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4

## 5 **Groundwater drawdown drives ecophysiological adjustments of woody** 6 **vegetation in a semi-arid coastal ecosystem**

7 ***Running head:*** functional responses to groundwater depth

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17

18 **Keywords:** water table lowering; groundwater table depth; plant functional types; coastal  
19 dune ecosystems; photosynthetic activity; plant water status; water-sources-use; water-  
20 uptake depth.

21

## 22 **Abstract**

23 Predicted droughts and anthropogenic water use will increase groundwater lowering rates  
24 and intensify groundwater limitation, particularly for Mediterranean semi-arid ecosystems.  
25 These hydrological changes may be expected to elicit differential functional responses of  
26 vegetation either belowground or aboveground. Yet, our ability to predict the impacts of

27 groundwater changes on these ecosystems is still poor. Thus, we sought to better  
28 understand the impact of falling water table on the physiology of woody vegetation. We  
29 specifically ask (a) how is woody vegetation ecophysiological performance affected by  
30 water table depth during the dry season? and (b) does the vegetation response to increasing  
31 depth to groundwater differ among water-use functional types? We examined a suite of  
32 physiological parameters and water-uptake depths of the dominant, functionally distinct  
33 woody vegetation along a water-table depth gradient in a Mediterranean semi-arid coastal  
34 ecosystem that is currently experiencing anthropogenic groundwater extraction pressure.  
35 We found that groundwater drawdown did negatively affect the ecophysiological  
36 performance of the woody vegetation. Across all studied environmental factors, depth to  
37 groundwater was the most important driver of ecophysiological adjustments. Plant  
38 functional types, independent of groundwater dependence, showed consistent declines in  
39 water content and generally reduced C and N acquisition with increasing depths to  
40 groundwater. Functional types showed distinct operating physiological ranges, but common  
41 physiological sensitivity to greater water table depth. Thus, although differences in water-  
42 source use exist, a physiological convergence appeared to happen among different  
43 functional types. These results strongly suggest that hydrological drought has an important  
44 impact on fundamental physiological processes, constraining the performance of woody  
45 vegetation under semi-arid conditions. By disentangling the functional responses and  
46 vulnerability of woody vegetation to groundwater limitation, our study establishes the basis  
47 for predicting the physiological responses of woody vegetation in semi-arid coastal  
48 ecosystems to groundwater drawdown..

## 50 **Introduction**

51 The seasonal cycle of water availability drives variation in Mediterranean ecosystem  
52 function. Water availability is considered to be the main factor limiting vegetation growth  
53 in this region, and changes in precipitation are already inducing changes in these  
54 ecosystems (e.g. Allen et al., 2010; Barbeta, Ogaya, & Peñuelas, 2013; Jump, Hunt, &  
55 Peñuelas, 2006; Peñuelas & Boada, 2003). Climate models broadly predict a decrease in  
56 water resources and negative impacts on ecosystem integrity, particularly on semi-arid  
57 ecosystems (Kirtman et al., 2013). These predicted meteorological droughts will diminish  
58 recharge and increase groundwater lowering rates, intensifying groundwater depletion  
59 (Taylor et al., 2012). Additionally, groundwater will be affected by the changing patterns of  
60 anthropogenic use, as increasing withdrawal combined with reduced recharge can decrease  
61 groundwater levels significantly (Kløve et al., 2014; Kopp et al., 2013). These trajectories  
62 raise concerns, as they can lead to insufficient supplies for both human society and  
63 ecosystems (Taylor et al., 2012).

64 Climate and human-induced changes in groundwater will directly affect groundwater-  
65 dependent ecosystems (Colón-Rivera, Feagin, West, Lopez Figueroa, & Benítez-Joubert,  
66 2014; Cooper, Sanderson, Stannard, & Groeneveld, 2006; Naumburg, Mata-Gonzalez,  
67 Hunter, Mclendon, & Martin, 2005). In particular, groundwater can serve as an important  
68 water resource for woody vegetation in semiarid landscapes (Barbeta & Peñuelas, 2017;  
69 Barbeta et al., 2015; Dawson & Pate, 1996; Evaristo & McDonnell, 2017; Garcia-Forner  
70 et al., 2016; Miller, Chen, Rubin, Ma, & Baldocchi, 2010; Palacio, Montserrat-Martí, &  
71 Ferrio, 2017), especially in sandy soils, where water retention is low, and there is strong  
72 soil moisture limitation in the top soil during dry seasons. Thus, limited plant access to

73 groundwater caused by groundwater lowering is expected to have major impacts on plant  
74 physiological performance (Rossatto, de Carvalho Ramos Silva, Villalobos-Vega, da  
75 Sternberg, & Franco, 2012; Zencich, Froend, Turner, & Gailitis, 2002). However, due to  
76 niche differentiation among species in response to ecohydrological factors, not all species  
77 are expected to respond in the same way (Araya et al., 2011; Silvertown, Araya, & Gowing,  
78 2015; Silvertown, Dodd, Gowing, & Mountford, 1999).

