b>Lignin per leaf (mg)</b>	<b>352.7±42.20</b>	<b>188.5±99.73</b>	* 298.3±21.50	<b>83.7±112.74</b>	* 404.0±81.78
	<b>Aerenchym (score: 1-3)</b>	<b>1.9±0.23</b>	<b>1.6±0.32</b>	<b>1.6±0.04</b>	<b>1.6±0.24</b>	<b>1.8±0.16</b>
	<b>Woodiness (score: 1-3)</b>	<b>2.0±0.17</b>	<b>1.8±0.43</b>	<b>2.0±0.00</b>	<b>2.1±0.26</b>	<b>2.1±0.20</b>
	<b>Hollowness (score: 1-3)</b>	<b>1.1±0.09</b>	<b>1.1±0.17</b>	<b>1.1±0.15</b>	<b>1.0±0.03</b>	<b>1.0±0.00</b>

288

289 *A comparison of palmiet and fynbos communities*

290 The ANOSIM revealed 62-72% dissimilarity between fynbos and palmiet plant  
291 communities. Palmiet communities tended to be characterized by *Prionium serratum*  
292 (Palmiet, 87-94%) some *Cliffortia odorata*, and ferns: *Todea barbara* and *Pteridium*  
293 *aquilinum* (**Table A4**). Fynbos communities were distinguished by *Restio paniculatus*  
294 (43-44%), *Cliffortia strobilifera* (17-23%), and to a lesser extent two graminoids  
295 *Epischoenus gracilis* and *Isolepis prolifera* (**Table A4**). Based on plant community  
296 structure from September 2014 the DCA confirmed that fynbos communities tend to be  
297 more diverse than palmiet ones (**Fig. 2**). Fynbos and palmiet communities cluster  
298 separately except for two fynbos plots which clustered closer to the palmiet communities.  
299 These two plots were both situated within palmiet communities, though were classified  
300 as non-palmiet communities as the cover of palmiet was less than 50%. The results from  
301 2015 showed similar trends and are displayed in **Fig. A1**.

302

303 *#Figure 2 approximately here#*

304

## 305 **4 DISCUSSION**

306 *Which environmental parameters explain patchiness in palmiet wetlands?*

307 Only two abiotic variables differed significantly between fynbos and palmiet patches in  
308 palmiet wetlands. These were soil pH, which was slightly higher in fynbos communities,  
309 and relative groundwater depth, which tended to be closer to the surface in one wetland  
310 (Goukou) but more variable for another (Theewaterskloof) for fynbos communities. In a

311 study on the Kromme palmiet wetland, Nsor (2007) also found soil pH to be a key  
312 environmental variable influencing community assembly. Additionally a study on  
313 riparian zones in South Africa confirmed that flow regimes were the key variable  
314 determining four different zones of differing plant communities (Reinecke 2013). There  
315 is no doubt that hydrological regime and geomorphological processes will play an  
316 important role in shaping wetland plant communities (Tooth and McCarthy 2007),  
317 however in the case of palmiet wetlands, longer term monitoring of water table depth is  
318 needed to yield more insight. In this case it is not clear whether water table depth is  
319 driving vegetation dynamics, or whether the vegetation is shaping local water table depth  
320 and pH through processes such as transpiration, photosynthesis and decomposition.

#### 321 *Can plant functional traits shed light on the super-dominance of Palmiet?*

322 Within palmiet wetlands there are at least two distinct plant communities: palmiet-  
323 dominated communities, and somewhat more diverse fynbos communities. The diversity  
324 within fynbos communities likely points to more than one community type (e.g. *Calopsis*  
325 *paniculata* vegetation -Community 1.1, *Cliffortia strobilifera* vegetation -Community 1.2;  
326 see Sieben et al. 2017b). Plants may be grouped into dominant matrix species, interstitial  
327 species, and ruderals (Boutin and Keddy 1993), or using a functional approach into  
328 dominants, subordinates and transients (Grime 1998). This applies to palmiet  
329 communities; *P. serratum* acting as the dominant matrix species, *Cliffortia odorata*, ferns  
330 *Todea barbara* and *Pteridium aquilinum* as well as various *Psoralea sp.* (depending on the  
331 region) acting as the sparse interstitial species. *Cliffortia odorata* has a creeping form and  
332 *Psoralea sp.* are spindly trees. Vegetation potassium (K) and magnesium (Mg)  
333 concentration was significantly higher in the palmiet communities relative to the fynbos;  
334 however, these differences are not reflected in the soil or groundwater, therefore it is not

335 clear why this difference should occur. This greater accumulation of K in palmiet could  
336 be the result of higher transpiration rates relative to fynbos communities (Brag 1972;  
337 Rebelo et al. 2020). Another possibility is that it is indicative of palmiet communities  
338 being older than the fynbos ones, and these tissue concentrations reflecting longer term  
339 uptake from soil and groundwater (e.g. from high cation flood pulses). Additionally, at  
340 low pH, Mg becomes more soluble and therefore in palmiet communities may be more  
341 available for plant uptake (Jackman and Black 1951; Lucas and Davis 1961).

