

Canopy plant composition and structure of Cape subtropical dune thicket are predicted by levels of fire exposure

Tiaan Strydom^{Corresp., 1, 2}, Tineke Kraaij^{1, 2}, B. Adriaan Grobler², Richard M. Cowling²

¹ Department of Conservation Management, Natural Resource Science and Management Cluster, Faculty of Science, Nelson Mandela University, George, Western Cape, South Africa

² African Centre for Coastal Palaeoscience, Nelson Mandela University, Gqeberha, Eastern Cape, South Africa

Corresponding Author: Tiaan Strydom
Email address: tiaanstrydom.nature@gmail.com

Background. Subtropical dune thicket (hereafter “dune thicket”) of the Cape Floristic Region experiences a wide range of fire exposure throughout the landscape, unlike other dry rainforest formations that rarely experience fire. We asked how fire exposure influences species composition and the architectural composition of dune thicket?

Methods. We used multivariate analysis and diversity indices based on cover abundance of species to describe the species composition, architectural guild composition and structure of dune thicket sites subject to different levels of fire exposure, namely low (fire return interval of > 100 years), moderate (fire return interval of 50-100 years), and high (fire return interval of 10-50 years).

Results. The diversity, cover abundance and architectural guild cover abundance of dune thicket canopy species were strongly influenced by the level of fire exposure such that each level was associated with a well-circumscribed vegetation unit. Dune thicket subject to low fire exposure comprises a floristically distinct, low forest characterized by shrubs with one to few upright stems (ca. 4 – 8 m tall) and a relatively small canopy spread (vertical growers). Of the 25 species in this unit, 40% were restricted to it. Dune thicket subject to moderate fire exposure had the highest abundance of lateral spreaders, which are multi-stemmed (ca. 3 – 6 m tall) species with a large canopy spread and lower stature than vertical growers. None of the 17 species found in this unit was restricted to it. Dune thicket subject to high fire exposure had the highest abundance of hedge-forming shrubs, these being low shrubs (ca. 0.6 – 1.4 m tall), with numerous shoots arising from an extensive system of below-ground stems. Of the 20 species in this unit, 40% were restricted to it. Multivariate analysis identified three floristic units corresponding to the three fire exposure regimes. Compositional structure, in terms of both species and architectural guilds, was most distinctive for dune thicket subject to high and low fire exposure, while the dune thicket subject to moderate fire exposure showed greatest compositional overlap with the other units.

Conclusion. Fire exposure profoundly influenced the composition and structure of dune thicket canopy species in the Cape Floristic Region. In the prolonged absence of fire, thicket is invaded by vertical-growing species that overtop and outcompete the multi-stemmed, laterally-spreading shrubs that dominate this community. Regular exposure to fire selects for traits that enable thicket species to rapidly compete for canopy cover post-fire via the prolific production of resprouts from basal buds below- and above-ground. The trade-off is that plant height is constrained, as proportionately more resources are allocated to below-ground biomass.

1 Canopy plant composition and structure of Cape subtropical dune thicket are
2 predicted by the levels of fire exposure

3

4 Tiaan Strydom^{1,2}, Tineke Kraaij^{1,2}, B. Adriaan Grobler², Richard M. Cowling²

5

6 ¹Department of Conservation Management, Natural Resource Science and Management Cluster,
7 Faculty of Science, Nelson Mandela University, George, Western Cape, South Africa

8

9 ²African Centre for Coastal Palaeoscience, Nelson Mandela University, Gqeberha, Eastern
10 Cape, South Africa

11

12

13

14 Corresponding Author:

15 Tiaan Strydom

16 Email address: tiaanstrydom.nature@gmail.com

17

18 Abstract

19 **Background.** Subtropical dune thicket (hereafter “dune thicket”) of the Cape Floristic Region
20 experiences a wide range of fire exposure throughout the landscape, unlike other dry rainforest
21 formations that rarely experience fire. We asked how fire exposure influences species
22 composition and the architectural composition of dune thicket?

23 **Methods.** We used multivariate analysis and diversity indices based on cover abundance of
24 species to describe the species composition, architectural guild composition and structure of
25 dune thicket sites subject to different levels of fire exposure, namely low (fire return interval of >
26 100 years), moderate (fire return interval of 50-100 years), and high (fire return interval of 10-50
27 years).

28 **Results.** The diversity, cover abundance and architectural guild cover abundance of dune thicket
29 canopy species were strongly influenced by the level of fire exposure such that each level was
30 associated with a well-circumscribed vegetation unit. Dune thicket subject to low fire exposure
31 comprises a floristically distinct, low forest characterized by shrubs with one to few upright
32 stems (ca. 4 – 8 m tall) and a relatively small canopy spread (vertical growers). Of the 25 species
33 in this unit, 40% were restricted to it. Dune thicket subject to moderate fire exposure had the
34 highest abundance of lateral spreaders, which are multi-stemmed (ca. 3 – 6 m tall) species with a
35 large canopy spread and lower stature than vertical growers. None of the 17 species found in this
36 unit was restricted to it. Dune thicket subject to high fire exposure had the highest abundance of
37 hedge-forming shrubs, these being low shrubs (ca. 0.6 – 1.4 m tall), with numerous shoots
38 arising from an extensive system of below-ground stems. Of the 20 species in this unit, 40%
39 were restricted to it. Multivariate analysis identified three floristic units corresponding to the
40 three fire exposure regimes. Compositional structure, in terms of both species and architectural
41 guilds, was most distinctive for dune thicket subject to high and low fire exposure, while the
42 dune thicket subject to moderate fire exposure showed greatest compositional overlap with the
43 other units.

44 **Conclusion.** Fire exposure profoundly influenced the composition and structure of dune thicket
45 canopy species in the Cape Floristic Region. In the prolonged absence of fire, thicket is invaded
46 by vertical-growing species that overtop and outcompete the multi-stemmed, laterally-spreading
47 shrubs that dominate this community. Regular exposure to fire selects for traits that enable

48 thicket species to rapidly compete for canopy cover post-fire via the prolific production of
49 resprouts from basal buds below- and above-ground. The trade-off is that plant height is
50 constrained, as proportionately more resources are allocated to below-ground biomass.

51 **Keywords**

52 biome boundaries, Cape Floristic Region, coastal dune vegetation, forest, fire frequency, fynbos
53 plant architecture, species diversity, structural composition

54 **Introduction**

55 Climatically and edaphically homogeneous landscapes may support structurally and floristically
56 distinct biomes, raising the question as to what determines the boundaries between them
57 (Hoffman et al., 2012; Butler et al., 2014; Coetsee, Bond & Wigley, 2014; Cowling & Potts,
58 2015; Cramer et al., 2019). In landscapes dominated by fire-prone vegetation such as savannas,
59 grasslands and heathlands, fire regime effects have been invoked to explain the boundaries
60 between fire-prone and fire-avoiding biomes, for example Afrotemperate forest patches in Cape
61 fynbos shrublands (Manders, 1990; Geldenhuys, 1994; Cowling & Potts, 2015) and rainforest
62 patches in savanna and grassland (Hoffman et al., 2009; Murphy & Bowman, 2012; Becket et al.,
63 2022). The coastal dunes of the Cape Floristic Region (CFR) are an interesting case in this
64 regard, since they can support three biomes, namely dune forest, subtropical dune thicket
65 (hereafter “dune thicket”) and dune fynbos, each of which experiences different fire regimes as
66 determined by topographically induced fire protection and species-specific flammability
67 properties (Pierce & Cowling, 1991; Cowling & Potts, 2015; Msweli et al., 2020; Cowling &
68 Hoffman, 2021). Here we report on compositional and architectural differences of thicket canopy
69 dominants in dune communities associated with different levels of fire exposure. We
70 investigated whether the historical fire frequencies purported for these communities’ influence
71 dune thicket composition and structure.

72 The effects of fire regimes on vegetation composition and structure have been studied
73 extensively in fire-prone vegetation across the globe (e.g. Bond & Van Wilgen, 1996; Williams
74 et al., 2012; Rundel et al., 2018; Becket et al., 2022). Even though dune thicket is not a fire-
75 dependent vegetation type, it experiences fire and is resilient to high fire severity as most, if not
76 all, thicket canopy species are capable of resprouting post-fire from dormant basal buds or

77 epicormic buds in the canopy (Cowling & Pierce, 1988; Strydom et al., 2020). Strydom et al.
78 (2020) found no evidence of a relationship between fire severity and thicket shrub survival.
79 However, a few single-stemmed tree species (*Apodytes dimidiata* E.Mey. ex Arn., *Chionanthus*
80 *foveolatus* (E.Mey.) Stearn, *Scolopia zeyheri* Szyszyl.), which mostly grow in deep, narrow dune
81 swales where community composition and structure are more typical of dune forest than of
82 thicket (Cowling, 1984; Cowling et al., 1997; Midgley et al., 1997), are more vulnerable to high
83 fire severity, displaying lower survival rates and weaker resprouting vigour than species which
84 have two or more stems at ground level (e.g. *Pterocelastrus tricuspidatus* Walp., *Searsia glauca*
85 (Thunb.) Moffett, *Sideroxylon inerme* Forssk. (Strydom et al., 2020, 2021). Furthermore, a
86 largely positive relationship between tree size and fire survival suggested that some species of
87 dune thicket may be negatively affected by frequent fires (Strydom et al. 2020).

88 The long-term effects of fire severity and frequency on species composition and structure of
89 dune thicket are, however, not known. Strydom et al. (2021) classified thicket species into
90 architectural guilds and post-fire resprouting guilds, which could be used in the current study to
91 assess structural composition of dune thicket in relation to long-term fire exposure. Three
92 architectural guilds were recognised, namely vertical growers (tall-stature (ca. > 4 m), single-
93 stemmed trees with a small to large canopy spread), lateral spreaders (moderate-stature (ca. 2-4
94 m), multi-stemmed shrubs with a large canopy spread), and hedge formers (low-stature, (ca. < 2
95 m) multi-stemmed shrubs with a large canopy spread). Hedge-forming species exhibited a high
96 mean survival rate (> 80%) and strong resprouting vigour post-fire; lateral- spreading species
97 also exhibited a high mean survival rate (> 80%) and moderate to strong resprouting vigour post-
98 fire; whereas vertical-growing species showed a lower mean survival rate (73%) and weaker
99 resprouting vigour post-fire (Strydom et al., 2020, 2021).

100 Several studies have investigated the influence and importance of fire on species composition
101 and structure of savanna-forest mosaics of Africa, Australia and Brazil (Charles-Dominique et al.,
102 2015; Hoffman et al., 2009; Murphy & Bowman, 2012 Flake et al., 2021a; Flake et al., 2021b;
103 Becket et al., 2022). In these systems, regular fires promote savanna tree and grass abundance
104 and suppress forest trees, which are mostly killed by fire; however, when the fire frequency
105 increases, savanna trees can also be suppressed, thereby favoring grasslands. Accordingly, if fire
106 is absent for too long, forest tree abundance will increase, and savanna tree and grass cover will

107 decrease (Hoffman et al., 2009; Flake et al., 2021b; Becket et al., 2022). Less is known about the
108 influence of fire on species composition and structure of closed-canopy vegetation types that
109 rarely burn, such as Afrotemperate forest (Watson & Cameron, 2001; Giddey, Baard & Kraaij,
110 2022a) and thicket (Cowling 1984; Vlok, Euston-Brown & Cowling, 2003; Cowling & Potts,
111 2015); however, some information on species-specific responses to fire is available, which leads
112 to the question of how fire exposure shapes community composition in these closed
113 communities.

114 Forest margins in forest-fynbos mosaics in the CFR burn to a greater or lesser extent (depending
115 on the fynbos fuel load and the severity of fire weather conditions) when the adjacent fynbos
116 burns (Giddey et al., 2021). The level of fire exposure that forest patches experience depend on
117 their position in the landscape in relation to topography and desiccating winds that drive fires
118 (Geldenhuys, 1994; Cowling & Potts, 2015). Forest margins and small forest patches typically
119 experience more frequent and severe fire than the forest core and large patches (Geldenhuys,
120 1994; Giddey, Baard & Kraaij, 2022a, Giddey, Baard & Kraaij, 2022b). Like the forest core, the
121 dune thicket core is seldom exposed to fire and will only burn under the most severe conditions,
122 likely less than once per century. The margins of dune thicket patches and small thicket clumps,
123 on the other hand, may burn whenever fire occurs in the dune fynbos matrix, typically every 10-
124 20 years (Cowling et al., 1997; van Wilgen et al., 2010; Kraaij et al., 2013).