79 Plant responses to changes in water availability are generally linked to varying capacities  
80 for water uptake and tolerance of water stress (Chaves Manuela, Maroco João, & Pereira  
81 João, 2003; West et al., 2012; Pivovarovoff et al., 2016; Grossiord et al., 2017; Ackerly,  
82 2004). Both meteorological drought and hydrological drought might initiate differential  
83 species responses either belowground or aboveground (Antunes, Díaz Barradas,  
84 Zunzunegui, Vieira, Pereira, et al., 2018; Imada, Yamanaka, & Tamai, 2008; Máguas et al.,  
85 2011; Zunzunegui, Díaz Barradas, & García Novo, 1998; Zunzunegui, Díaz Barradas, &  
86 García Novo, 2000). After drawdown events, regional water tables commonly continue to  
87 decline, with the vegetation usually responding through progressive and unidirectional  
88 changes in abundance and composition (Froend & Sommer, 2010; Sommer & Froend,  
89 2011). Variations in composition can be manifested as a shift towards species not  
90 dependent on specific hydrological conditions (e.g., relatively shallow groundwater), with  
91 the progressive change in hydrology continuing to force a transition in the flora towards an  
92 alternative ecohydrological state (Sommer & Froend, 2011, 2014). These variations are  
93 expected to be primarily based on ecophysiological processes of acclimation and stress  
94 tolerance. Phenotypic plasticity and physiological adjustments in plants allow some species  
95 to sustain (or increase) resource-use efficiency rates, subsequently maintaining their fitness  
96 under varying environmental conditions (Ernande & Dieckmann, 2004; Valladares et al.,

97 2014). Still, there are some species that, by lower tolerance of water stress, decrease their  
98 physiological performance and ultimately face die back and a decline in the community  
99 (Horton, Kolb, & Hart, 2001; Lloret & Granzow-de la Cerda, 2013; Padilla & Pugnaire,  
100 2007; Zunzunegui, Barradas, Ain-Lhout, Clavijo, & Novo, 2005). Interestingly,  
101 ecophysiological processes of acclimation and structural changes forced by (long-term)  
102 cyclic droughts may further mitigate the negative effects of extreme droughts and of  
103 human-induced hydrological changes (Barbeta et al., 2013, 2015; Helman, Lensky, Yakir,  
104 & Osem, 2017; Matesanz & Valladares, 2013). However, there are costs and limits to the  
105 functional benefits that acclimation processes can deliver in a given environment  
106 (McDowell et al., 2008; Valladares, Gianoli, & Gómez, 2007).

107 Our ability to predict with confidence the impacts of hydrological droughts on ecosystems  
108 with high human and climate pressure such as coastal semi-arid woodlands is still poor.  
109 Understanding current water, N and C use responses to declining water table and soil  
110 moisture in the semi-arid Mediterranean region is essential for predicting the altered  
111 functioning of these key ecosystems under scenarios of future groundwater limitation  
112 (Schröter et al., 2005). The evaluation of physiological adjustments can improve the  
113 categorization of plant functional responses to hydrological drought, ultimately helping to  
114 better inform and make more accurate predictions regarding plant responses to future  
115 changes in groundwater availability. Through an ecophysiological perspective, we can  
116 potentially identify mechanisms underlying the hydrological impacts that threaten the  
117 persistence of ecosystems in their current structures and compositions.

118 Thus, in this study, we sought to better understand the impact of groundwater drawdown  
119 (i.e., falling water table) on the physiology of overlying woody vegetation. Accordingly, we  
120 aimed to assess functional responses of woody species to increasing water table depth in a

121 semi-arid Mediterranean coastal dune ecosystem under anthropogenic groundwater  
122 abstraction. We specifically ask: how is woody vegetation ecophysiological performance  
123 affected by water table depth during the dry season? Are there other environmental factors  
124 that influence variation in ecophysiological responses in the dry season? Does the  
125 vegetation response to increasing depths to groundwater differ among water-use functional  
126 types?