342 While fynbos communities had more plant species than palmiet communities there was  
343 no difference in the number of functional types. This suggests that although palmiet  
344 communities are more species poor (and less even, with Palmiet dominating), the suite  
345 of species is optimal for exploiting the niche space provided by the wetland (i.e. there is  
346 convergence on the same number of functional types). Community weighted means for  
347 stem diameter, leaf length-width ratio, leaf area as well as cellulose and lignin  
348 concentration in the leaves were significantly higher in palmiet communities relative to  
349 fynbos communities. These mean values in palmiet communities were highly influenced  
350 by the dominant species: Palmiet. The palmiet community's overall larger stem diameter  
351 than that of the fynbos may be confirmation of the community being fire retardants as  
352 opposed to promoters (Rebelo 2001), allowing fires to pass over the crown of the plants,  
353 leaving the stems intact. The larger stem diameter may equally confer benefits for  
354 withstanding the mechanical disturbance of floods. There is evidence of the co-evolution  
355 of rivers and vegetation on geological time-scales that give rise to traits that allow the  
356 vegetation to tolerate disturbances (Gibling et al. 2014). The significantly higher leaf  
357 length-width ratio (long strap-like leaves) may be an adaptation to the mechanical  
358 disturbance of floods (Colmer and Voisenek 2009; Catford and Jansson 2014).

359 Additionally, the higher cellulose and lignin concentration of the leaves, but lower  
360 biogenic silica concentration may indicate high stem flexibility (Schoelynck et al. 2010),  
361 representing another adaptation to flood events (Colmer and Voesenek 2009; Catford  
362 and Jansson 2014). We did not measure below ground traits in this study, however  
363 another study on palmiet wetland communities has shown that rhizome internode length  
364 (a measure for clonality) was important in explaining vegetation spatial patterns (Sieben  
365 2012).

### 366 *Ecological hypotheses of palmiet wetland development*

367 Since there is no clear evidence of abiotic conditions explaining patchiness in palmiet  
368 wetlands from these results, other explanatory factors for these patterns are possible.  
369 Disturbance and competition, or a combination of these, may also shape vegetation  
370 patterns. Little is known about how palmiet wetlands have formed over time, but it is  
371 acknowledged that pristine, unchanneled valley-bottom palmiet wetlands are typically  
372 located on slopes that are steeper than would be expected to be suitable for wetland  
373 formation (Pulley et al. 2018; Grenfell et al. 2020). A geomorphological theory for the  
374 development of palmiet wetlands suggests that gully cut-and-fill cycles laterally plane  
375 valley floors and contribute to gradually widening the valley-bottom and reducing  
376 longitudinal slope. Proposed geomorphological drivers for this erosion are impingement  
377 of the valley-bottom by alluvial fans, or more commonly the exceedance of slope through  
378 aggradation (Grenfell et al. 2010; Pulley et al. 2018; Grenfell et al. 2020).

379 Other drivers may potentially include extreme (1:100 year) fires and floods which could  
380 cause localized erosion, initiating gully formation in some cases. Whilst Palmiet is fire-  
381 adapted (Boucher and Withers 2004), severe fire, especially during drought, could locally  
382 damage stem and root stocks. Once these gullies have leveled the longitudinal profile, the

383 shallower slope would encourage deposition of organic matter and clastic sediment  
384 (Pulley et al. 2018). This would create an opportunity for competition for establishment  
385 (juvenile trait subset) within the potential species pool. Those species with superior  
386 colonization ability would have a competitive advantage initially (Shipley et al. 1989).

387 In cases where this gully erosion exceeds the scale that the system has evolved to cope  
388 with (e.g. with the introduction of European-style farming and irrigation, railways, dams  
389 and roads), it is possible that the system exceeds a threshold and switches to another  
390 stable state (Suding et al. 2004; Brown et al. 2017; Tooth 2018; Grenfell et al. 2020). This  
391 is evidenced by cases where the alluvium of the entire valley-floor is washed downstream  
392 for hundreds of meters (e.g. parts of the Kromme and Duivenhoks rivers), or the  
393 unprecedented synchronous phase of incision across the wetland in Pietersielieskloof  
394 palmiet wetland (Grenfell et al. 2020). Recruitment in this harsh environment of floods,  
395 droughts, grazing and fire, is challenging and therefore success is limited in the short-to-  
396 medium term (Rebelo 2017). Though the erosion process itself is “natural” (Pulley et al.  
397 2018), in many cases this process has accelerated (Brown et al. 2017) and intensified in  
398 the Anthropocene to a point that is not beneficial for nature and society. On geological  
399 time-scales these wetland ecosystems will probably self-restore, but in the interim it  
400 represents a large loss of ecosystem services to society, justifying rehabilitative  
401 intervention (Tooth 2018; Grenfell et al. 2020). Little is known about which species are  
402 best to use for palmiet wetland rehabilitation, as little is known about the genesis of  
403 palmiet wetlands. We present three possible hypotheses from an ecological perspective,  
404 which may guide future research and rehabilitation initiatives.