125 Watson and Cameron (2001) investigated the influence of fire on Afrotemperate forest
126 composition and found tree diversity to be higher in the fire-sheltered forest core, which
127 contained a unique suite of species that were absent from the fire-exposed forest margin. They
128 found that the young trees of *Gonioma kamassi* E.May, *Ilex mitis* (L.) Radlk., and *Podocarpus*
129 *latifolius* hort. ex Carrière. that occurred in the forest margin had high mortality rates (75-100%)
130 post-fire, suggesting that fire-induced mortality can lead to a change in species composition.
131 Similarly, Giddey, Baard & Kraaij (2022b) found that Afrotemperate forest tree species showed
132 differential post-fire survival responses, although some individuals of virtually all species were
133 able to survive fire by resprouting. Certain species, e.g., *Olea capensis* subsp. *macrocarpa*
134 (C.H.Wright) I. Verd, *Podocarpus latifolius*, *Elaeodendron croceum* DC. and *Halleria lucida* L.
135 showed high mortality rates (> 60%) whereas others, like *Ocotea bullata* (Burch.) Baill.,
136 *Lachnostylis hirta* Müll.Arg., *Cassine peragua* L. and *Rapanea melanophloeos* Mez, showed low

137 mortality rates (< 40%) and strong resprouting capabilities. Like forest trees, single-stemmed
138 vertical-growing species in dune thicket, i.e. *Chionanthus foveolatus*, *Apodytes dimidiata* and
139 *Scolopia zeyheri*, had higher mortality rates post-fire (40-60%) compared to multi-stemmed
140 lateral spreaders e.g. *Mystroxydon aethiopicum* (14%), *Pterocelastrus tricuspidatus* (10%) and
141 hedge forming species *Searsia glauca* (19%) (Strydom et al., 2020).

142 Given that dune thicket shrub species have variable post-fire survival rates, resprouting abilities
143 and architecture (Strydom et al., 2020; Strydom et al., 2021), and need to compete for light and
144 belowground resources in a post-fire environment, we asked the question: How does fire
145 exposure influence the species composition and structure (~architectural guild composition) of
146 dune thicket in the same landscape? Based on the ecologies of the respective architectural guilds,
147 it should be possible to predict their occurrence in relation to gradients of fire exposure. We also
148 expect differences in floristic composition to parallel the differences in architectural guild
149 composition in relation to fire exposure. While there are some data consistent with these
150 predictions (Cowling 1984; Cowling et al. 1997; Midgley et al. 1997), they remain to be
151 rigorously tested. Thus, we investigated whether the degree of fire exposure influences species
152 composition and architectural guild (sensu Strydom et al., 2021) composition of dune thicket
153 canopy species in a coastal dune landscape.

154

155 **Methods**

156 *Study area*

157 The study was conducted in a landscape comprising parallel ridges and associated swales of
158 coastal dunes west of Cape St Francis in the southeastern CFR (*Fig. 1*). The geology comprises
159 Holocene aeolianites (Schelmoek Formation) overlying Pleistocene calcarenites (possibly
160 Nahoon Formation) (Roberts et al., 2006; Cowling et al., 2019). Soils are mostly deep,
161 calcareous sands with high organic matter content (Cowling, 1984). The climate is warm-
162 temperate, and rainfall occurs year-round but with relatively dry summers. The mean annual
163 rainfall for the region is ca. 700 mm. The mean annual temperature is 17 °C with a minimum of
164 4 °C and maximum of 32 °C, with the warmest months being December-February and the
165 coldest being July-August. The wind regime is fierce, with east to southeasterly winds

166 dominating in summer, and west to southwesterly winds in winter; gale force winds occur
167 mainly in the spring and summer months.

168 The vegetation of the study area comprises a mosaic of thicket and fynbos vegetation, with
169 scattered and small (1-5 ha) patches of forest (Cowling, 1984; Cowling et al., 2019). Both thicket
170 and forest canopy species produce bird-dispersed propagules that established in shaded
171 microsites (Cowling et al., 1997; Strydom et al., 2019). The understorey vegetation comprises a
172 relatively depauperate flora of forbs and graminoids (Cowling, 1984). The herb and graminoid
173 layer in these dune thickets are not well developed and comprise only a few species when present
174 (Cowling, 1984). Fynbos, which invariably has an admixture of low thicket shrubs, is confined
175 largely to the well-drained slopes and crests of the hairpin parabolic ridges that run in an east to
176 west direction, which aligns with the prevailing wind directions (*Fig. 1*). Thicket is mainly
177 associated with the lower slopes and swales of the dune landscape; here, owing to the presence
178 of an impermeable layer (calcarnite or quartzitic sandstone) near the soil surface, soil moisture is
179 more accessible to plant roots than on the deeper soils of the dune ridges. The small patches of
180 forest are restricted to narrow dune swales with steep-sided dune ridges. Soil chemical and
181 physical variables are similar across the landscape except for organic carbon, which is higher in
182 forest than thicket or fynbos.

183 The grazing/browsing regime in the study has changed in the past several years. Prior to the
184 colonial era (starting ca. 1750), the area experienced episodic grazing by cattle and sheep
185 belonging to nomadic Khoe-khoe pastoralists (Cowling, 1984) as well as browsing by
186 indigenous herbivores including two megaherbivores (Boshoff & Kerley, 2001; Radloff, 2008).
187 The colonial era saw the extirpation of megaherbivores and increase in grazing of livestock
188 belonging to sedentary pastoralists of European origin alongside browsing by small medium-
189 sized indigenous herbivores. Since the early 1960s, grazing domestic livestock has declined and
190 herbivory is now entirely by small to medium-sized indigenous herbivores.

191 The dune topography of the study area (*Fig. 1*) influences the potential occurrence of fire in the
192 landscape (Cowling, 1984; Cowling & Hoffman, 2021). Dune ridges and slopes, comprising
193 highly flammable fynbos (Cowling, 1984; Calitz, Potts & Cowling, 2015; Msweli et al., 2022),
194 are exposed to the full brunt of the region's strong wind regime; these sites likely burn in every
195 conflagration. The thicket-dominated dune-swales, comprising species of lower flammability

196 (Cowling, 1984; Calitz, Potts & Cowling, 2015; Msweli et al., 2022), and subject to a milder
197 wind regime than the slopes, burn only under extreme fire hazard conditions. The deep, narrow
198 swales that support forest are protected from fire, even under the most severe conditions, as were
199 experienced in a wildfire in the summer of 2016.

200 In the absence of detailed fire records, we identified a fire-exposure gradient in the dune
201 landscape in relation to topographical position and presumed historical occurrence of fire as
202 gleaned from ten aerial photographs (1961, 1969, 1985, 2000, 2006, 2009, 2011, 2013, 2016,
203 2019) (*Fig. S1*) (CDNGI Geospatial Portal, 2022; Google Earth, 2022), repeat photography
204 (Cowling & Hoffman, 2021), and anecdotal accounts (*Table S2*) from long-term residents in the
205 area of the occurrence of wildfires since the 1930s. Note that the regime for the dune fynbos-
206 thicket mosaic is likely biased towards lower fire frequencies owing to fire suppression practices
207 initiated with a shift from pastoralism to resort development in the early 1960s. The aerial
208 photographs and anecdotal accounts of fire occurrence confirmed that the distribution of dune
209 forest was stable and had not burnt since 1942. Thicket appears to have expanded into fynbos in
210 the dune swales and lower slopes over the same period but especially since the early 1960s, a
211 finding that supported by analysis of repeat photography (Cowling & Hoffman, 2021).

212 The study area experienced a fire in January 2016, which burnt large parts of dune fynbos and
213 thicket on slopes and broad swales (Strydom et al., 2020), leaving the fire-protected forest of the
214 deep, narrow swales unburnt. The fairly crude estimations of fire occurrence revealed by these
215 sources enabled us to categorize fire exposure in terms of three broad categories: (i) low fire
216 exposure (i.e. fire return intervals of >100 years) associated with deep, narrow dune swales (*Fig.*
217 *1*) that provide refuge from strong winds and wind-driven fires, and which support dune forest
218 vegetation; (ii) moderate fire exposure (i.e. fire return intervals of 50-100 years) associated with
219 dune swales, that experience moderate exposure to wind, and which support dune thicket; and
220 (iii) high fire exposure (i.e. fire return intervals of 10-50 years) associated with dune crests and
221 upper slopes that experience the strongest wind and fire exposure in the dune landscape, and
222 which support a dune fynbos-thicket mosaic comprising ericoid shrubs, restioids and dwarf
223 thicket shrubs.

224 *Data collection*

225 During April 2018, we surveyed 17 belt transects in each of the three dune thicket fire-exposure
226 categories, focusing on native canopy-forming shrubs and trees, but excluding fynbos shrubs in
227 the high fire-exposure sites (taxonomic authorities for all study species are listed in *Table 1*).
228 Alien trees were absent from our transects. We used transects of 50 m x 5 m in low and moderate
229 fire-exposed sites. We surveyed the latter, which burnt in 2016, at a post-fire age of almost three
230 years by measuring the burnt shrub skeletons which resembled the architecture of the mature pre-
231 fire individuals. In high fire-exposed sites we surveyed 17 belt transects of 5 m x 2 m. The
232 smaller transect size used here was due to extreme stem density of the dwarf dune thicket shrubs
233 (mean density of 5.2 stems/m² vs 0.4 stems/m² in moderate and low fire exposure). These
234 transect sizes produced reasonably comparable survey effort across transects, i.e. the mean
235 number of stems assessed per transect was 95 in low fire-exposure, 73 in moderate, and 52 in
236 high fire-exposure. Variation in slope, aspect and soil type (Cowling, 1984; Cowling & Potts,
237 2015) of the surveyed transects were broadly comparable amongst the different fire-exposure
238 sites (*Table S3*). In sites associated with low and moderate fire exposure, individuals with a stem
239 diameter > 5 cm were recorded and all stems that were connected at the base at ground level
240 were considered an individual. In high fire exposure no threshold was set as individual shrubs
241 have small stems and all stems that were connected at the base at ground level were considered
242 an individual. In all fire exposure categories individual plant canopy height and the widest and
243 shortest canopy diameter were measured to estimate cover abundance of species and
244 architectural guilds of canopy shrubs (detailed below).

245

246 *Data analysis*

247 We used the Sørensen similarity coefficient to assess the similarity in species composition of the
248 different fire exposure categories in terms of the proportion of shared species pooled across all
249 transects within the respective fire-exposure categories ($C_s = 2 \times c / S_1 + S_2$) (c = number of
250 species in common between both communities, S_1 = number of species in community one; S_2 =
251 number of species in community two) (Sørensen 1948). We used projected canopy cover (%) to
252 estimate cover abundance of dune thicket species (rather than numbers of individuals per species,
253 due to difficulty with identifying individuals in the case of clonal plants) and architectural guilds
254 in all fire exposure categories. Canopy cover can exceed 100% as dune thicket shrub canopies

255 often overlap. The canopy area (m^2) of each individual shrub was calculated as the area of an
256 oval ($a/2 \times b/2 \times \pi$) where a = widest canopy diameter, and b = shortest canopy diameter. The
257 total canopy area (m^2) for each species per transect was calculated as the sum of the canopy area
258 of all the individuals of that species within the transect. To calculate % canopy cover of each
259 species per transect we divided the total canopy area of the species by the area of the transect and
260 multiplied by 100.

261

262 To calculate the % canopy cover per architectural guild for each transect, we assigned each
263 species, based on its observed architecture in each transect and fire-exposure category, to an
264 architectural guild (i.e. hedge former, lateral spreader, or vertical grower). This categorisation
265 was based on the physical dimensions associated with each architectural guild as defined by
266 Strydom et al. (2021). The total canopy areas of all species assigned to an architectural guild
267 were summed to obtain the total canopy area of each guild per transect. Thereafter the % canopy
268 cover was calculated for each architectural guild by dividing with the area of the transect and
269 multiplying by 100.

270

271 We calculated species diversity (with species data pooled across transects within fire exposure
272 categories) using Shannon-Wiener index (Spellerberg & Fedor, 2003) and did pairwise
273 comparisons between the three fire-exposure categories using Hutcheson t-test (Hutcheson,
274 1970). Transects were used as the unit of replication in all subsequent analyses.

275 Canopy cover data were normally distributed, and a one-way ANOVA followed by a post-hoc
276 (Tukey) test was used to compare canopy cover (which indicates canopy overlap when
277 exceeding 100%) between the fire-exposure categories. Canopy height data were not normally
278 distributed and a Kruskal Wallis test followed by a post-hoc (Dunn's) test were used to compare
279 canopy height between the fire-exposure categories.

280

281 Although our primary interest was in the effect of fire exposure on species and structural
282 composition, we used distance-based Redundancy Analysis (db-RDA) (using the 'dbrda'
283 function from the 'vegan' version 2.5-7 R package; Oksanen et al., 2020), with fire exposure,
284 slope and aspect as environmental factors, to assess the potential influence of these factors on
285 dune thicket composition. These, and all subsequent analyses, were conducted in R version 4.1.1

286 (R Core Team, 2021). Prior to db-RDA, the species and architectural-guild cover abundance data
287 were square root transformed and subjected to Wisconsin double standardisation, after which
288 Bray-Curtis dissimilarity matrices were compiled for use in subsequent analyses. We then
289 constructed maximal db-RDA models (i.e., constrained by all environmental factors) and used
290 the ‘cca.anova’ function to assess the significance of the environmental factors’ marginal effects
291 on species and structural composition through permutational tests (999 permutations). In the
292 following steps, we only included factors that had significant marginal effects in the final db-
293 RDA of guilds and species (i.e., those used for ordination plots). As our focus was on the effect
294 of fire exposure, where factors other than fire exposure were found to have significant marginal
295 effects on composition, we used partial db-RDA to control for these factors.