127

## 128 **METHODS**

### 129 **Study site**

130 The study was conducted at a semi-arid Mediterranean coastal dune ecosystem at  
131 Biological Reserve of Doñana, southwest of Spain (Fig. S1a). The site has a typical thermo-  
132 Mediterranean climate, with total annual rainfall (September 2012–September 2013) of 566  
133 mm (weather station at BRD: 36°59'19"N; 6°26'35"W). During the hydrological year of  
134 2012-2013 the evapotranspiration was higher than precipitation; with a negative water  
135 balance of -197 mm. Top-soil moisture was reduced by 85% from spring to summer,  
136 reaching a mean value of  $0.017 \text{ cm}^3 \cdot \text{cm}^{-3}$  in the dry season.

137 Topography defines a spatial gradient of depth to groundwater which has been exacerbated  
138 due to human water extraction and rainfall reduction. The excessive pumping for human  
139 use led to groundwater table lowering in the site, which is threatening Doñana habitats (De  
140 Castro Ochoa & Muñoz-Reinoso, 1997; Muñoz-Reinoso, 2001; Muñoz-Reinoso & de  
141 Castro, 2005; Muñoz-Reinoso & García Novo, 2005; Serrano & Zunzunegui, 2008; Díaz-  
142 Paniagua & Aragonés, 2015).

143 The water table level (height relative to sea level) was measured every month with a  
144 portable probe in PVC piezometers (diameter 6 cm) installed in 7 sampling points (Serrano  
145 & Zunzunegui 2008). The belowground vertical distance from soil surface to water table  
146 (i.e. depth to groundwater), across the study area was estimated using a digital terrain  
147 model (DTM) and through a geo-statistical approach as in Antunes *et al.* (2018a). We  
148 observed a shallower groundwater table depth in winter months and a general summer  
149 lowering of the water table.

150 Nineteen sampling plots (20 m x 20 m), separated by at least 200 m, were distributed  
151 throughout the study area, which presented a spatial gradient of depths to groundwater (Fig.  
152 S1b). Our sampling plots end up distributed along a spatial gradient of depth to  
153 groundwater that ranged in summer (August), from 0.94 to 12.28 m.

154 As all sampling plots were in similar sandy soils and under the same meteorological  
155 drought pressure during the dry season, we can focus on specific responses of vegetation to  
156 water table depth and top-soil moisture variations.

157

## 158 **Plant species**

159 The sand mantle is mostly covered by a Mediterranean scrub with local patches of  
160 *Juniperus phoenicea* and *Quercus suber* woodlands, and the presence of *Pinus pinea*  
161 (Muñoz-Reinoso & García Novo, 2005). We focused our study on woody plant species. In  
162 each plot, we sampled two dominant scrub species and the dominant tree species (either  
163 one or two species). When possible, we sampled three individuals per species in each plot.  
164 Fifteen woody plant species, with distinct functional characteristics (Díaz Barradas *et al.*,  
165 1999), and a total of 191 plants were sampled (Table 1). In a previous study (Antunes *et al.*,

166 2018b) these species clustered in five water-use functional groups, with distinct summer  
 167 water-use patterns, exploring soil water from shallower to deeper soil layers. The species in  
 168 this study and their respective functional type classification are described in Table 1.

169

170 **Table 1.** Species names, number of individual plants sampled (n), functional type classification  
 171 (based on water used by plants in the dry season), their description, and water sources depth used by  
 172 each functional type during the dry season (mean  $\pm$  standard deviation and maximum estimated  
 173 depth; different letters stands for significant differences between functional types).