405 *a) Hypothesis 1. Succession towards Palmiet-dominated communities*

406 One hypothesis to explain patchiness in palmiet wetland vegetation is that fynbos  
407 communities (possibly with Palmiet interspersed, but not dominated by it) are an earlier  
408 successional stage, and that autogenic succession is at work, propelling the system  
409 towards a climax community, dominated by Palmiet (Mitsch and Gosselink 2015). This is  
410 based on the findings that (1) fynbos communities tend to be more species rich,  
411 characteristic of the pioneer stage, and (2) Palmiet-dominated communities had higher  
412 tissue K and Mg, possibly due to being older. A conceptual diagram for this process is  
413 given in **Fig. 3**. This hypothesis is underpinned by the following two assumptions: (1)  
414 fynbos species are superior juvenile competitors and have higher success establishing  
415 from the potential seed pool, and (2) Palmiet is a superior adult competitor, able to take  
416 over by predominantly clonal growth (vegetative reproduction) by expanding existing  
417 patches. These clonal root systems are likely to be very old and analogous to the  
418 'underground forests' formed by species in tropical Africa (Maurin et al. 2014). Palmiet  
419 is cited to be an ecosystem engineer (Sieben 2012), due to its ability to modify its  
420 environment to its advantage. One way in which Palmiet may modify its environment is  
421 through the production of thick above-ground roots which form a convoluted mass  
422 sometimes as much 20 cm to 1 m above the ground surface (**Plate 1: b,c,e**). In fynbos  
423 communities within palmiet wetlands there are no such structures, and fynbos grows  
424 straight from the peat or soil. It is possible that this root formation is an adaptation for  
425 flood events: the root system prevents uprooting during flood events, and the height of  
426 the plants from the ground may result in a decrease in anoxia in the root zone.

427 Patches of palmiet (e.g. looking at a cross-section across the valley) also appear to be  
428 slightly raised in the center as a result of this root development at scale (**Fig. 4**). Possibly  
429 an adaptation to maximize light exposure, or a result of accumulation of sediment from

430 diffuse flows (e.g. **Plate 1: g**), this phenomenon is known in other wetlands in drylands,  
431 and thought to be critical for chemical sedimentation (Tooth and McCarthy 2007). These  
432 raised mounds eventually alter the pathway of water through the valley-bottom, creating  
433 preferential flow paths (Pulley et al. 2018). The sediment deposition (aggradation) may  
434 also be the phenomenon that accounts for the steeper longitudinal slope of Palmiet  
435 wetlands relative to the bedrock (Pulley et al. 2018; Grenfell et al. 2020). Literature  
436 suggests that this would be likely to result in localized erosion (Pulley et al. 2018; Grenfell  
437 et al. 2020), which would restart the cycle of vegetation colonization and succession in  
438 these highly dynamic wetland ecosystems.

439  
440 *#Figure 3 approximately here#*

441  
442 *#Figure 4 approximately here#*

443

444 *b) Hypothesis 2. Succession towards fynbos communities*

445 A second hypothesis is that fynbos communities are the climax community, with the  
446 Palmiet-dominated community as the pioneer, an alternative form of autogenic  
447 succession (Mitsch and Gosselink 2015). Following severe gully erosion, it has been noted  
448 that palmiet establishes in small patches within these gullies (**Plate 1**). It has been  
449 proposed that Palmiet traps sediments and organic material, and that as these patches  
450 expand, the wetland would be raised, until the gully was refilled (Barclay 2016, **Fig. 5**).  
451 Palmiet patches have also been observed to close up over water-filled gullies, or water-  
452 bodies, by means of their root system (**Fig. 6**). As sediment accumulates and the habitat  
453 becomes more suitable for other species, it is possible that fynbos species could establish

454 and outcompete Palmiet. It is well known that Palmiet does not tolerate shade (e.g.  
455 following invasion by alien trees), so could be out-competed by other shrubs (Boucher  
456 and Withers 2004). This hypothesis is underpinned by the following two assumptions:  
457 (1) Palmiet is a superior juvenile competitor, especially in extreme conditions (e.g.  
458 following gully erosion), and (2) fynbos species are able to outcompete Palmiet once it  
459 has reached a mature state. In this situation, Palmiet transforms a habitat from one that  
460 is inhospitable to other species, to one that is ideal, through the trapping of sediment: an  
461 altruistic ecosystem engineer.

462

463 *#Figure 5 approximately here#*

464

465 *#Figure 6 approximately here#*

466

### 467 *c) Hypothesis 3. Non-directional maturity*

468 An alternative hypothesis is that all communities may be 'mature' palmiet wetland  
469 communities and that there is no temporal succession towards a 'climax' palmiet  
470 community (Niering 1989; Mitsch and Gosselink 2015). This hypothesis would rely on  
471 the assumption that both Palmiet and other palmiet wetland fynbos species have equal  
472 or similar juvenile colonization abilities (Shipley et al. 1989), depending on conditions or  
473 challenges to establishment. Evidence to support this hypothesis is provided in **Fig. 7**  
474 which shows the stability of patches of Palmiet-dominated communities over a 60-year  
475 period in the Goukou wetland. The Palmiet-dominated patches do not appear to expand  
476 nor shrink over this time. Conversely, palmiet patch expansion where there is no

477 competition from other communities seems to be much more rapid (e.g. establishing  
478 across a channel) (**Fig. 5**). From the change in the small patches of Palmiet at Jonkershoek  
479 over the past 13 years (**Fig. 6**), it appears that palmiet patches could potentially expand  
480 at a rate of as much as 15 m<sup>2</sup> per month. It is, however, possible that clonal expansion of  
481 palmiet communities into existing fynbos communities, or *vice versa*, take place on much  
482 greater timescales than can be captured by aerial photographic history. If this were the  
483 case, this would have important consequences for restoration using the species Palmiet.