296
297 Next, we used Cluster Analysis (CA) and ordinations based on db-RDA (see details above) and
298 Non-Metric Multidimensional Scaling (NMDS) to explore the effect of fire exposure on patterns
299 of species and architectural guild cover abundance among the 51 transects spread across the three
300 fire-exposure categories. Our hierarchical CA was based on a Bray-Curtis dissimilarity matrix
301 and used Ward’s agglomeration method (‘ward.D’ option in the ‘hclust’ function). The NMDS
302 analysis was implemented via the ‘metaMDS’ function of the ‘vegan’ version 2.5-7 R package
303 (Oksanen et al., 2020), which has incorporated various procedures to facilitate a robust solution
304 (Minchin, 1987). Cover abundance data were square root transformed and subjected to
305 Wisconsin double standardisation, after which a Bray-Curtis dissimilarity matrix was used to
306 ordinate the data. The ordination was run 999 times with random starts to prevent the NMDS
307 from becoming trapped in local optima, and the solution with minimal stress was then selected.
308 To facilitate interpretation of the results, the final NMDS solution was centred and rotated by
309 principal components so that the variance of points was maximised along the first NMDS axis.
310 We further used permutational multivariate analysis of variance (PERMANOVA), implemented
311 via the ‘adonis’ function of the ‘vegan’ version 2.5-7 R package (Oksanen et al., 2020), to test
312 for differences in cover abundances of species and architectural guilds among the fire exposure
313 categories. The ‘pairwiseAdonis’ version 0.4 R package (Martinez Arbizu, 2017) was then used
314 for post-hoc multilevel pairwise comparisons between the three fire-exposure categories. For
315 further investigation of species abundance across fire-exposure categories we used a rank
316 abundance curve.

317

318 **Results**319 *Species diversity and composition*

320 A total of 35 thicket shrub and low tree species were recorded in the vegetation survey (*Table 1*).
321 Vegetation experiencing low fire exposure comprised 25 species, of which nine were exclusive
322 to this category. Vegetation experiencing moderate fire exposure comprised 17 species, none of
323 which were exclusive to this category. Vegetation experiencing high fire exposure comprised 20
324 species of which eight species were exclusive to this category. Nine species were shared among
325 all fire exposure categories (*Table 1; Fig S5*).

326 Species with the highest cover abundance in low fire-exposed sites were *Mystroxyton*
327 *aethiopicum*, followed by *Pterocelastrus tricuspidatus*, *Sideroxyton inerme* and *Dovyalis*
328 *ramnoides*. In moderate fire-exposed sites, the most abundant species was *Pterocelastrus*
329 *tricuspidatus*, followed by *Searsia glauca*, *Sideroxyton inerme* and *Mystroxyton aethiopicum*. In
330 high fire-exposed sites, the dominant species was *Olea exasperata*, followed by *Searsia glauca*,
331 *Maytenus procumbens* and *Sideroxyton inerme*. Low fire-exposed sites supported several forest
332 species, namely *Apodytes dimidiata*, *Chionanthus foveolatus*, *Scolopia mundii*, *Psydrax obovata*
333 and *Celtis africana*. High fire-exposed sites were the exclusive habitat for several dune-endemic
334 thicket species e.g., *Cussonia thyrsoiflora*, *Rapanea gilliana*, *Robsonodendron maritimum* and
335 *Searsia crenata*. Nine species that occurred across all fire-exposure sites showed consistent
336 differences in canopy coverage in relation to them (*Fig. 1; Table 1; Fig. S4*).

337 The Sørensen similarity coefficient (Ss) showed higher compositional similarity between low
338 and moderate fire-exposure categories (Ss = 71%) than between low and high fire-exposure (Ss
339 = 40%), or between moderate and high fire-exposure (Ss = 60%). The Shannon-Wiener diversity
340 index value (H) was significantly lower for sites subject to moderate fire-exposure (H = 1.3) than
341 for those subject to low fire exposure (H = 2.3; $t = 5.76$, $P < 0.001$) and to high fire-exposure (H
342 = 2.2; $t = 4.90$; $P = 0.001$), while it did not differ between low and high fire-exposure sites ($t =$
343 0.32 , $P = 0.76$).

344 Permutational significance tests of the maximal db-RDA model (*Table S5*) confirmed that slope
345 was not a significant predictor ($P = 0.190$) of dune thicket species composition, but aspect did
346 have a marginal effect ($P = 0.031$), which was mostly associated with variation in species

347 composition within fire-exposure groups, especially within high fire exposure, rather than
348 between fire-exposure groups (*Fig. S6*). Fire exposure had the most significant marginal effect
349 on species composition of dune thicket ($P = 0.001$).

350 The partial db-RDA (effect of aspect controlled for) and NMDS ordinations based on species
351 abundances identified three dune thicket units that aligned with our fire exposure categories (*Fig.*
352 *2, 3; Fig. S7*). These ordinations illustrated the dissimilarities between the fire-exposure
353 categories in terms of the species' cover abundances in the transects. There were some
354 similarities between certain transects of moderate fire exposure and those of low and high fire
355 exposure, but most overlap occurred between transects of low and moderate fire exposure. The
356 similarities between transects of low and moderate fire exposure were a result of similar cover
357 abundances of shared species, such as *Pterocelastrus tricuspidatus*, *Sideroxylon inerme*,
358 *Mystroxydon aethiopicum*, and *Dovyalis rotundifolia*. PERMANOVA ($F = 15.051$, $P = 0.001$)
359 and post-hoc pairwise multi-level comparison (adjusted $P = 0.003$ for all comparisons) showed
360 that there were significant differences in the cover abundances of species between all three fire-
361 exposure categories (*Table S8*). These differences were accounted for by species that showed
362 high fidelity to sites of either low or high fire exposure. Overall, sites subject to moderate fire
363 exposure had the lowest compositional distinctiveness and the lowest species diversity whereas
364 sites in low and high fire exposure had distinctive floras of similarly high diversity.

365 *Architectural guild composition*

366 Analysis of the maximal db-RDA model (*Table S9*) showed that slope ($P = 0.917$) and aspect (P
367 $= 0.350$) did not have significant marginal effects on the structural composition of dune thicket;
368 however, the level of fire exposure did ($P = 0.001$). The db-RDA and NMDS ordinations of
369 architectural guild cover identified three units that aligned with the three fire-exposure
370 categories, but with a stronger overlap between low and moderate fire-exposure than was the
371 case for species composition (*Fig. 4,5; Fig. S10*). There were similarities between certain
372 transects of low and moderate fire exposure, showing similar cover abundance in architectural
373 guilds, especially in terms of lateral spreaders (*Fig. 3,4*). The structural homogeneity of dune
374 thicket in high fire-exposure settings was pronounced as 14 of the 17 transects – all comprising
375 exclusively hedge-forming shrubs – were indistinguishable in the db-RDA and NMDS
376 ordinations. PERMANOVA ($F = 59.237$, $P = 0.001$) and post-hoc pairwise multi-level

377 comparison (adjusted $P = 0.003$ for all comparisons) showed that there were significant
378 differences between the architectural guild cover abundances of the three fire-exposure
379 categories (*Table S11*).

380 The hedge-forming guild dominated high fire-exposure sites (median cover abundance = 103%)
381 (*Fig. 6a*), had low cover abundance (7%) in sites of moderate fire exposure, and was close to
382 being absent (0%) from sites of low fire exposure. Lateral spreaders were almost absent (median
383 cover abundance = 0%) in sites subject to high fire exposure, moderately abundant (47%) in sites
384 of moderate fire exposure, and most abundant (103%) in sites subject to low fire exposure.
385 Vertical growers were largely absent from moderate and high fire-exposure sites (median cover
386 abundance = 0%) but relatively abundant (38%) in sites subject to low fire exposure.

387 The canopy cover, and thus canopy overlap, differed significantly between the fire-exposure
388 categories ($F = 11.467$; $P < 0.001$); it was significantly higher (mean canopy cover of 145%) in
389 low fire exposure than high (101 %) ($P < 0.001$) and moderate (74 %) ($P = 0.014$) fire exposure,
390 and significantly higher in high fire exposure than in moderate fire exposure ($P < 0.001$). Dune
391 thicket in low fire-exposure sites was significantly taller (median height of 4m) than in moderate
392 fire-exposed sites (3m) and shortest in high fire-exposed sites (0.6m) ($H = 1631.494$; $P < 0.001$)
393 (*Fig. 6b*).

394

395 **Discussion**

396 *Species diversity and composition*

397 The floristic units we identified in relation to three fire-exposure categories corresponded to
398 communities recognized in Cowling's (1984) phytosociological study undertaken in our study
399 area. Thus, the high fire-exposure sites resembled Cowling's *Restio eleocharis* – *Maytenus*
400 *procumbens* dune fynbos-thicket community, characterized by a high cover of hedge-forming
401 thicket canopy species, notably *Maytenus procumbens*, *Olea exasperata*, *Euclea racemosa*,
402 *Lauridia tetragona*, *Searsia glauca*, *S. crenata*, *S. laevigata* and *Rapanea gilliana* (Endangered)
403 (Victor, 2006), as well as a variety of fynbos shrubs and herbs. This community is described as a
404 successional phase of the fynbos-thicket transition in these dune landscapes. The moderately
405 fire-exposed sites correspond to Cowling's (1984) *Mystroxydon aethiopicum* – *Cussonia*

406 *thyrsiflora* dune thicket community. Dominant canopy species include *Mystroxyton aethiopicum*,
407 *Pterocelastrus tricuspidatus*, *Sideroxyton inerme*, *Chionanthus foveolatus*, *Cassine peragua* and
408 *Scutia myrtina*. Cowling (1984) sampled only one site that resembled our low fire-exposure unit.
409 Here the dominant canopy species comprised a mix of forest (e.g. *Canthium spinosum*,
410 *Zanthoxylon capense*) and thicket (e.g. *Mystroxyton aethiopicum*, *Sideroxyton inerme*) species.
411 Cowling (1984) did not consider the role of fire in maintaining the boundary between the dune
412 communities of the study area, stressing instead the roles of soil moisture and drainage, whereas
413 fynbos communities occupied drier, excessively drained dune crest and upper slopes whereas
414 forest and thicket occupied swales which enjoyed higher soil moisture conditions owing to lower
415 depth to the water table. Following Cowling's (1984) floristic analysis, we term the vegetation of
416 high fire exposure, "fynbos-thicket", that of moderate fire exposure, "thicket", and that of low
417 fire exposure, "forest-thicket".

418 Our results indicate that the diversity and cover abundance of thicket canopy-forming species are
419 strongly influenced by the degree of fire exposure in the landscape. These results are robust as
420 the various ordinations performed, constrained and unconstrained, showed very similar patterns.
421 Sites at the upper and lower margins of fire exposure, namely fynbos-thicket and forest-thicket,
422 had the highest diversity and compositional distinctiveness. The former was dominated by
423 hedge-forming species e.g. *Olea exasperata*, *Rapanea gilliana*, and *Robsonodendron maritimum*;
424 the latter including a high abundance of vertically growing species, namely *Acokanthera*
425 *oppositifolia*, *Allophylus decipiens*, *Apodytes dimidiata*, *Cassine peragua*, *Celtis africana*,
426 *Dovyalis rhamnoides*, *Gymnosporia nemorosa* and *Scolopia zeyheri*. These vertical growers are
427 restricted to the tiny forest-thicket patches in the study area and are commonly found in coastal
428 forests throughout the CFR (Mucina, Geldenhuys & Rutherford, 2006; Geldenhuys, 1993;
429 Gadow et al., 2016). The prolonged absence of fire in these sites, and associated build-up of soil
430 organic carbon and persistent shade, enables the recruitment, via birds, and persistence of forest
431 species here and nowhere else in the dune landscape (Cowling et al., 1997). On the other hand,
432 thicket, which is subject to moderate fire exposure, has a relatively low diversity of canopy
433 species and is overwhelmingly dominated by *Pterocelastrus tricuspidatus*, with *Euclea*
434 *racemosa*, *Sideroxyton inerme* and *Searsia glauca* as subdominants. These species produce large
435 canopies with multiple stems, which likely hinders the establishment of shade-intolerant species
436 found in high fire exposure. The moderate fire return interval might hinder forest species' (i.e.,

437 vertical growers) competitive ability and they are likely outcompeted post fire by the dominant
438 lateral spreaders and hedge formers that are strong resprouters (Strydom et al., 2021), thereby
439 limiting species diversity. The higher level of disturbance in fynbos-thicket could potentially be
440 driving diversity as geoxyles and dune-endemic hedge formers are abundant, while the short fire-
441 return intervals keep the lateral-spreading species smaller and shorter, thereby limiting
442 competition for light.