Species	n	Summer water-use functional type*	Description	Water sources used (dry season)*	Potential water-uptake depth (m) [mean $\pm$ SD (max)]
<i>Cistus libanotis</i>	6	NXs	narrow-leaved xerophytic shrubs	shallow	0.17 $\pm$ 0.15 <sup>a</sup> (0.7)
<i>Halimium calycinum</i>	11				
<i>Rosmarinus officinalis</i>	9				
<i>Corema album</i>	9				
<i>Cistus salvifolius</i>	6	Os	aphyllous/spike or semi-deciduous broad-leaf shrubs		0.6 $\pm$ 0.38 <sup>ab</sup> (1.4)
<i>Lavandula stoechas</i>	6				
<i>Stauracanthus genistoides</i>	3				
<i>Ulex australis</i>	3				
<i>Halimium halimifolium</i>	42	sMs	semi-deciduous mesophytic shrub		0.86 $\pm$ 1.2 <sup>ab</sup> (5.5)
<i>Erica scoparia</i>	33	eH	evergreen hygrophytic shrubs and trees		0.96 $\pm$ 1.25 <sup>b</sup> (6.12)
<i>Phillyrea angustifolia</i>	7				
<i>Salix atrocinerea</i>	3				
<i>Quercus suber</i>	5				
<i>Pinus pinea</i>	24	eXt	evergreen xerophytic trees	deep	1.9 $\pm$ 1.61 <sup>c</sup> (5.79)
<i>Juniperus phoenicea</i>	24				

\* based on Antunes *et al.*, 2018b

174

## 175 **Physiological parameters**

176 Ecophysiological traits measured included leaf C and N concentrations and isotope ratios  
 177 and spectral reflectance indices from plants sampled at the 19 sampling plots (Fig. S1). In



178 each sampling plot, all the following physiological measurements were carried out during  
179 the dry season, in late summer, 2-10 September 2013.

180

#### 181 *Leaf carbon and nitrogen isotope composition*

182 Mature leaves (2-10, depending on leaf size) were collected from each plant. The bulk leaf  
183 samples were dried at 60 °C for at least 48 h, and milled to fine powder in a ball mill  
184 (Retsch MM 2000, Germany) for isotopic analysis. Leaf  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  and C and N  
185 concentrations were determined by continuous flow isotope ratio mass spectrometry (CF-  
186 IRMS) on a Sercon Hydra 20-22 (Sercon, UK) stable isotope ratio mass spectrometer,  
187 coupled to a EuroEA (EuroVector, Italy) elemental analyser. Uncertainty of the isotope  
188 ratio analysis, calculated using values from 6 to 9 replicates of secondary isotopic reference  
189 material interspersed among samples in every batch analysis, was  $\leq 0.1\%$ .

190

#### 191 *Reflectance indices*

192 We used a nondestructive optical method, based on the reflectance of light by an intact leaf.  
193 Spectral reflectance was measured using a UniSpec Spectral Analysis System (PP Systems,  
194 Haverhill, Massachusetts, USA) and carried out in 6 different leaves per plant. The mean  
195 value of the 6 measurements per plant was considered. The following reflectance indexes  
196 were calculated:

197 Chlorophyll index (CHL) =  $R750/R705$ , where  $R750$  and  $R705$  are the reflectance at  
198 wavelengths of 750 nm and 705 nm (Peñuelas *et al.*, 1995). This index has been found to  
199 be well correlated with leaf chlorophyll content on a number of plant species, and can

200 provide information about photosynthetic potential, primary production and nutrient status  
201 (Richardson *et al.*, 2002).

202 Photochemical Index (PRI) =  $(R531-R570) / (R531+R570)$ , where  $R531$  and  $R570$  are the  
203 reflectance at wavelengths of 531 nm and 570 nm (Peñuelas, Llusia, Pinol, & Filella,  
204 1997). There is an emerging consistency in the relationship between PRI and light use  
205 efficiency, which can be used as an index of photosynthetic activities (Wong & Gamon,  
206 2015).

207 Water Index (WI) =  $R900/R970$ , where  $R900$  and  $R970$  are the reflectance at wavelengths  
208 of 900 nm and 970 nm (Peñuelas *et al.*, 1997). This index is highly related to plant water  
209 content, so it can be used as a proxy for water status in the plant (Claudio *et al.*, 2006).

210 Normalized difference vegetation index (NDVI) =  $(R900-R680) / (R900+R680)$ , where  
211  $R900$  and  $R680$  are the reflectance at wavelengths of 900 nm and 680 nm, respectively  
212 (Gamon *et al.*, 1995). NDVI allows the assessment of biomass "greenness," and therefore  
213 of plant photosynthetic capacity (Mänd *et al.*, 2010).