484

485 *#Figure 7 approximately here#*

486

#### 487 *d) Implications for wetland restoration/rehabilitation*

488 Several restoration programmes seek to use Palmiet as a pioneer species in replanting  
489 efforts on the basis that it is an ecosystem engineer, and therefore would be able to  
490 colonize a degraded river or wetland system, creating habitat for other species to follow  
491 at a later stage. However, only one of our three hypotheses suggest that Palmiet would be  
492 appropriate for use as a pioneer (hypothesis 2), and one hypothesis implies that it may  
493 be appropriate in certain conditions (hypothesis 3). It is also possible that all three  
494 hypotheses hold in certain circumstances, and do not in others. For example, fynbos  
495 species may be superior juvenile competitors in palmiet wetlands after severe fire, where  
496 there is still alluvium to colonize, whereas Palmiet may be a superior competitor where  
497 there is an open body of water to colonize, or a water-filled gully. Either way it seems  
498 clear that palmiet expanding from existing patches with healthy root beds, or 'islands',  
499 into open water takes place rapidly, whereas palmiet recruiting from seedlings takes

500 place much more slowly, which is the opposite of some other dominant wetland  
501 macrophytes (Terer et al. 2014).

502 This has critical implications for restoration activities. Firstly, perhaps Palmiet may not  
503 be the best species to use for initial stages of palmiet wetland restoration compared to  
504 other fynbos wetland species. More research is needed on the efficacy of different palmiet  
505 wetland species in rehabilitation efforts in cases where rapid growth and ground cover  
506 is needed. Secondly, if Palmiet is planted, it may experience better establishment and  
507 higher survival if planted in patches, rather than individually. Further research is needed  
508 into these dynamics as well as the long-term impacts of groundwater level fluctuations  
509 and the influence of fire, and their interactions. Furthermore, these three hypotheses  
510 remain to be interrogated from a geomorphological and hydrological perspective. An  
511 interdisciplinary approach combining ecology, hydrology and geomorphology is  
512 recommended.

## 513 **5 CONCLUSION**

514 Soil pH and relative groundwater depth were two key environmental parameters that  
515 were correlated with plant community assembly in palmiet wetlands. Long-term  
516 monitoring is needed to understand the relationship between relative groundwater  
517 depth and plant community assembly in palmiet wetlands. Palmiet communities were  
518 characterized by higher community weighted means for stem diameter, leaf length-width  
519 ratio, leaf area as well as cellulose and lignin concentration. These suggest adaptations to  
520 fire (thicker stems – fire retardants) and floods (long, thin leaves, flexible shoots and  
521 thicker stems). We propose three hypotheses to explain the presence of patchiness in  
522 palmiet wetland vegetation. The hypotheses shed light on palmiet restoration strategies  
523 and highlight gaps for future research.

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535 **Conflicts of interest/Competing interests (include appropriate disclosures)**

536 The authors have no conflicts of interest to declare.

537 **Availability of data and material (data transparency)**

538 Data will be made available upon acceptance.

539 **Code availability (software application or custom code)**

540 Code will be made available upon acceptance.

541 **Authors' contributions (optional: please review the submission guidelines from**  
542 **the journal whether statements are mandatory)**

543 AJR, KJE, PM conceived the study, AJR performed data analysis, AJR wrote the manuscript  
544 and KJE, PM, ES, contributed and edited it.

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## 707 CAPTIONS

708

709 **Fig. 1** The location of the 20 study plots (yellow and blue circles) and three study wetlands within the Cape  
710 Floristic Region (green) of South Africa. Blue circles indicate the location of piezometers, and the black  
711 shapes indicate the quaternary catchments the wetland are located within. The global aridity index is  
712 plotted, with most of the wetlands located in areas classified as semi-arid (Trabucco and Zomer 2018).

713

714 **Fig. 2** Detrended Correspondence Analysis (DCA) of the plant communities in fynbos and palmiet patches  
715 in three South African palmiet wetlands sampled in September 2014. Fynbos sites are in orange, palmiet in  
716 green. Symbols: ▲ Theewaterskloof, ■ Goukou, ● Kromme. Species names are given in black, and +  
717 indicates species with a lower abundance that are masked by other labels. Parameters that were interesting  
718 or significantly different (bold) between palmiet and fynbos wetland patches were overlain and are  
719 indicated by the arrows. Soil parameters are in brown, vegetation composition in green, functional  
720 diversity indices in blue. CWM: community weighted mean, LLWR: leaf length-width ratio, Lig: lignin, Cel:  
721 cellulose, SD: stem diameter, LA: leaf area, Si: silicon, No\_sp: number of species, Veg.K: K in vegetation,  
722 Veg.Mg: Mg in vegetation, MicrobialC: microbial carbon, CEC: cation exchange capacity, SWC: soil water  
723 content. For full species names see **Table A5**. Stippled circles encompass sites from fynbos and palmiet  
724 communities

725

726 **Fig. 3** Conceptualization of autogenic succession in palmiet wetlands over a time period of thousands of  
727 years. The section of palmiet wetland is represented by the gray rectangle with various disturbances  
728 represented.