443 Our results on compositional differences along a fire-exposure gradient are broadly consistent
444 with those from other systems where fire-sensitive and fire-dependent systems coexist in the
445 same landscape. The degree of fire exposure is an important influence in the composition of
446 vegetation in forest-fynbos systems in the CFR (Manders, 1990; Geldenhuys, 1994) and in the
447 tropical forest-savanna systems of Africa, Brazil and Australia (Charles-Dominique et al., 2015;
448 Hoffman et al., 2009; Murphy & Bowman, 2012 Flake et al., 2021a; Flake et al., 2021b; Becket
449 et al., 2022). In both systems, regular fires maintain the more open, fire-dependent ecosystems
450 (fynbos, savanna) by preventing invasion of fire-sensitive forest species (Geldenhuys, 1994;
451 Hoffman et al., 2009). Our system differs from the aforementioned in that it includes a closed
452 community (thicket) that burns only in unusually fierce fires. Survival of dune thicket species
453 after fire is high (84%) (Strydom et al., 2020) in comparison to that of Cape Afrotropical forest
454 (45%) (Giddey, Baard & Kraaij, 2022b). This is likely due to differences in fire resiliency traits
455 such as allocation to bark thickness and fire-protected bud banks (Clarke et al., 2013; Charles-
456 Dominique et al., 2015; Corrêa Scalon et al., 2020). While bark thickness of our thicket species
457 has not been investigated, all are capable of resprouting from epicormic, basal and underground
458 bud banks (Strydom et al., 2020; Strydom et al., 2021). Furthermore, thicket species are
459 generally more flammable than forest trees (Calitz, Potts & Cowling, 2015), thus requiring
460 strategies that confer fire resilience traits described above. Consistent with this is the higher
461 allocation of resources among thicket species to vegetative reproduction via ramets, than in
462 vertically growing forest trees that allocate more to sexual reproduction, as suggested by the
463 higher numbers of seedlings observed for the latter (Midgley & Cowling, 1993; Midgley, 1996;
464 Kruger, Midgley & Cowling, 1997). This would explain why forest is invariably restricted to
465 fire-free refugia (Geldenhuys 1994; Govender et al., 2006; Cowling & Potts, 2015), whereas the
466 more fire-resilient thicket can persist in fire-exposed sites, and expand into adjacent, more open
467 fynbos-thicket communities in the prolonged absence of fire (Cowling & Hoffman, 2022).

468 Thicket can establish on the drier dune crest and steep upper slopes of fynbos sites but has
469 restricted growth and canopy cover and does not outcompete fynbos on these sites (Cowling &
470 Hoffman, 2022), possibly because seedlings and ramets are outcompeted for soil moisture by the
471 mass of fine roots associated with fynbos shrubs (Lu et al., 2022).

472 *Structural composition*

473 The degree of fire exposure in our dune landscape profoundly influences the structural
474 composition of vegetation as represented by the architecture of dune thicket canopy species. This
475 is also true of other systems such as forest-savanna (Higgins et al., 2007; Smith et al., 2010;
476 Ryan, 2002) and forest-fynbos mosaics (Kruger, 1984; van Wilgen, Higgins & Bellstedt, 1990).
477 At high fire exposure, thicket species comprise a diverse array of hedge formers characterized by
478 many relatively thin and low shoots arising from robust underground stems (Cowling, 1983;
479 Grobler & Cowling, 2022; *Fig. S12*). This architecture is consistent with the geoxylic structure
480 of species commonly found in the fire-swept African savannas (the “underground forests” of
481 White, 1976), where it is regarded as an adaptation to frequent fire (Maurin et al., 2014; Lamont,
482 He & Pausas, 2017; Pausas et al., 2018). Interestingly, many of the geoxylic hedge formers in
483 fynbos-thicket are endemic to the dune landscapes of the CFR, namely *Olea exasperata*,
484 *Rapanea gilliana*, *Robsonodendron maritimum* and *Searsia crenata* (Cowling, 1984; Grobler &
485 Cowling, 2021). This growth form can provide an alternative means of surviving fire, allowing
486 for multiple stems to occupy an extensive area and protecting woody biomass and buds
487 belowground (Maurin et al., 2014; Wigley et al., 2019). Indeed, hedge formers produce
488 numerous ramets after fire, similar in abundance to seedlings (genets) produced by non-sprouting
489 fynbos shrubs in fynbos-thicket (Cowling & Pierce, 1988, *Fig. S13*). Geoxylic hedge formers
490 require frequent fire for persistence, otherwise they are outcompeted by taller shrubs and trees
491 that invest more in above ground biomass (Fidelis et al., 2014). This is evident in moderate and
492 low fire-exposed dune thicket where the geoxylic species are largely absent.

493 Under moderate fire exposure, hedge formers are largely replaced by lateral spreaders – notably
494 *Pterocelastrus tricuspidatus* (*Fig. S14*) – which invest more in aboveground shoots but still
495 retain fire resilience. The thicket community unit associated with this fire environment comprises
496 a closed, multi-stemmed, 3 – 6 m high vegetation. Vertical growing species are represented by

497 seedlings (Cowling et al., 1997) and occasional saplings which are in the center of clumps as
498 understory or emergent individuals.

499 Under conditions of low fire exposure, thicket is invaded by vertical-growing forest tree species
500 like *Apodytes dimidiata*, *Chionanthus foveolatus*, *Celtis africana*, *Scolopia zeyheri*, and *Psydrax*
501 *obovata*, which establish from bird-dispersed propagules (Cowling et al., 1997). We propose that
502 vertical growers will ultimately dominate thicket only in those sites that are protected from
503 regular fire, as is the case for Afrotropical forest trees in fynbos-dominated landscapes
504 (Geldunheys, 1994; Calitz, Potts & Cowling, 2015). The lower flammability of forest species
505 (Calitz, Potts & Cowling, 2015), as well as soil amelioration via nutrient input from the
506 prolonged deposition of litter (Cowling 1984), would further promote forest development.
507 Similar processes are associated with the invasion of fynbos by Afrotropical forest (Coetzee et
508 al., 2015; Cowling & Potts, 2015) and the invasion of tropical African savanna by rainforest
509 (Hoffman, Orthen & Franco, 2004; Beckett et al., 2021; Flake et al., 2021a; Flake et al., 2021b;
510 Geiger et al., 2011).

511 In dune thicket, certain species that predominantly present as lateral spreaders, i.e. *Sideroxylon*
512 *inerme*, *Myroxylon aethiopicum* and *Pterocelastrus tricuspidatus*, have high phenotypic
513 plasticity (Fig. S15) (Strydom et al., 2021) which enables persistence in low, moderate and high
514 fire-exposure environments. Under low fire exposure these species are dominant and can shed
515 lateral branches in favor of fewer vertical branches, shifting from a lateral spreader to a vertical
516 grower via architectural modification (Halle, Olderman & Tomlinson, 1978; Strydom et al.,
517 2021). In high fire-exposure conditions, they can adopt hedge-like architectures, where
518 *Sideroxylon inerme* has a fair canopy dominance. Other species, such as *Euclea racemosa* and
519 *Olea exasperata*, mostly dominant in high fire-exposure sites as hedge formers, can – because of
520 competition from taller-growing species – invest resources into one or more stems that reach
521 canopy height, thereby adopting a vertical grower architecture. Similarly, the architecture of
522 highly plastic *Vachellia karroo* (Hayne) Banfi & Galasso is determined by its environment; in
523 light-limited forest, individuals resemble vertical growers, in fire-swept open savanna they
524 resemble lateral growers, and in fire-free arid shrubland, they resemble hedge formers (Archibald
525 & Bond, 2003). Interestingly, we have observed no case of a predominantly vertical-growing
526 species being sufficiently plastic to adopt lateral-spreading or hedge-forming architectures. This

527 likely underpins their inability to persist in landscapes subject to moderate and high fire
528 exposure.

529 In high fire exposure the underground stem (geoxylic) structure of certain hedge formers (*Euclea*
530 *racemosa*, *Olea exasperata*, *Rapanea gilliana*, *Searsia lavigata*) is likely an adaptation to
531 recurrent fire (Maurin et al., 2014; Lamont, He & Pausas, 2017) and, given our knowledge of the
532 sequential temporal emergence of dominant disturbance regimes (herbivory vs. fire) through
533 evolutionary history (Cowling et al., 2005; Keeley & Rundel, 2005; Pennington et al., 2010), we
534 would expect these geoxylic species to be more recently diversified than their laterally-spreading
535 or vertically-growing sister species. Examples of closely related pairs of species from the Cape
536 that have different architectures include: *Rapanea gilliana*, a hedge-forming geoxylic shrub
537 endemic to fire-exposed dune fynbos-thicket in the southeastern Cape, which is likely derived
538 from the vertical-growing, arborescent *Rapanea melanophloeos*, a typical component of local
539 forests (Cowling, 1983); and *Olea exasperata*, another geoxylic hedge-former restricted to CFR
540 coastal dunes, which is derived from the vertical-growing forest species *Olea capensis* (Besnard
541 et al., 2009). Based on the evidence presented above, we hypothesise that the vertical growing
542 and lateral spreading architectures would be associated with basal lineages, whereas hedge
543 formers, especially geoxylic species, are likely associated with lineages of younger age.
544 However, comprehensive phylogenetic data are lacking to test this hypothesis.

545 **Conclusions**

546 The coastal dunes of the southeastern CFR comprise three biomes – forest, thicket and fynbos –
547 that are associated with increasing exposure to recurrent fire. We show here that fire exposure
548 has a profound effect on the floristic and structural composition of these biomes. Forest-thicket,
549 which seldom or ever burns, comprises a diverse assemblage of laterally spreading shrubs and
550 vertically-growing trees, the latter being restricted to small populations in the rare fire-free
551 habitats of the dune landscape. Many of the vertical growers are poor resprouters that recruit
552 mainly from seedlings. Fynbos-thicket is similarly diverse, comprising many hedge-forming
553 species, most of which have extensive belowground stems indicative of a geoxylic structure.
554 These species are capable of vigorous post-fire resprouting and include several dune-endemic
555 taxa that do not grow in the other biomes. Thicket, which is subject to intermediate fire exposure
556 comprises a relatively depauperate flora of laterally-spreading, multi-stemmed and fire-resilient

557 shrubs, some of which show high architectural plasticity (i.e. they can grow as either hedge
558 formers or vertical foragers, depending on the degree of fire exposure). We suggest that the
559 primary selective force for sprouting in these thicket lineages was browsing by megaherbivores
560 in the Paleogene; fire likely became a factor of the evolution of subtropical grass-dominated
561 ecosystems during the Neogene. However, more research is required to test this hypothesis.
562 More research is also required on the belowground architecture of these thicket lineages and how
563 this influences competitive interactions between architectural types in relation to fire exposure.

564 Acknowledgements

565 We thank Zanri Strydom for her assistance in collecting the data, and the reviewers who
566 provided useful suggestions which facilitated improvement of the manuscript.

567

568 References

- 569 **Archibald S, Bond WJ. 2003.** Growing tall vs growing wide: Tree architecture and allometry of
570 *Acacia karroo* in forest, savanna, and arid environments. *Oikos* 102(1):3-14
571 <https://doi.org/10.1034/j.1600-0706.2003.12181.x>.
- 572 **Becket H, Staver AC, Charles-Dominique T, Bond WJ. 2022.** Pathways of savannization in a
573 mesic African savanna-forest mosaic following an extreme fire. *Journal of Ecology*
574 110(4):902-915 <https://doi.org/10.1111/1365-2745.13851>.
- 575 **Besnard G, Rubio De Casas R, Christin PA, Vargas P. 2009.** Phylogenetics of *Olea*
576 (Oleaceae) based on plastid and nuclear ribosomal DNA sequences: Tertiary climatic
577 shifts and lineage differentiation times. *Annals of Botany* 104(1):143-160.
578 <https://doi.org/10.1093/aob/mcp105>.
- 579 **Bond WJ, van Wilgen BW. 1996.** Fire and the evolutionary ecology of plants. In: Fire and
580 Plants. *Population and Community Biology Series*, vol 14. Springer, Dordrecht.
581 https://doi.org/10.1007/978-94-009-1499-5_6.
- 582 **Bond WJ, Midgley GF, Woodward FI. 2003.** What controls South African vegetation—
583 climate or fire? *South African Journal of Botany* 69(1):79-91
584 [https://doi.org/10.1016/S0254-6299\(15\)30362-8](https://doi.org/10.1016/S0254-6299(15)30362-8)

- 585 **Boshoff AF, Kerley LJ. 2001.** Potential distributions of the medium-to large-sized mammals in
586 the Cape Floristic Region, based on historical accounts and habitat requirements. *African*
587 *Zoology*, 36(2):245-273. <https://doi.org/10.1080/15627020.2001.11657142>
- 588 **Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso, JM, Hobbs**
589 **RJ, Pellant M, Pyke D. 2004.** Effects of invasive alien plants on fire regimes.
590 *BioScience* 54(7):677-688. <https://doi.org/10.1641/0006->
591 [3568\(2004\)054\[0677:EOIAPoch\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAPoch]2.0.CO;2).
- 592 **Butler DW, Fensham RJ, Murphy BP, Haberle SG, Bury SJ, Bowman DM. 2014.**
593 Aborigine-managed forest, savanna and grassland: biome switching in montane eastern
594 Australia. *Journal of Biogeography* 41(8):1492-1505.
- 595 **Calitz W, Potts AJ, Cowling RM. 2015.** Investigating species-level flammability across five
596 biomes in the Eastern Cape, South Africa. *South African Journal of Botany* 101:32-39.
- 597 **CDNGI Geospatial Portal V 16.5.0105 Build: 00054. 2022.** Chief Directorate: National Geo-
598 spatial information. Department: Rural Development & Land Reform, Republic of South
599 Africa. Accessed: 21 March 2022. Available: <http://www.cdngiportal.co.za/cdngiportal/>.
- 600 **Charles-Dominique T, Beckett H, Midgley GF, Bond WJ. 2015.** Bud protection: a key trait
601 for species sorting in a forest- savanna mosaic. *New Phytologist* 207(4):1052-1060.
602 <https://doi.org/10.1111/nph.13406>.
- 603 **Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox**
604 **JE. 2013.** Resprouting as a key functional trait: how buds, protection and resources drive
605 persistence after fire. *New Phytologist* 197(1):19-35 <http://doi.org/10.1111/nph.12001>.
- 606 **Coetsee C, Bond WJ, Wigley BJ. 2015.** Forest and fynbos are alternative states on the same
607 nutrient poor geological substrate. *South African Journal of Botany* 101:57-65
608 <https://doi.org/10.1016/j.sajb.2014.11.007>.
- 609 **Corrêa Scalon M, Maia Chaves Bicalho Domingos F, Jonatar Alves da Cruz W, Marimon**
610 **Júnior BH, Schwantes Marimon B, Oliveras I. 2020.** Diversity of functional trade-offs
611 enhances survival after fire in Neotropical savanna species. *Journal of Vegetation*
612 *Science* 31(1):139-150 <https://doi.org/10.1111/jvs.12823>.