214

### 215 **Estimation of potential water uptake depth**

216 To determine the isotopic composition of available water sources, samples were collected  
217 from two distinct water pools: shallow soils (region in the soil profile above 60 cm) and  
218 groundwater (deep water-source) (Dawson *et al.*, 2002; Berry *et al.*, 2017), on the same  
219 days of physiological sampling (summer, 2-10 September 2013). In each sampling plot, soil  
220 samples were collected at 3 depths: 10 cm, 30 cm, and 50 cm, with 3 replicates per depth.  
221 Groundwater samples were collected in piezometers (sampled after bailing to remove  
222 stored casing water) or wells reaching the water table (n=3) (Newman *et al.*, 2010). Since it  
223 did not rain in the two weeks prior to sampling, we did not consider rainwater as an

224 available water source for plants during the period of sampling. Lignified woody stems of  
225 each individual selected for physiological measurements were also collected at the same  
226 dates of soil sampling (2-10 September 2013). Soil and twig sampling, storage and water  
227 extraction by vacuum distillation followed the methodology detailed in Antunes *et al.*,  
228 2018b (Ehleringer & Dawson, 1992; West *et al.*, 2008a). Oxygen stable isotope ratio  
229 analysis of all water samples was performed by headspace equilibration, on an Isoprime  
230 (Micromass, UK) IRMS, coupled in continuous flow mode to a Multiflow (Micromass,  
231 UK) auto-sampler and sample equilibration system. Analytical uncertainty was <0.1%.

232 The relative contribution of different water sources to the composition of the xylem water  
233 was estimated by individual-based Bayesian stable isotope mixing models, using the  
234 graphical user interface and model framework MixSIAR for R (Parnell *et al.*, 2013; Stock  
235 & Semmens, 2013), as described in Antunes *et al.* (2018b) (and supporting information -  
236 Appendix 1).

237 After the quantification of water sources used by plants in the dry sampling period, we  
238 estimated the potential maximum water uptake depth of each individual plant. For that we  
239 used a weighted average of the contribution of the different soil layers to the xylem water  
240 (derived from MixSIAR), as follows:

$$241 \text{ Potential water-uptake depth (m)} = \frac{(SW_{10} * 0.10) + (SW_{30} * 0.30) + (SW_{50} * 0.50) + (GW * GW_{\text{depth}})}{100}$$

242 being  $SW_{10}$ ,  $SW_{30}$ ,  $SW_{50}$  and  $GW$  the % of contribution of the soil layers; 0.10, 0.30 and  
243 0.50 the soil layer depths in m, and 'GW depth' the summer depth to groundwater in m  
244 (minus the hypothetical capillary fringe of 0.5 m) (see Appendix 2 for further details). For  
245 GW depth values we used the information of August (monthly mean) map of water table  
246 depth, obtained as in Antunes *et al.* (2018a) (Fig. S1b).

247 **Environmental variables**

248 (i, ii) Spring and summer depths to groundwater (i.e. belowground vertical distance from  
249 soil surface to water table) were calculated per sampling plot using the maps of water table  
250 depth of April and August, respectively.

251 (iii) Annual mean depth to groundwater was obtained per sampling plot by calculating the  
252 mean of monthly water table depths from October 2012 to September 2013 (hydrological  
253 year).

254 (iv) Seasonal variation of depth to groundwater was calculated per sampling plot, as GW  
255 diff (m) = summer depth to GW – spring depth to GW, yielding an estimation of water  
256 table lowering from April to September.

257 (v, vi) Spring and summer top-soil water contents were obtained by measuring the soil  
258 water moisture ( $\text{cm}^3.\text{cm}^{-3}$ ) in April and September using a ML3 ThetaProbe Soil Moisture  
259 Sensor (Delta-T Devices). Soil moisture (~10 cm deep) was measured at three points per  
260 sampling plot and a mean value considered.

261 (vii) Seasonal variation in surface soil water content ( $\text{SWC}_{10}$ ) was calculated at each  
262 sampling point, as  $\text{SWC}_{10}$  diff (%) = summer  $\text{SWC}_{10}$  – spring  $\text{SWC}_{10}$ .

263 (viii) Distance to the sea was calculated as the linear distance (m) from the sampling point  
264 to the nearest shore line (in ArcGIS 10.4.1).

265

266 **Statistical analysis**

267 Multicollinearity among potential environmental explanatory variables was handled by  
268 dropping collinear covariates when correlated at Pearson  $|r| > 0.7$  (Dormann *et al.*, 2013)  
269 (Table S1). This selection resulted in a reduced set of five potential explanatory variables:  
270 Summer depth to groundwater ('GW depth'), Seasonal variation of depth to groundwater

271 ('GW diff'), Spring top-soil water content ('SWC<sub>sp10</sub>'), Summer top-soil water content  
272 ('SWC<sub>s10</sub>') and Distance to the sea ('Sea Distance').