729

730 **Fig. 4** Conceptualized cross section through a wetland dominated by palmiet, and that of a more diverse  
731 fynbos community in the mid-region of the Goukou catchment. The gray stippled line represents the peat  
732 bed of an average transect in the Goukou. In the fynbos community: yellow represents graminoids, green:  
733 shrubs, brown: ferns, black: trees with some individual Palmiet plants. In the case of the palmiet-dominated  
734 wetland, the brown root zone and raised center is apparent. In this case, it is hypothesized that the fynbos  
735 community may be the result of disturbance and recent colonization, and there is no presence of peat.

736

737 **Fig. 5** Conceptual diagram of Palmiet recolonization following disturbance (after Barclay 2016). The gray  
738 stippled area indicates peat, blue: water, green: palmiet and interstitial vegetation, brown: sediment and  
739 organic build-up from Palmiet. (a) intact palmiet wetland with raised center, stimulating gully formation at  
740 the edge of the wetland, (b) alluvium washed out and gully eroded to bed-rock, (c) Palmiet starts to colonize  
741 the gully from the edges, using its superior root stock, (d) sediment and organic matter build up, until (e)  
742 the gully is refilled and the wetland is “intact” once more. As a result of sediment deposition, the habitat  
743 becomes more suitable for other facultative wetland species, which may start to invade and outcompete  
744 Palmiet in patches.

745

746 **Fig. 6** Aerial photograph time series showing expansion of palmiet patches behind the Jonkershoek dam  
747 from 2005 to 2018. The light green region in the map of South Africa represents the Cape Floristic Region.  
748 White arrows indicate change in palmiet patches. The values in m<sup>2</sup> show the area of the palmiet wetland in  
749 each time-step, calculated from Google Earth Imagery ©.

750

751 **Fig. 7** Aerial photograph time series of the Goukou palmiet wetland from 1954-2014. The light green region  
752 in the map of South Africa represents the Cape Floristic Region. Black arrows represent four large palmiet

753 patches which tend to be lighter than the adjacent fynbos communities. The darkest areas on the  
754 photographs are invasive alien trees, invading tributaries and the periphery of the wetland.

755 **APPENDIX**

756 **Table A1.** The percentage cover of palmiet in each of the plots from three palmiet wetlands, South Africa, and the mean value for 2014 and 2015 combined. Where the  
 757 presence of palmiet exceeded 60% cover, these were assigned to the palmiet community (n=10), and where it was lower, these were assigned to the fynbos community  
 758 (n=10).  
 759

Site	Community	% Palmiet 2014	% Palmiet 2015	mean
T7	Palmiet	95	95	95
T8	Palmiet	85	80	82.5
T9	Fynbos	7	20	13.5
T10	Fynbos	25	35	30
T11	Fynbos	50	55	52.5
T12	Palmiet	85	70	77.5
G1	Fynbos	50	50	50
G2	Palmiet	95	60	77.5
G3	Palmiet	95	70	82.5
G4	Fynbos	20	30	25
G5	Fynbos	0	0	0
G6	Fynbos	0	0	0
G7	Fynbos	0	0	0
G8	Fynbos	7	45	26
G9	Fynbos	0	0	0
K1	Palmiet	95	100	97.5
K2	Palmiet	100	100	100
K3	Palmiet	95	100	97.5
K5	Palmiet	100	100	100
K6	Palmiet	90	95	92.5

760

761 **Table A2.** The 13 functional traits collected for the 22 dominant wetland species. All methods were based on the standardised protocol of Pérez-Harguindeguy et al. (2013).

762 For categorical traits the codes assigned are shown in brackets.

	<b>Trait</b>	<b>Measurement method used</b>	<b>Unit</b>	<b>Scale</b>	
Morphological/ Anatomical Traits	Shoot Length	Average shoot length of 10 mature plants	mm	Ratio	
	Stem Diameter	Average diameter of 10 stems at base level	mm	Ratio	
	Total Biomass	Average value of total biomass divided by number of mature shoots (in case of a tuft or rhizome)	g	Ratio	
	Leaf Length/Width Ratio (LLWR)	Ratio between the length and the width of a leaf based on an average of 10 leaves	mm/m	Ratio	
	Leaf Dry Mass	Average leaf mass after being oven dried at 60°C for 72 hours (10 leaves)	mg	Ratio	
	Leaf Area	Area of a single surface of a leaf based on an average of 10 leaves	mm <sup>2</sup>	Ratio	
	Specific Leaf Area (SLA)	The total surface area of a leaf divided by its dry mass (based on an average of 10 leaves)	mm <sup>2</sup> /m	Ratio	
	Presence of Aerenchym	Scale of 1 to 3 (1 = no aerenchym, 2 = less than 50% aerenchym, 3 = predominantly aerenchym)	g	Class	Ordinal
	Woodiness of Stem	Scale of 1 to 3 (1 = no woody tissue, 2 = less than 50% woody tissue, 3 = predominantly woody tissue)	Class	Class	Ordinal
	Hollowness of Stem	Scale of 1 to 3 (1 = stem not hollow, 2 = hollow space less than 50%, 3 = hollow space more than 50%)	Class	Class	Ordinal
Biochemical Traits	Si Content	Biogenic silica was extracted from 25 mg dry plant (leaf and stem) material from 10 plants and analysed using ICP-OES	%	Ratio	
	Absolute amount of Cellulose per leaf	Cellulose content (%) multiplied by average dry leaf mass to get an amount of Si per leaf	mg	Ratio	
	Absolute amount of Lignin per leaf	Lignin content (%) multiplied by average dry leaf mass to get an amount of Si per leaf	mg	Ratio	

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**Table A3:** Statistical results of the linear mixed models for community parameters. Parameters in bold indicate no significant effect of wetland. NS indicates not significant.