- 613 **Cowling RM. 1983.** Phytochorology and vegetation history in the south-eastern Cape, South
614 Africa. *Journal of Biogeography* 10(5):393-419 <https://doi.org/10.2307/2844748>.
- 615 **Cowling RM. 1984.** A syntaxonomic and synecological study in the Humansdorp region of the
616 fynbos biome. *Bothalia* 15:175-228.
- 617 **Cowling RM, Pierce SM. 1988.** Secondary succession in coastal dune fynbos: variation due to
618 site and disturbance. *Vegetatio* 76(3):131-139 <https://doi.org/10.1007/BF00045474>.
- 619 **Cowling RM, Kirkwood D, Midgley JJ, Pierce SM. 1997.** Invasion and persistence of bird-
620 dispersed, subtropical thicket and forest species in fire-prone coastal fynbos. *Journal of*
621 *Vegetation Science* 8(4):475-488. <https://doi.org/10.2307/3237199>.
- 622 **Cowling RM, Procheş Ş, Vlok JHJ, Van Staden J. 2005.** On the origin of southern African
623 subtropical thicket vegetation. *South African Journal of Botany* 71(1):1-23.
624 [https://doi.org/10.1016/S0254-6299\(15\)30144-7](https://doi.org/10.1016/S0254-6299(15)30144-7).
- 625 **Cowling RM, Potts AJ. 2015.** Climatic, edaphic and fire regime determinants of biome
626 boundaries in the eastern Cape Floristic Region. *South African Journal of Botany* 101:73-
627 81 <https://doi.org/10.1016/j.sajb.2015.03.182>.
- 628 **Cowling RM, Logie C, Brady J, Middleton M, Grobler BA. 2019.** Taxonomic, biological and
629 geographical traits of species in a coastal dune flora in the southeastern Cape Floristic
630 Region: Regional and global comparisons. *PeerJ* (7):1-28
631 <https://doi.org/10.7717/peerj.7336>.
- 632 **Cowling RM, Hoffman MT. 2021.** Multi-decadal vegetation change in dune vegetation of the
633 south-eastern Cape Floristic Region: Is thicket expansion without fire inevitable? *South*
634 *African Journal of Botany* 142:73-81 <https://doi.org/10.1016/j.sajb.2021.05.032>.
- 635 **Cramer MD, Power SC, Belev A, Gillson L, Bond WJ, Hoffman MT, Hedin LO. 2019.** Are
636 forest-shrubland mosaics of the Cape Floristic Region an example of alternate stable
637 states? *Ecography* 42:717-729 <https://doi.org/10.1111/ecog.03860>.
- 638 **Crane PR, Friis EM, Pedersen KR. 1995.** The origin and early diversification of
639 angiosperms. *Nature* 374(6517):27-33.

- 640 **Fidelis A, Appezzato-da-Glória B, Pillar VD, Pfdenhauer J. 2014.** Does disturbance affect
641 bud bank size and belowground structures diversity in Brazilian subtropical grasslands?
642 *Flora-Morphology, Distribution, Functional Ecology of Plants* 209(2) 110-116
643 <https://doi.org/10.1016/j.flora.2013.12.003>.
- 644 **Flake SW, Abreu RCR, Durigan G, Hoffmann WA. 2021a.** Savannas are not old fields:
645 Functional trajectories of forest expansion in a fire-suppressed Brazilian savanna are
646 driven by habitat generalists. *Functional Ecology* 35(8):1797-1809
647 <https://doi.org/10.1111/1365-2435.13818>.
- 648 **Flake SW, Honda EA, Pilon NAL, Hoffmann WA, Durigan G. 2021b.** Not all trees can make
649 a forest: Tree species composition and competition control forest encroachment in a
650 tropical savanna. *Journal of Ecology* 110(2):301-312 [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.13820)
651 [2745.13820](https://doi.org/10.1111/1365-2745.13820).
- 652 **Gadow KV, Zhang G, Durrheim G, Drew D, Seydack A. 2016.** Diversity and production in an
653 Afromontane Forest. *Forest Ecosystems* 3(1):1-12.
- 654 **Geiger EL, Gotsch SG, Damasco G, Haridasan M, Franco AC, Hoffmann WA. 2011.**
655 Distinct roles of savanna and forest tree species in regeneration under fire suppression in
656 a Brazilian savanna. *Journal of Vegetation Science* 22(2):312-321
657 <https://doi.org/10.1111/j.1654-1103.2011.01252.x>.
- 658 **Geldenhuys CJ. 1993.** Floristic composition of the southern Cape forests with an annotated
659 check-list. *South African Journal of Botany* 59(1):26-44 [https://doi.org/10.1016/S0254-](https://doi.org/10.1016/S0254-6299(16)30771-2)
660 [6299\(16\)30771-2](https://doi.org/10.1016/S0254-6299(16)30771-2).
- 661 **Geldenhuys CJ. 1994.** Bergwind fires and the location pattern of forest patches in the southern
662 Cape landscape, South Africa. *Journal of Biogeography* 21(1):49-62
663 <https://doi.org/10.2307/2845603>.
- 664 **Giddey B, Baard JA, Vhengani L, Kraaij T. 2021.** The effect of adjacent vegetation on fire
665 severity in Afrotemperate forest along the southern Cape coast of South Africa. *Southern*
666 *Forests: a Journal of Forest Science* 83(3):225-230
667 <https://doi.org/10.2989/20702620.2021.1936686>.
- 668 **Giddey B, Baard JA, Kraaij T. 2022a.** Verification of the differenced Normalised Burn Ratio

- 669 (dNBR) as an index of fire severity in Afrotropical Forest. *South African Journal of*
670 *Botany* 146:348-353 <https://doi.org/10.1016/j.sajb.2021.11.005>.
- 671 **Giddey B, Baard JA, Kraaij T. 2022b.** Fire severity and tree size affect post-fire survival of
672 Afrotropical forest trees. *Fire Ecology* 18(5):1-13 [https://doi.org/10.1186/s42408-022-](https://doi.org/10.1186/s42408-022-00128-5)
673 00128-5.
- 674 **Google Earth Pro V 7.3.4.8573. (March 21, 2022).** Cape St Francis, South Africa. 34° 09'
675 46.09" S, 24° 44' 53.55" E, Eye alt 10.39 km. SIO, NOAA, U.S. Navy, NGA, GEBCO.
676 CNES/Airbus 2022, Maxar Technologies 2022.
- 677 **Grobler BA, Cowling RM. 2021.** The composition, geography, biology and assembly of the
678 coastal flora of the Cape Floristic Region. *PeerJ* 9:e11916
679 <https://doi.org/10.7717/peerj.11916>.
- 680 **Govender N, Trollope WSW, Van Wilgen BW. 2006.** The effect of fire season, fire
681 frequency, rainfall and management on fire intensity in savanna vegetation in South
682 Africa. *Journal of Applied Ecology* 43(4):748-758 DOI 10.1111/j.1365-
683 2664.2006.01184.x.
- 684 **Halle F, Oldeman RAA, Tomlinson PB. 1978.** *Tropical Trees and Forest: an Architectural*
685 *Analysis*. Berlin: Springer Verlag.
- 686 **Higgins SI, Bond WJ, February EC, Bronn A, Euston-Brown DI, Enslin B, Govender N,**
687 **Rademan L, O'Regan S, Potgieter AL & Scheiter S. 2007.** Effects of four decades of
688 fire manipulation on woody vegetation structure in savanna. *Ecology* 88(5):1119-1125.
- 689 **Hoffmann WA, Orthen B, Franco AC. 2004.** Constraints to seedling success of savanna and
690 forest trees across the savanna–forest boundary. *Oecologia* 140:252-260.
- 691 **Hoffmann WA, Adasme R, Haridasan M, Carvalho M, Geiger EL, Pereira MAB. 2009.**
692 Tree topkill, not mortality, governs the dynamics of alternate stable states at savanna-
693 forest boundaries under frequent fire in central Brazil. *Ecology* 90:1326-1337.
694 <https://doi.org/10.1890/08-0741.1>.

- 695 **Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LC, Lau OL, Haridasan M,**
696 **Franco AC. 2012.** Ecological thresholds at the savanna-forest boundary: how plant traits,
697 resources and fire govern the distribution of tropical biomes. *Ecology Letters* 15(7):759-
698 768.
- 699 **Hutcheson K. 1970.** A test for comparing diversity based on Shannon formula. *Journal of*
700 *Theoretical Biology* 29:151-154.
- 701 **IUCN. 2022.** The IUCN Red List of Threatened Species. Version 2022-1. <https://www.iucnredlist.org>.
702 Accessed on [18 June 2022]. **Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock**
703 **RA. 2011.** Fire as an evolutionary pressure shaping plant traits. *Trends in Plant*
704 *Science* 16(8):406-411 <https://doi.org/10.1016/j.tplants.2011.04.002>.
- 705 **Keeley JE, Rundel PW. 2005.** Fire and the Miocene expansion of C4 grasslands. *Ecology*
706 *Letters* 8(7):683-690 <https://doi.org/10.1111/j.1461-0248.2005.00767.x>.
- 707 **Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. 2012.** Fire in Mediterranean
708 Ecosystems, Cambridge: Cambridge University Press.
- 709 **Keeley JE, Syphard AD. 2017.** Different historical fire–climate patterns in California.
710 *International Journal of Wildland Fire* 26:253-268 <https://doi.org/10.1071/WF16102>.
- 711 **Kelly LT et al. 2020.** Fire and biodiversity in the Anthropocene. *Science* 370:eabb0355 DOI:
712 10.1126/science.abb0355.
- 713 **Kraaij T, Baard JA, Cowling RM, van Wilgen BW, Das S. 2013.** Historical fire regimes in a
714 poorly understood, fire-prone ecosystem: eastern coastal fynbos. *International Journal of*
715 *Wildland Fire* 22(3):277-287 <https://doi.org/10.1071/WF11163>.
- 716 **Kruger FJ, Bigalke RC. 1984.** Fire in fynbos. In *Ecological effects of fire in South African*
717 *ecosystems* (pp. 67-114). Springer, Berlin, Heidelberg.
- 718 **Kruger LM, Midgley JJ, Cowling RM. 1997.** Resprouters vs reseederers in South African forest
719 trees; a model based on forest canopy height. *Functional Ecology* 11(1):101-105
720 <https://doi.org/10.1046/j.1365-2435.1997.00064.x>.
- 721 **Kun Z, DellaSala D, Keith H, Kormos C, Mercer B, Moomaw WR, Wiezik M. 2020.**

- 722 Recognizing the importance of unmanaged forests to mitigate climate change. *GCB*
723 *Bioenergy* 12(12):1034-1035. <https://doi.org/10.1111/gcbb.12714>.
- 724 **Lamont BB, He T, Pausas JG. 2017.** African geoxyles evolved in response to fire; frost came
725 later. *Evolutionary Ecology* 31(5):603-617 <https://doi.org/10.1007/s10682-017-9905-4>.
- 726 **Low AB, Rebelo TG. 1996.** Vegetation of South Africa, Lesotho and Swaziland. Department of
727 Environmental Affairs and Tourism, Pretoria.
- 728 **Lu M, Bond WJ, Sheffer E, Cramer MD, West AG, Allsopp N, February EC, Chimphango**
729 **S, Ma Z, Slingsby JA, Hedin LO. 2022.** Biome boundary maintained by intense
730 belowground resource competition in world's thinnest-rooted plant
731 community. *Proceedings of the National Academy of Sciences* 119(9): p.e2117514119.
- 732 **Mackey B, Kormos CF, Keith H, Moomaw WR, Houghton RA, Mittermeier RA, Hugh S.**
733 **2020.** Understanding the importance of primary tropical forest protection as a mitigation
734 strategy. *Mitigation and Adaptation Strategies for Global Change* 25(5): 763-787
735 <https://doi.org/10.1007/s11027-019-09891-4>.
- 736 **Manders PT. 1990.** Fire and other variables as determinants of forest / fynbos boundaries in the
737 Cape Province. *Journal of Vegetation Science* 1(4):483-490
738 <https://doi.org/10.2307/3235782>.
- 739 **Martinez Arbizu P. 2017.** pairwiseAdonis: Pairwise Multilevel Comparison using Adonis. R
740 package version 0.4.
- 741 **Maurin O, Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya AM, Van der Bank M,**
742 **Bond WJ. 2014.** Savanna fire and the origins of the 'underground forests' of Africa. *New*
743 *Phytologist* 204(1):201-214 <https://doi.org/10.1111/nph.12936>.
- 744 **Meerts P. 2017.** Geoxylic suffrutices of African savannas: short but remarkably similar to
745 trees. *Journal of Tropical Ecology* 33(4):295-298
746 <https://doi.org/10.1017/S0266467417000165>.
- 747 **Meller P, Stellmes M, Fidelis A, Finckh M. 2021.** Correlates of geoxyle diversity in
748 Afrotropical grasslands. *Journal of Biogeography* 49(2):339-352
749 <https://doi.org/10.1111/jbi.14305>.