273 A multivariate principal component analyses (PCA) was performed with the individual  
274 physiological traits measurements aiming to integrate the complete set of physiological  
275 traits measured in all woody species, and defined the patterns of physiological performance  
276 of the dominant vegetation (accounting with specific relative position within the  
277 community physiological axis). Then, Spearman correlations between the environmental  
278 variables and PCA (meaningful) axes were performed to examine the relationships between  
279 those variables and the vegetation physiological traits (Serrano *et al.*, 2015). All  
280 environmental variables that showed a significant correlation ( $p < 0.05$ ) were considered for  
281 further analysis.

282 We tested if the measured ecophysiological traits were different among water-use  
283 functional types (considering each physiological trait separately and the PCA axis factor  
284 scores), using an analysis of variance (ANOVA). Post-hoc pairwise comparisons were  
285 performed with Tukey's HSD.

286 In order to select the most meaningful environmental variables, and describe their influence  
287 on the functional responses of the vegetation, we performed a stepwise multiple regression  
288 model selection by Akaike Information Criterion (AIC) (backward elimination of  
289 variables), using (i) PC1 factor scores, (ii) WI (reflectance-based water index), and (iii)  
290 Potential water-uptake depth as response variables, separately. To identify the most  
291 important independent variable(s) in the regression models, we inferred the relative  
292 importance of regressors using the 'relaimpo' package of R (Grömping, 2006). The two most  
293 important environmental predictors were selected for further analysis.

294 To further characterize the relationship between the most important selected environmental  
295 predictors and the functional responses of (i) overall vegetation, and (ii) each plant  
296 functional type, we performed Generalized Additive Models (GAMs), using the function  
297 “gam” of the “mgcv” R package (Wood 2017). For both vegetation and plant functional  
298 types, the responses considered were (i) individual PC1 factor scores (extracted from the  
299 PCA performed with the physiological traits), (ii) WI (reflectance-based water index), and  
300 (iii) potential water-uptake depth. For regression models and GAMs, SWC<sub>S10</sub> was log-  
301 transformed.

302 All statistical analyses were performed in R version 3.4.3 (R Core Team, 2017).

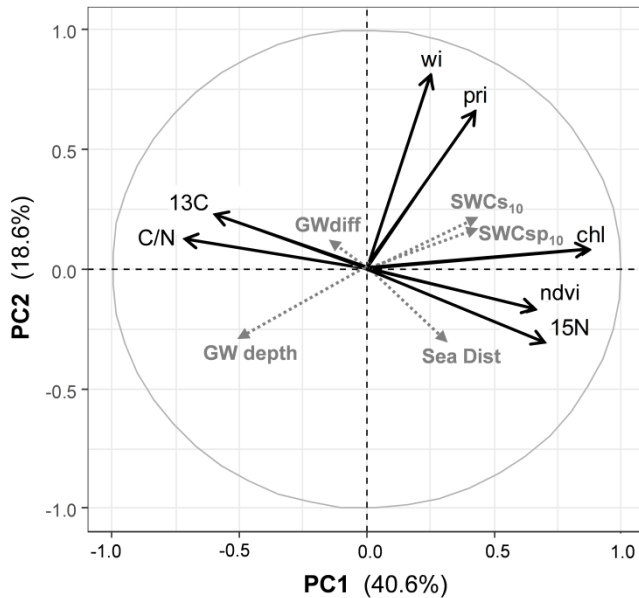
303

## 304 **RESULTS**

### 305 **Influence of environmental factors on ecophysiological patterns of woody vegetation**

306 Through a multivariate approach, we integrated the complete set of physiological traits  
307 measured in all woody species and defined the patterns of physiological performance of the  
308 dominant vegetation (accounting with physiological trade-offs and plants' relative position  
309 within the overall vegetation's physiological axis, Fig. 1 and Fig. S2). The first two axes of  
310 the principal component analysis (PCA), PC1 and PC2, accounted for 40.6% and 18.6% of  
311 the variance, respectively. PC1 reflected a gradient of physiological performance related  
312 with carbon and nitrogen acquisition, from low to high values of chlorophyll content index  
313 (CHL), normalized difference vegetation index (NDVI) and leaf  $\delta^{15}\text{N}$ ; and high to low  
314 values of  $\delta^{13}\text{C}$  and leaf C/N (Fig. 1; Table S2). While PC2 reproduced a plant water status  
315 gradient, from low to high values of plant water index (WI) and Photochemical Index (PRI)