		Theewaterskloof		Goukou		
		Palmiet	Fynbos	Palmiet	Fynbos	
General	Number of species	NS		<b>F=33.65, ndf=1, ddf=12, p=0.000</b>		
	<b>Number of functional types</b>			NS		
	<b>% Cover by dominant</b>			NS		
Diversity Indices	<b>Functional richness</b>			NS		
	<b>Functional evenness</b>			NS		
	<b>Functional diversity</b>			NS		
	<b>Functional dispersion</b>			NS		
	<b>Rao's entropy</b>			NS		
Community Means	Weighted	<b>Shoot length (mm)</b>			NS	
		<b>Stem diameter (mm)</b>			<b>F=9.41, ndf=1, ddf=12, p=0.010</b>	
		<b>Total biomass (g)</b>			<b>F=7.26, ndf=1, ddf=12, p=0.020</b>	
		<b>Leaf length-width ratio</b>			<b>F=8.20, ndf=1, ddf=12, p=0.014</b>	
		<b>Leaf mass (mg)</b>			NS	
		<b>Leaf area (mm<sup>2</sup>)</b>			<b>F=6.79, ndf=1, ddf=12, p=0.023</b>	
		<b>Specific leaf area (mm<sup>2</sup>/mg)</b>			NS	
		<b>Si concentration (%)</b>			<b>F=4.88, ndf=1, ddf=12, p=0.050</b>	
		<b>Cellulose per leaf (mg)</b>			<b>F=5.29, ndf=1, ddf=12, p=0.040</b>	
		<b>Lignin per leaf (mg)</b>			<b>F=6.32, ndf=1, ddf=12, p=0.027</b>	
		<b>Aerenchym (score: 1-3)</b>			NS	
		<b>Woodiness (score: 1-3)</b>			NS	
		<b>Hollowness (score: 1-3)</b>			NS	

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**Table A4:** Results of the SIMPER analysis comparing palmiet and fynbos communities in palmiet wetlands for 2014 and 2015.

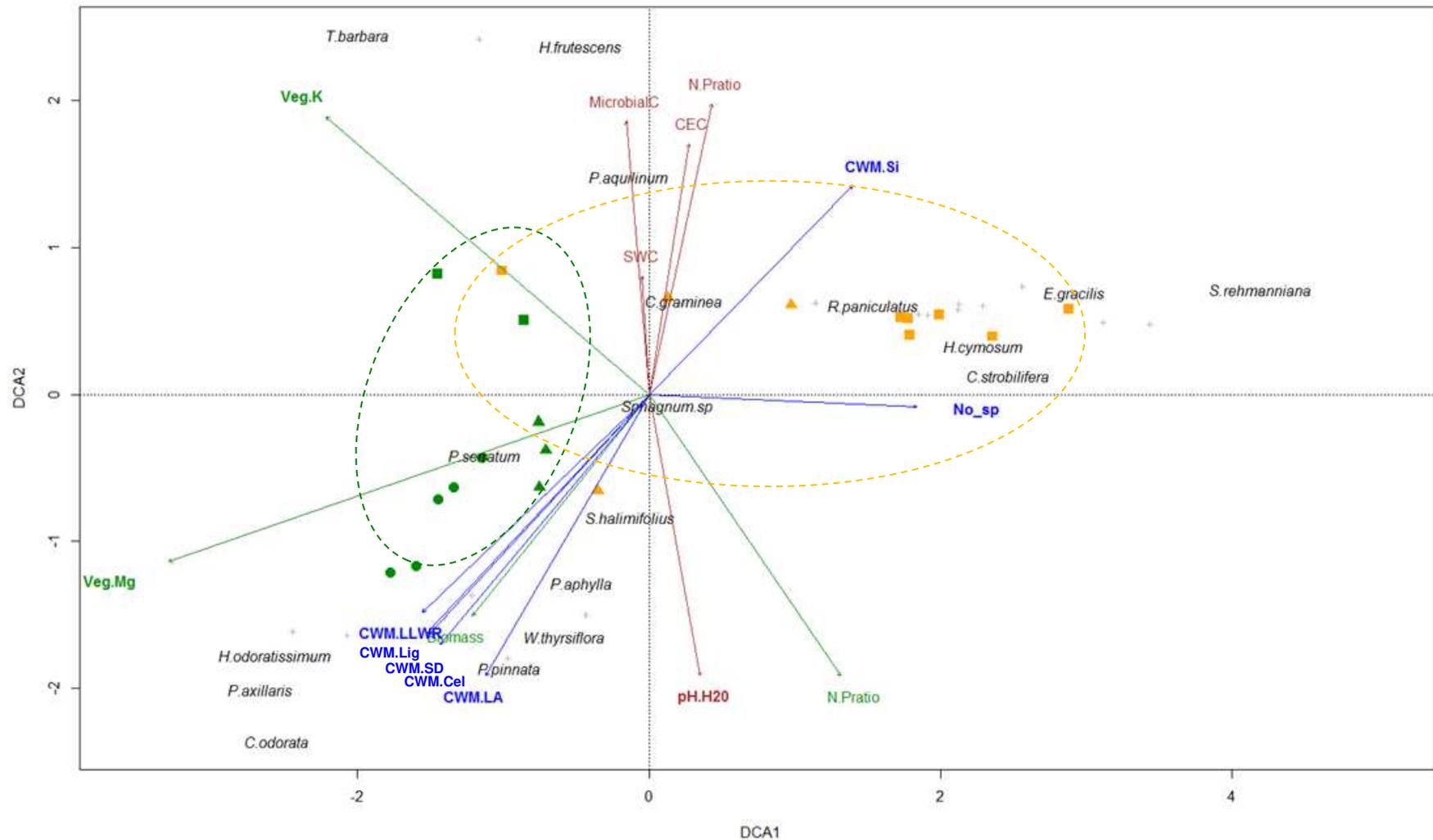
Year	Species	Average contribution	Standard deviation	Cumulative sum of most influential species	Fynbos sites (%)	Palmiet sites (%)
2014	<i>Prionium serratum</i>	0.24	0.099	0.31	23.5	87.0
	<i>Restio paniculatus</i>	0.15	0.117	0.51	43.5	4.5
	<i>Cliffortia strobilifera</i>	0.07	0.068	0.60	19.5	0.6
	<i>Epischoenus gracilis</i>	0.04	0.056	0.65	10.8	0.0
	<i>Cliffortia odorata</i>	0.03	0.069	0.69	0.0	10.0
	<i>Todea barbara</i>	0.03	0.058	0.73	1.5	7.0
2015	<i>Prionium serratum</i>	0.28	0.087	0.33	15.9	93.5
	<i>Restio paniculatus</i>	0.15	0.111	0.51	42.8	2.4
	<i>Cliffortia strobilifera</i>	0.06	0.064	0.57	16.6	0.3
	<i>Pteridium aquilinum</i>	0.05	0.068	0.63	6.2	11.6
	<i>Epischoenus gracilis</i>	0.05	0.072	0.69	13.6	0.0
	<i>Isolepis prolifera</i>	0.04	0.109	0.73	9.5	0.0