- 750 **Midgley JJ, Cowling RM, Seydack AWH, van Wyk GF. 1997.** Indigenous Forest. In:
751 Cowling RM, Richardson DM, Pierce SM. (eds) *Vegetation of Southern Africa*.
752 Cambridge University Press, Cambridge UK.
- 753 **Midgley JJ, Cowling RM. 1993.** Regeneration patterns in a subtropical transition thicket; where
754 are all the seedlings? *South African Journal of Botany* 59:496-499.
- 755 **Midgley JJ, 1996.** Why the world's vegetation is not totally dominated by resprouting plants;
756 because resprouters are shorter than reseeders. *Ecography* 19(1):92-95.
- 757 **Minchin PR. 1987.** An evaluation of the relative robustness of techniques for ecological
758 ordination. *Vegetatio* 69:89-07 https://doi.org/10.1007/978-94-009-4061-1_9.
- 759 **Morrison DA, Renwick JA. 2000.** Effects of variation in fire intensity on regeneration of co-
760 occurring species of small trees in the Sydney region. *Australian Journal of Botany*
761 48(1):71-79. DOI 10.1071/BT98054.
- 762 **Msweli ST, Potts AJ, Fritz H, Kraaij T. 2020.** Fire weather effects on flammability of
763 indigenous and invasive alien plants in coastal fynbos and thicket shrublands (Cape
764 Floristic Region). *PeerJ* 8:e10161 DOI 10.7717/peerj.10161.
- 765 **Murphy BP, Bowman DM. 2012.** What controls the distribution of tropical forest and
766 savanna? *Ecology Letters* 15(7):748-758 [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2012.01771.x)
767 [0248.2012.01771.x](https://doi.org/10.1111/j.1461-0248.2012.01771.x).
- 768 **Mucina L, Geldenhuys CJ, Rutherford MC. 2006.** Afrotropical, subtropical and azonal
769 forests. In: Mucina L, Rutherford MC, eds. *The Vegetation of South Africa, Lesotho and*
770 *Swaziland*. Pretoria. *Strelitzia* 19 pp.584-614.
- 771 **Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Peter R, Minchin**
772 **RB, O'Hara G, Simpson L, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H.**
773 **2020.** vegan: Community Ecology Package. R package version 2.5-7. [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)
774 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan)
- 775 **Pausas JG, Lamont BB, Paula S, Appezzato-da- Glória B, Fidelis A. 2018.** Unearthing
776 belowground bud banks in fire-prone ecosystems. *New Phytologist*, 217(4):1435-1448
777 <https://doi.org/10.1111/nph.14982>.

- 778 **Pennington RT, Lavin M, Särkinen T, Lewis GP, Klitgaard BB, Hughes CE. 2010.**
779 Contrasting plant diversification histories within the Andean biodiversity hotspot.
780 *Proceedings of the National Academy of Sciences* 107(31):13783-13787.
- 781 **Pierce SM, Cowling RM. 1991.** Disturbance regimes as determinants of seed banks in coastal
782 dune vegetation of the southeastern Cape. *Journal of Vegetation Science*, 2(3):403-412
783 <https://doi.org/10.2307/3235933>.
- 784 **Radloff FGT. 2008.** *The ecology of large herbivores native to the coastal lowlands of the*
785 *Fynbos Biome in the Western Cape, South Africa* (Doctoral dissertation, Stellenbosch:
786 Stellenbosch University). **R Core Team (2021).** R: A language and environment for
787 statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL
788 <https://www.R-project.org/>.
- 789 **Roberts DL, Botha GA, Maud RR, Pether J. 2006.** Coastal Cenozoic deposits. In: Johnson
790 MR, Anhaeusser CR, Thomas RJ.(Eds.) *The Geology of South Africa* (pp. 605-628).
791 Pretoria: Geological Society of South Africa, Johannesburg/Council for Geoscience.
- 792 **Ruiz-Peinado R, Oviedo JAB, Senespleda EL, Oviedo FB, del Río Gaztelurrutia M. 2017.**
793 Forest management and carbon sequestration in the Mediterranean region: A
794 review. *Forest Systems* 26(2):10.
- 795 **Ryan KC. 2002.** Dynamic interactions between forest structure and fire behavior in boreal
796 ecosystems. *Silva Fennica* 36(1):13-39.
- 797 **Smit IP, Asner GP, Govender N, Kennedy-Bowdoin T, Knapp DE & Jacobson J. 2010.**
798 Effects of fire on woody vegetation structure in African savanna. *Ecological*
799 *Applications* 20(7):1865-1875.
- 800 **Sørensen TA. 1948.** A method of establishing groups of equal amplitude in plant sociology
801 based on similarity of species content and its application to analyses of the vegetation on
802 Danish commons. *Biol. Skar.* 5:1-34.
- 803 **South African Government, 2022.** National Forest Act: List of protected tree species.
804 <https://www.gov.za/documents/national-forests-act-list-protected-tree-species-7>.
805 Accessed on [19 June 2022].
- 806 **Spellerberg I, Fedor P. 2003.** A tribute to Claude Shannon (1916–2001) and a plea for more

- 807 rigorous use of species richness, species diversity and the ‘Shannon-Wiener’ Index.
808 *Global Ecology and Biogeography* 12:177–179.
- 809 **Strydom T, Kraaij T, Difford M, Cowling RM. 2020.** Fire severity effects on resprouting of
810 subtropical dune thicket of the Cape Floristic Region. *PeerJ* 8:e9240
811 <https://doi.org/10.7717/peerj.9240>.
- 812 **Strydom T, Grobler BA, Kraaij T, Cowling RM. 2021.** Pre-and post-fire architectural guilds
813 of subtropical dune thicket species in the southeastern Cape Floristic Region. *Journal of*
814 *Vegetation Science* 32:e13079 <https://doi.org/10.1111/jvs.13079>.
- 815 **van Wilgen BW, Higgins KB, Bellstedt DU. 1990.** The role of vegetation structure and fuel
816 chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of
817 South Africa. *The Journal of Ecology* 78(1):210-222.
- 818 **van Wilgen BW, Forsyth GG, de Klerk H, Das S, Khuluse S, Schmitz P. 2010.** Fire
819 management in Mediterranean-climate shrublands: A case study from the Cape fynbos,
820 South Africa. *Journal of Applied Ecology* 47(3):631-638 [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2664.2010.01800.x)
821 [2664.2010.01800.x](https://doi.org/10.1111/j.1365-2664.2010.01800.x).
- 822 **Victor J.E. 2006.** *Rapanea gilliana* (Sond.) Mez. National Assessment: Red List of South
823 African Plants version 2020.1. [http://redlist.sanbi.org/species.php?species=2565-](http://redlist.sanbi.org/species.php?species=2565-2)
824 [2](http://redlist.sanbi.org/species.php?species=2565-2) Accessed on [18 June 2022]. **Vlok, JHJ, Euston-Brown DIW, Cowling RM. 2003.**
825 Acocks’ Valley Bushveld 50 years on: new perspectives on the delimitation,
826 characterisation and origin of subtropical thicket vegetation. *South African Journal of*
827 *Botany* 69(1):27-51 [https://doi.org/10.1016/S0254-6299\(15\)30358-6](https://doi.org/10.1016/S0254-6299(15)30358-6).
- 828 **Watson LH, Cameron MJ. 2001.** The influence of fire on a southern cape mountain forest.
829 *Southern African Forestry Journal* 191(1):39-42
830 <https://doi.org/10.1080/20702620.2001.10434149>.
- 831 **White F. 1976.** The underground forests of Africa: a preliminary review. *Garden's Bulletin*.
832 Singapore, 29:57-71.
- 833 **Williams RJ, Gill AM, Bradstock RA. eds. 2012.** *Flammable Australia: fire regimes,*
834 *biodiversity and ecosystems in a changing world*. CSIRO publishing.

835 **Wigley BJ, Staver AC, Zytkowski R, Jagodzinski AM, Wigley-Coetsee C. 2019.** Root trait
836 variation in African savannas. *Plant and Soil* 441(1–2):555-565
837 <https://doi.org/10.1007/s11104-019-04145-3>.

838

Figure 1

Fire exposure and associated thicket structure of the dune landscape.

(a) Dune landscape of the study area showing parallel dune ridges and associated swales. (b) Narrow and steep-sided dune swale that is seldom, if ever, exposed to fire and supports ca. 4 - 8 m-tall dune forest. (c) Broad and shallow dune swale that supports ca. 3 - 6 m-tall dune thicket that only burns in the most severe fires at intervals of ca. 50-100 years. (d) Dune crests and slopes that supports ca. 0.6 - 1.4 m-tall dune fynbos-thicket that are exposed to fires at intervals of ca. 10-50 years.



Figure 2

(a) Partial distance-based Redundancy Analysis (dbRDA) ordination plot (constrained by fire exposure) and (b) Mutlidimensional scaling (MDS) ordination plot (unconstrained) for cover abundance data of dune thicket species.

The partial distance-based Redundancy Analysis (dbRDA) ordination and Mutlidimensional scaling (MDS) ordination were plotted using Bray-Curtis dissimilarity matrix based on cover abundance data of species and projected onto two-dimensional space. The shapes (square, circle, triangle) are transects colored according to their location in pre-determined fire-exposure categories for dune thicket (green = low fire exposure; blue = moderate fire exposure; orange = high fire exposure). The dashed ellipses indicate 95% confidence intervals around the centroids of each of these categories. The effect of aspect has been controlled for in this dbRDA. The legend (color coded) shows the architectural guild which is most common in the respective fire-exposure categories.

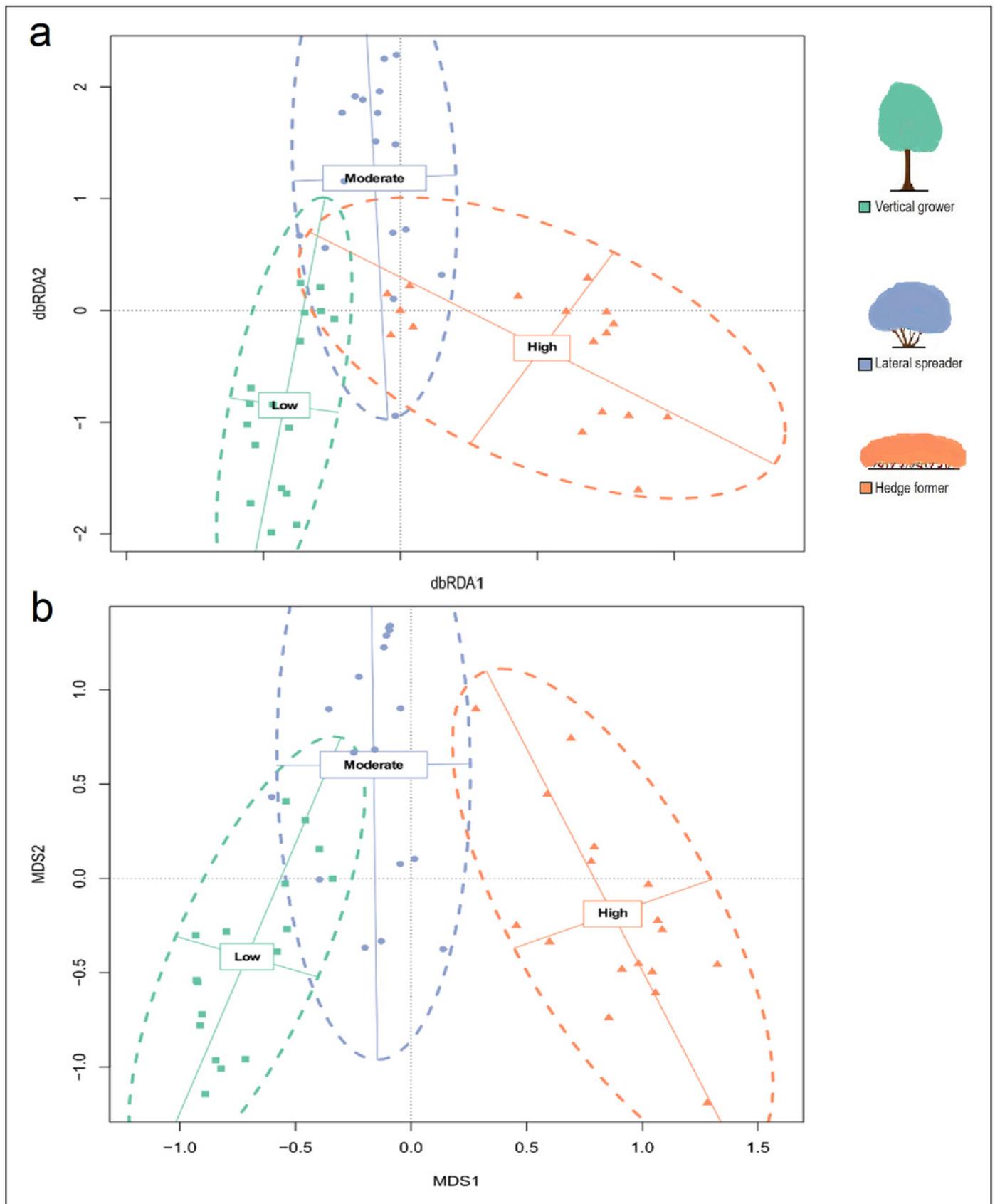


Figure 3

Non-Metric Multidimensional Scaling (NMDS) ordination plot for cover abundance of dune thicket species.