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782 **Table A5:** Full names of species used in the Detrended Correspondence Analysis. Species are given as presence/absence for each year, for each  
 783 of the wetlands and for each community in the wetlands.

Year Wetland Community	2014					2015				
	Theewaterskloof		Goukou		Kromme	Theewaterskloof		Goukou		Kromme
	Palmiet	Fynbos	Palmiet	Fynbos	Palmiet	Palmiet	Fynbos	Palmiet	Fynbos	Palmiet
<i>Acacia mearnsii</i> De Wild.	0	0	0	0	1	0	0	0	0	0
<i>Blechnum capense</i> Burm.f.	0	0	0	0	1	0	0	0	0	1
<i>Carpacoe spermacoea</i> (Rchb.ex Spreng.) Sond.	0	0	0	0	0	0	0	1	1	0
<i>Carpha capitellata</i> (Nees) Boeck.	0	1	0	0	0	0	0	0	0	0
<i>Carpha glomerata</i> Nees	1	0	0	0	0	0	0	0	0	0
<i>Centella asiatica</i> (L.) Urb.	0	1	0	0	0	0	0	0	0	0
<i>Cliffortia graminea</i> L.f.	0	1	0	0	0	0	1	0	0	0
<i>Cliffortia odorata</i> L.f.	0	0	0	0	1	0	0	0	0	1
<i>Cliffortia strobilifera</i> L.	1	1	1	1	1	0	1	1	1	1
<i>Cyclopia maculata</i> (Andrews) Kies	0	0	1	1	0	0	0	1	1	0
<i>Cyperus thunbergii</i> Vahl	0	1	0	0	0	0	0	0	0	0
<i>Didymodoxa</i> sp. E. Mey. ex Wedd.	0	0	0	0	0	0	0	0	0	0
<i>Dilatris viscosa</i> L.f.	0	0	0	0	0	0	1	0	0	0
<i>Elegia asperiflora</i> (Nees) Kunth	0	0	1	1	0	0	0	0	0	0
<i>Elegia capensis</i> (Burm.f.) Schelpe	0	1	0	0	1	0	1	0	0	1
<i>Elegia</i> sp.L.	0	1	0	0	0	0	0	0	0	0
<i>Schoenus gracillimus</i> T.L. Elliott & Muasya	0	0	1	1	0	0	0	1	1	0
<i>Erica bergiana</i> L.	0	1	0	0	0	0	1	0	0	0
<i>Ficinia nodosa</i> (Rottb.) Goetgh., Muasya & D.A. Simpson	0	0	1	1	0	0	0	0	0	0
<i>Ficinia</i> sp. Schrad.	1	0	0	0	0	0	0	0	0	0
<i>Gnidia oppositifolia</i> L.	0	1	0	0	0	0	1	0	0	0
<i>Helichrysum cymosum</i> (L.) D.Don.	0	0	1	1	0	0	0	1	1	1
<i>Helichrysum helianthemifolium</i> (L.) D.Don. ex D.Don.	0	0	1	1	0	0	0	1	1	0
<i>Helichrysum odoratissimum</i> (L.) Sweet	0	0	0	0	1	0	0	0	0	1
<i>Hippia frutescens</i> (L.) L.	0	0	1	1	0	0	0	1	1	0
<i>Histiopteris incisa</i> (Thunb.) J. Sm.	0	0	1	1	0	0	0	0	0	0

<i>Isolepis prolifera</i> (Rottb.) R. Br.	0	1	0	0	0	0	1	0	0	0
<i>Juncus lomatoxyllus</i> Spreng.	0	0	1	1	0	0	0	1	1	0
<i>Laurembergia repens</i> (L.) P.J. Bergius	0	0	1	1	0	0	0	1	1	0
<i>Osteospermum sp.</i>	0	0	1	1	0	0	1	1	1	0
<i>Osteospermum sp.</i>	0	0	0	0	0	1	0	0	0	0
<i>Osteospermum moniliferum</i> L.	0	0	0	0	1	0	0	0	0	0
<i>Otholobium sp.</i>	0	0	0	0	1	0	0	0	0	0
<i>Panicum coloratum</i> L.	0	0	1	1	0	0	0	1	1	0
<i>Persicaria decipiens</i> (R.Br.) K.L. Wilson	0	0	1	1	0	0	0	0	0	0
<i>Platycaulos callistachyus</i> (Kunth) H.P. Linder	0	0	0	0	0	0	0	1	1	0
<i>Prionium serratum</i> (L.f.) Drège	1	1	1	1	1	1	1	1	1	1
<i>Psoralea aphylla</i> L.	1	1	0	0	0	1	1	0	0	0
<i>Psoralea axillaris</i> L.f.	0	0	0	0	1	0	0	0	0	1
<i>Psoralea floccosa</i> C.H. Stirt., Muasya & Bello	0	0	1	1	0	0	0	0	0	0
<i>Psoralea monophylla</i> (L.) C.H. Stirton	0	0	0	0	0	0	0	1	1	0
<i>Psoralea pinnata</i> L.	0	0	0	0	0	1	0	0	0	0
<i>Psoralea plauta</i> C.H. Stirton	0	0	1	1	0	0	0	0	0	0
<i>Pteridium aquilinum</i> (L.) Kuhn	1	1	1	1	0	1	1	1	0	0
<i>Cyperus polystachyos</i> Rottb.	1	0	0	0	0	1	0	0	0	0
<i>Restio paniculatus</i> Rottb.	1	1	1	1	0	1	1	1	1	0
<i>Searsia rehmanniana</i> (Engl.) Moffett.	0	0	0	0	1	0	0	0	0	0
<i>Senecio coleophyllus</i> Turcz.	1	0	0	0	0	1	0	0	0	0
<i>Senecio halimifolius</i> L.	0	0	0	0	0	0	1	0	0	0
<i>Sphagnum sp.</i> L.	1	1	0	0	0	0	1	0	0	0
<i>Thelypteris confluens</i> (Thunb.) C.V. Morton	0	0	0	0	0	0	1	0	0	0
<i>Todea barbara</i> T. Moore	0	0	1	1	0	0	0	1	0	0
<i>Ursinia serrata</i> (L.f.) Poir.	0	0	1	1	0	0	0	0	0	0
<i>Wachendorfia thyrsoflora</i> Burm.	1	1	0	0	0	1	1	0	0	0
<i>Watsonia angusta</i> Ker Gawl.	0	0	1	1	0	0	0	1	1	0
<i>Zantedeschia aethiopica</i> (L.) Spreng.	0	0	1	1	0	0	0	1	1	0



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**Fig. A1** Detrended Correspondence Analysis (DCA) of the plant communities in fynbos and palmiet patches in three South African palmiet wetlands sampled in March 2015.

Fynbos sites are in orange, palmiet in green. Symbols: ▲ Theewaterskloof, ■ Goukou, ● Kromme. Species names are given in black, and + indicates species with a lower

abundance that are masked by other labels. Parameters that were interesting or significantly different (bold) between palmiet and fynbos wetland patches were overlain

789 and are indicated by the arrows. CWM: community weighted mean, LLWR: leaf length-width ratio, Lig: lignin, Cel: cellulose, SD: stem diameter, LA: leaf area, Si: silicon, No\_sp:  
790 number of species, Veg.K: K in vegetation, Veg.Mg: Mg in vegetation, MicrobialC: microbial carbon, CEC: cation exchange capacity, SWC: soil water content. Stippled circles  
791 encompass sites from fynbos and palmiet communities. Soil parameters are in brown, vegetation composition in green, functional diversity indices in blue. For full species  
792 names see **Table A4**



794 **Plate 1.** Photographs of palmiet wetlands showing (a) one of the preferential flow paths through the  
 795 wetland (dispersed flow), (b) the length of the raised stems of palmiet, (c) the “tussock-like” extensions of  
 796 palmiet, (d) a thick palmiet root, (e) the complex palmiet root system, (f) the tussock-like structure of  
 797 palmiet, (g) a degraded palmiet wetland with two palmiet patches: one in the foreground, one in the back  
 798 right. This photo shows the raised nature of the palmiet patches, lower at the edges, higher at the center,  
 799 (h) vegetative reproduction of palmiet, (i) a patch of palmiet growing in a recently formed gully in the  
 800 Kromme.