The ordination was plotted using the Bray-Curtis dissimilarity matrix based on cover abundance data of species and projected onto two-dimensional space. (a) The shapes (square, circle, triangle) are transects colored according to their location in pre-determined fire-exposure categories for dune thicket (green = low fire exposure; blue = moderate fire-exposure; orange = high fire exposure) and (b) species according to their location in the fire exposure categories. The dashed ellipses indicate 95% confidence intervals for these categories. NMDS solution: $k = 2$, stress = 16.1%, non-metric $R^2 = 0.974$, linear $R^2 = 0.874$. NMDS axis 1 reflects the fire-exposure gradient, which is aligned along the axis of most variation in species cover abundance. The legend (color coded) shows the architectural guild which is most common in the respective fire-exposure categories.

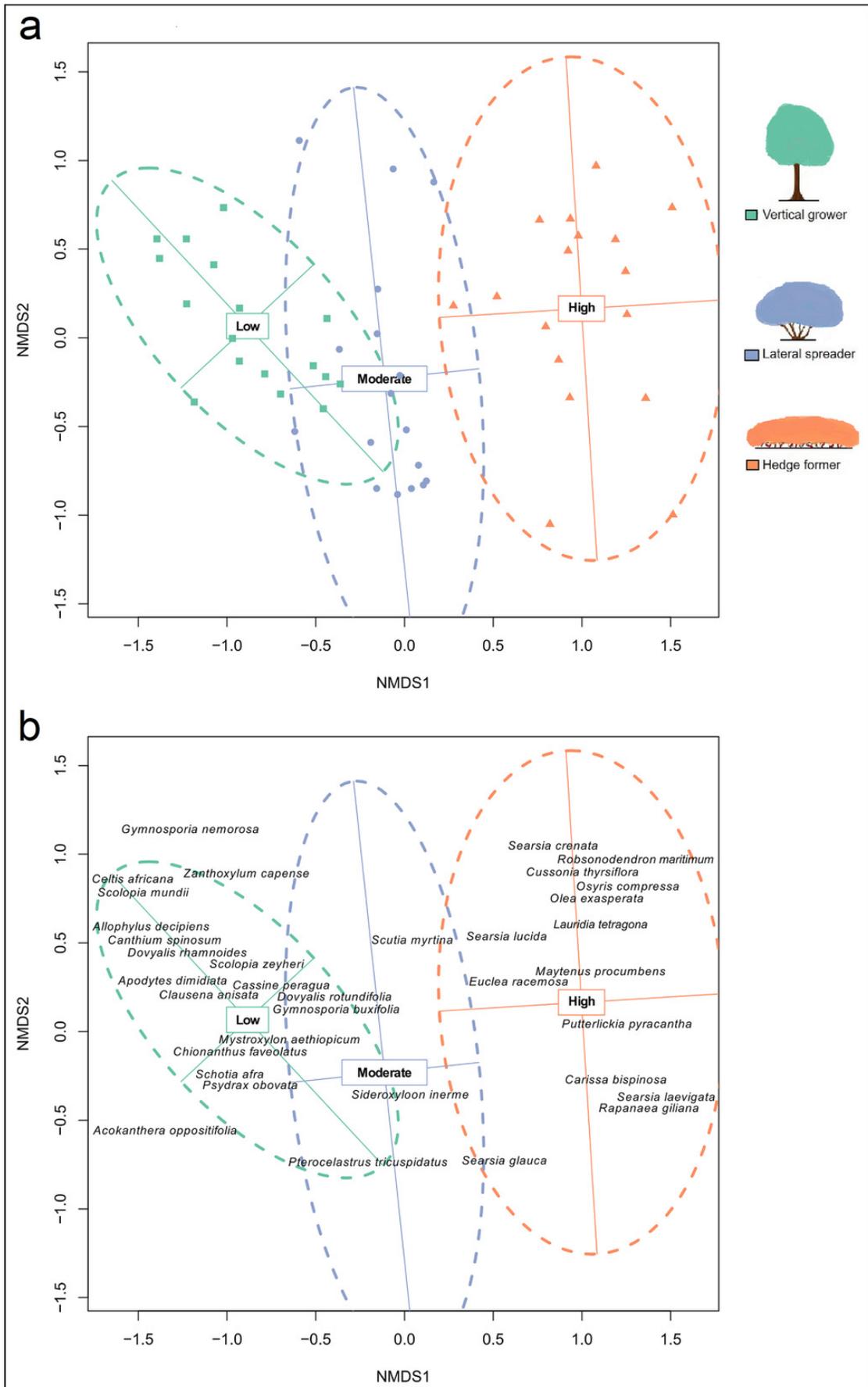


Figure 4

Maximal distance-based Redundancy Analysis (dbRDA) ordination plot (constrained by fire exposure) and (b) Mutlidimensional scaling (MDS) ordination plot (unconstrained) for cover abundance data of dune thicket architectural guilds.

The maximal distance-based Redundancy Analysis (dbRDA) ordination and Mutlidimensional scaling (MDS) ordination were plotted using Bray-Curtis dissimilarity matrix based on cover abundance data of architectural guilds and projected onto two-dimensional space. The shapes (square, circle, triangle) are transects colored according to their location in pre-determined fire-exposure categories for dune thicket (green = low fire exposure; blue = moderate fire exposure; orange = high fire exposure). The dashed ellipses indicate 95% confidence intervals around the centroids of each of these categories. The legend (color coded) shows the architectural guild which is most common in the respective fire-exposure categories.

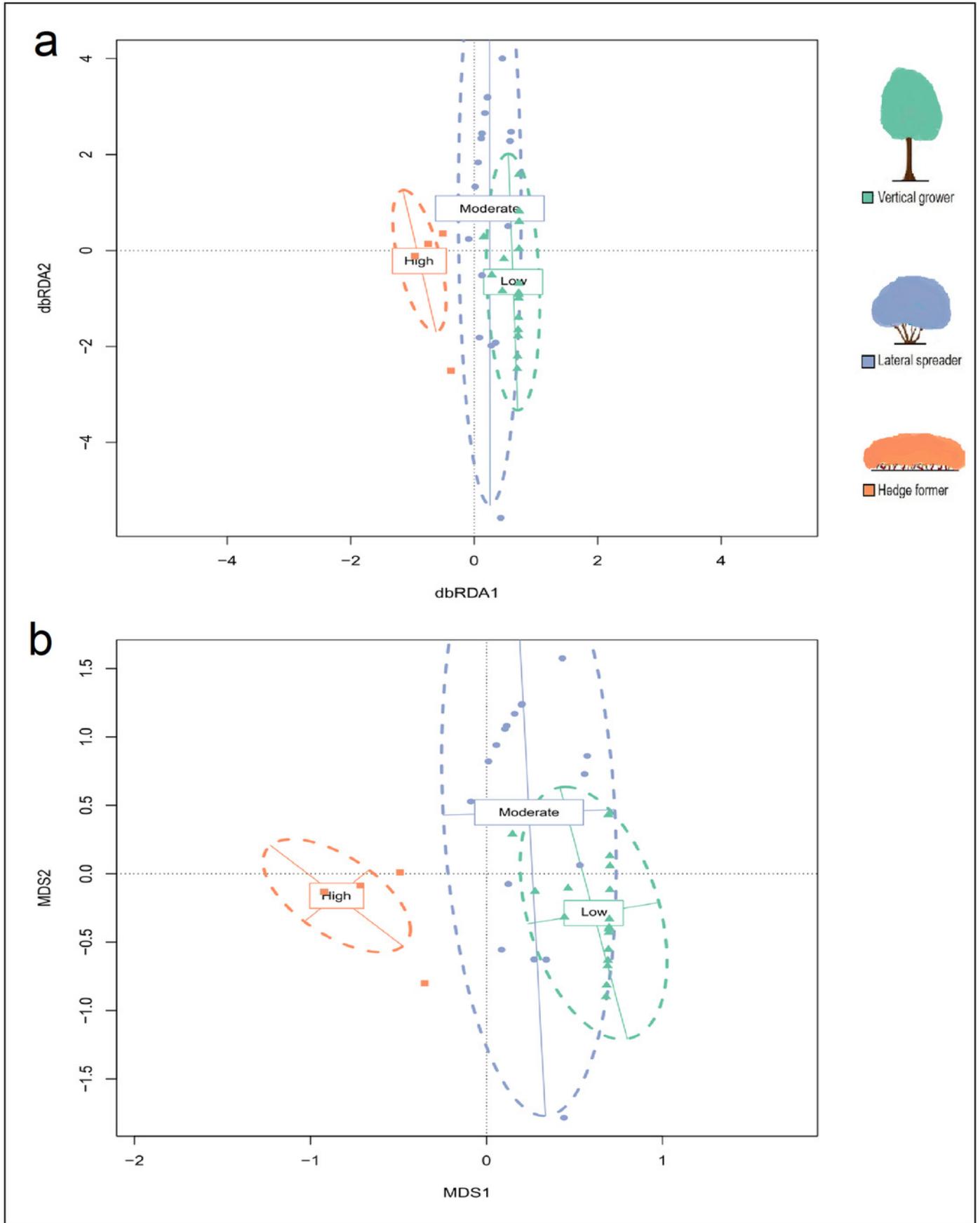


Figure 5

Non-Metric Multidimensional Scaling (NMDS) ordination plot for cover abundance of dune thicket architectural guilds.

The ordination was plotted with the use of the Bray-Curtis dissimilarity matrix based on cover abundance data of architectural guilds and projected onto two-dimensional space. The shapes (triangle, square and circle) are transects coloured according to their location in pre-determined fire-exposure categories (green = low fire exposure; blue = moderate fire exposure; orange = high fire exposure) and the cross dashed ellipses indicate 95% confidence intervals for these categories. Because of extreme structural homogeneity in high fire exposure, 14 of 17 transects plotted on top each other (indicated by an asterisk in the triangle). NMDS solution: $k = 2$, stress = 1.4%, linear $R^2 = 0.999$, non-metric $R^2 = 1$. NMDS axis 1 reflects the fire-exposure gradient, which is aligned along the axis of most variation in architectural guild cover abundance. The legend (color coded) shows the architectural guild which is most common in the respective fire-exposure categories.

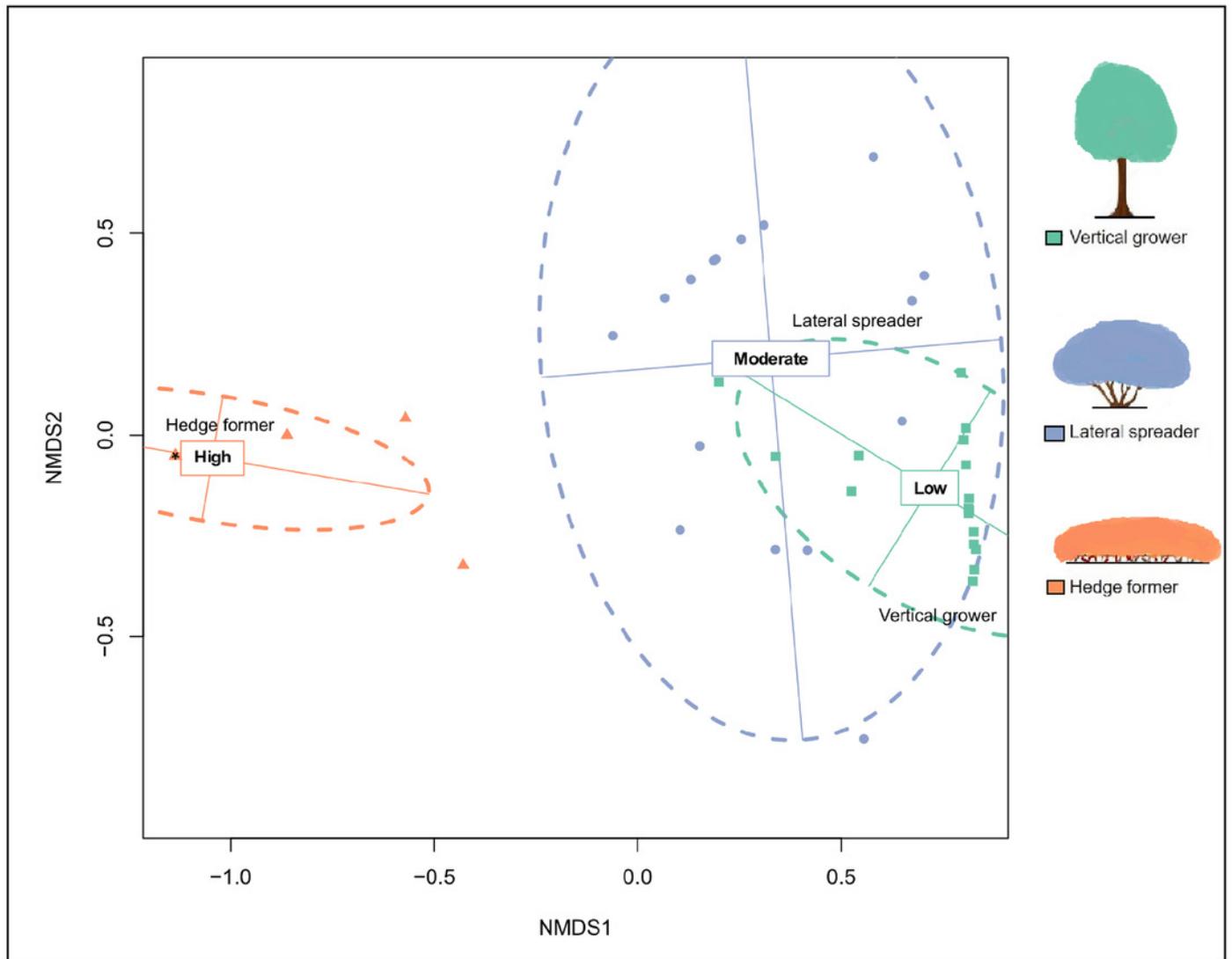


Figure 6

Canopy cover (a) and height (b) differences across three fire-exposure categories. Note that canopy cover values may exceed 100% owing to canopy overlap.

The legend (color coded) shows the architectural guild which is most common in the respective fire-exposure categories. Disparate small letters denote significant differences among fire-exposure categories based on Kruskal Wallis H test results and Dunn's multiple comparisons.

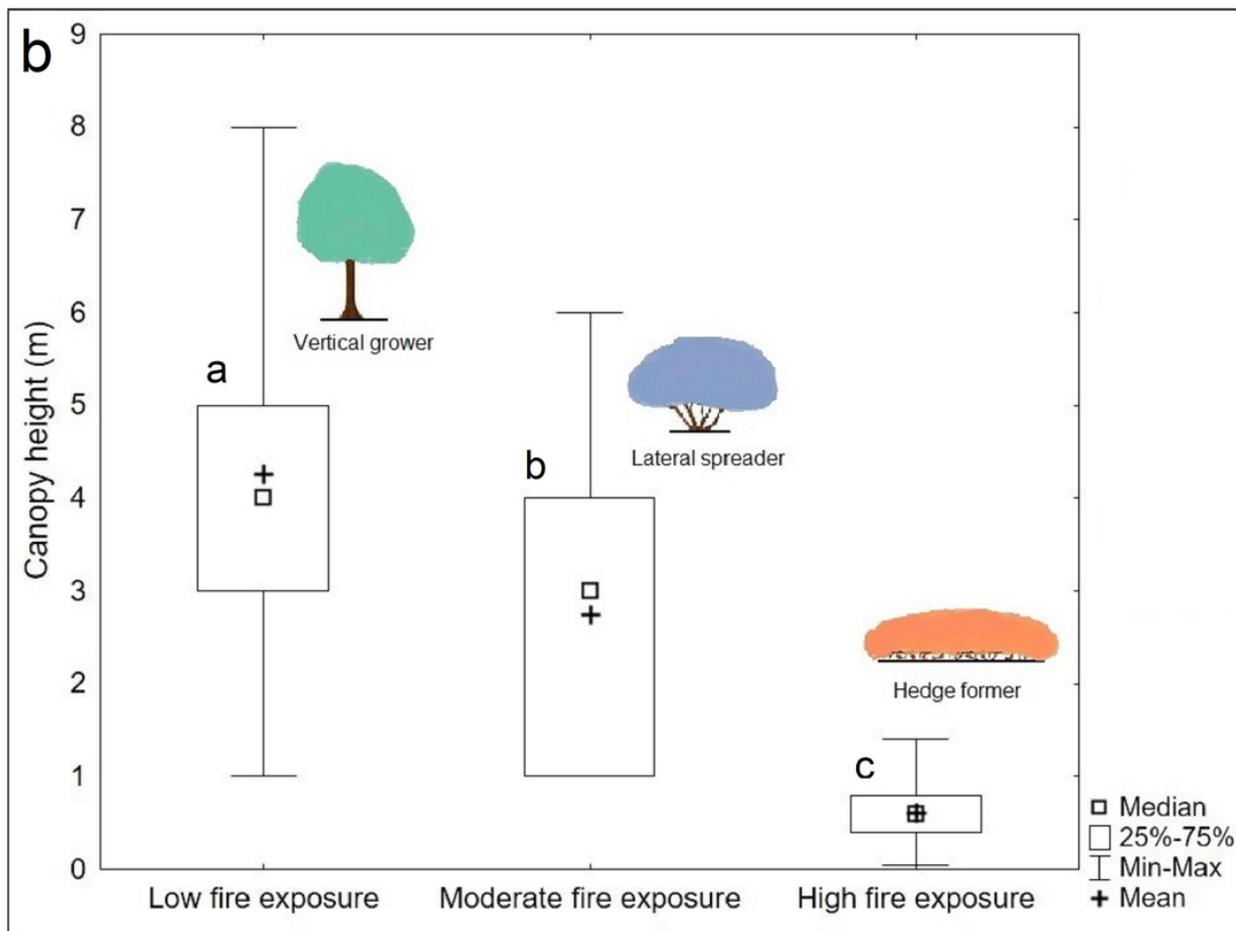
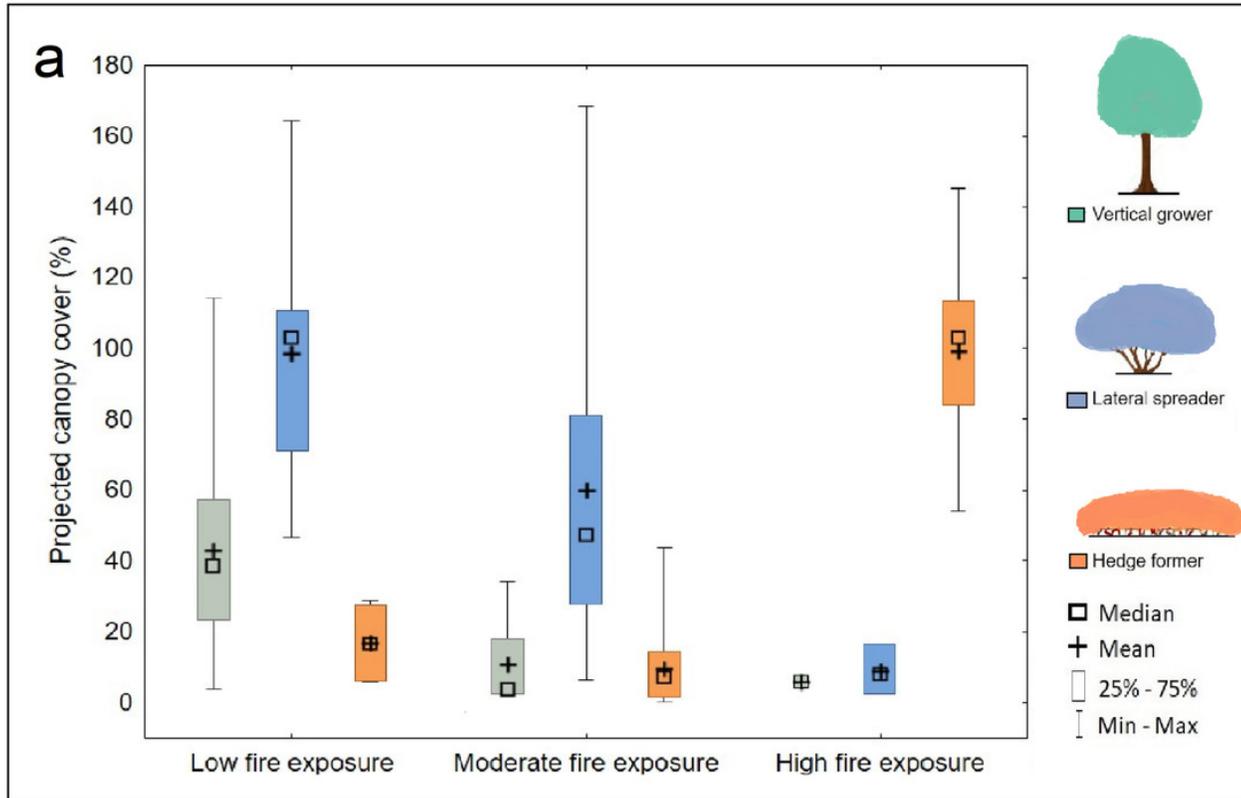


Table 1 (on next page)

Composition, canopy cover abundance and architectural guild allocation (Strydom et al., 2021) of canopy species in three fire exposure categories (low, moderate, high).

Architectural guilds included vertical grower (V), lateral spreader (L), and hedge former (H). Species allocated to more than one guild showed architectural plasticity across fire exposure categories.

- 1 **Table 1:** Composition, canopy cover abundance and architectural guild allocation (Strydom et al.,2021) of
 2 canopy species in three fire exposure categories (low, moderate, high).
 3 Architectural guilds included vertical grower (V), lateral spreader (L), and hedge former (H).
 4 Species allocated to more than one guild showed architectural plasticity across fire exposure
 5 categories.

Species	Projected canopy cover (%)		
	Low fire exposure	Moderate fire exposure	High fire exposure
<i>Canthium spinosum</i> (L.f.) J.St.-Hill.	6.8 (V)		
<i>Chionanthus foveolatus</i> E.Mey. Stearn	4.2 (V)		
<i>Allophylus decipiens</i> Radlk.	1.4 (V)		
<i>Apodytes dimidiata</i> E.Mey. ex Am.	1.4 (V)		
<i>Scolopia mundii</i> Warb.	0.5 (V)		
<i>Schotia afra</i> Thunb.	0.2 (V)		
<i>Acokanthera oppositifolia</i> (Lam.) Codd	0.1 (V)		
<i>Gymnosporia nemorosa</i> Szyszyl.	0.1 (V)		
<i>Celtis africana</i> Burm.f.	0.04 (V)		
<i>Dovyalis rhamnoides</i> Engl.	11.5 (V)	0.1 (V)	
<i>Psydrax obovata</i> Bridson	6.3 (V)	0.8 (V)	
<i>Scolopia zeyheri</i> Warb.	5.1 (V)	0.6 (V)	
<i>Zanthoxylum capense</i> Harv.	3 (V)	1.3 (V)	
<i>Clausena anisata</i> Hook.f., De Wild. & Staner	1.0 (V)	0.04 (V)	
<i>Gymnosporia buxifolia</i> (L.) Szyszyl	0.3 (L)	0.1 (L)	
<i>Mystroxydon aethiopicum</i> (Thunb.) Loes.	33.4 (L)	2.9 (L)	0.02 (H)
<i>Pterocelastrus tricuspidatus</i> Walp.	30.9 (L,V)	50.2 (L,V)	2.5 (L,H)
# <i>Sideroxylon inerme</i> Forssk.	25.5 (L,V)	6.1 (L,V)	8.5 (L,H)
<i>Cassine peragua</i> L.	5.2 (V)	0.6 (V)	0.2 (H)
<i>Scutia myrtina</i> (Burm.f.) Merr.	1.7 (H)	0.6 (H)	0.1 (H)
<i>Dovyalis rotundifolia</i> Engl.	1.3 (V)	0.4 (V)	0.3 (H)
<i>Searsia glauca</i> (Thunb.) Moffett.	3.0 (H)	7.7 (H)	22.9 (H)
* <i>Euclea racemosa</i> L.	0.8 (V)	4.7 (V)	2.7 (H)
†* <i>Olea exasperata</i> Jacq.	0.5 (V)	0.01 (H)	28.7 (H)
<i>Osyris compressa</i> A.DC.	1.0 (L)		3.1 (H)
<i>Searsia lucida</i> (L.) F.A.Barkley.		1.7 (H)	3.8 (H)
†* <i>Searsia crenata</i> (Thunb.) Moffett		0.02 (H)	1.1 (H)
<i>Maytenus procumbens</i> (L.f.) Loes.			10.7 (H)
† <i>Robsonodendron maritimum</i> (Bolus) R.H.Archer			7.9 (H)
@†* <i>Rapanea gilliana</i> Mez			3.0 (H)
<i>Lauridia tetragona</i> (L.f.) R.H. Archer			1.6 (H)
<i>Carissa bispinosa</i> (L.) Merxm.			1.5 (H)
<i>Putterlickia pyracantha</i> (L.) Szyszyl.			1.5 (H)
<i>Cussonia thyrsoiflora</i> Thunb.			1.2 (H)
* <i>Searsia laevigata</i> (Moffett) Moffett.			0.1 (H)

6

7 Note:

8 Most thicket species are classified as least concerned on the IUCN red list of threatened species (IUCN,
9 2022) but one species is classified as endangered (Victor, 2006). One species are protected by law (South
10 African Government, 2022) and a few species are endemic (Cowling et al., 2019).

11 #Protected

12 @Endangered

13 +Cape dune endemic

14 *Geoxyle (recruit from below ground stems)

15

16

17