316 (Fig. 1; Table S2). Since PC2 was mainly reflecting WI (Table S2), plus the WI was the  
 317 most significant physiological trait associated with depth to groundwater (Fig. S5) and a  
 318 previous study showed that WI could be an important response factor to water table depth  
 319 (Antunes *et al.*, 2018a), we used WI as a response variable in the subsequent analysis.  
 320



321

322 **Fig. 1** First and second axis of a principal component analysis (PCA) based on individual  
 323 physiological measurements (n=191). For physiological parameters considered see Methods  
 324 section. The first axis (PC1) explains 40.6% of the variance and reflects a gradient of  
 325 photosynthetic activity and nitrogen acquisition, while the second one (PC2) explains 18.6% and  
 326 reproduces a water status gradient. Abiotic (non autocorrelated) variables were included as  
 327 supplementary variables (grey dashed arrows). Abiotic supplementary variables considered:  
 328 depth to groundwater (GW depth), Distance to the sea (Sea Dist), Spring soil water content at 10 cm depth  
 329 (SWC<sub>sp10</sub>), Summer soil water content at 10 cm depth (SWC<sub>s10</sub>), Seasonal difference of GW depth  
 330 (i.e. seasonal water table lowering) (GWdiff).  
 331

332 Thus, using PC1 as a proxy of carbon and nitrogen acquisition (*C and N acquisition*)  
 333 related with photosynthetic capacity, and WI as a proxy of plant *water status*, we explored  
 334 the influence of the environmental variables on plants' physiology. Additionally, as  
 335 described in the methods, we also considered the potential water-uptake depth (WUD) as a

336 response variable. There was a significant correlation between the five candidate  
 337 environmental predictors and the C and N acquisition axis (PC1) (Table 2).

338

339 **Table 2.** Spearman correlations (rho coefficient) between the axes of the principal component  
 340 analysis performed with the physiological variables (PC1, 40.6% and PC2, 18.6%) and the  
 341 (selected) environmental variables: Summer depth to groundwater (GW depth), Seasonal variation  
 342 of depth to groundwater (GW diff), Spring top-soil water content (SWC<sub>sp10</sub>), Summer top-soil  
 343 water content (SWC<sub>s10</sub>) and Distance to the sea (Sea Distance). \*\*\* p<0.001; \*\* p<0.01; \*p<0.05.

	PC1		PC2	
GW depth	-0.51	***	-0.29	***
GW diff	-0.14	*	0.13	
SWC <sub>sp10</sub>	0.45	***	0.17	*
SWC <sub>s10</sub>	0.46	***	0.23	**
Sea Distance	0.34	***	-0.32	***

344

345 The multiple regression analysis showed that only spring top-soil water content (SWC<sub>sp10</sub>)  
 346 did not significantly influence PC1. 47.4% of PC1 deviance was explained by depth to  
 347 groundwater (GW depth), summer top-soil water content (log(SWC<sub>s10</sub>)), seasonal  
 348 difference of GW depth (GW diff) and distance to sea (Sea Dist) (Table 3). The variables  
 349 GW depth, log(SWC<sub>s10</sub>) and Sea Dist explained 39.3% of WI's variance, while GW diff  
 350 and spring SWC<sub>10</sub> were non-significant variables (and thereby excluded from the WI  
 351 model) (Table 3). WUD was mostly explained by groundwater related variables (Table 3).

352

353 **Table 3.** Results of Multiple Regression between ecophysiological response variables and the  
 354 predictors obtained by stepwise selection. Deviance explained (%) by each abiotic predictor,  
 355 deviance explained by the model, adjusted R<sup>2</sup>, F value and the model are represented in the table.  
 356 The ecophysiological response variables considered were the first axis of the PCA (PC1, as a proxy  
 357 of carbon and nitrogen acquisition), Water Index (WI, a proxy of plant water status) and Potential  
 358 water-uptake depth (WUD). Predictor variables not selected (p>0.05), and not included in the  
 359 model, are denoted as 'ns'. Predictors that explain more than 10% of the deviance are in bold, and  
 360 considered the most important variables in the regression model. \*\*\* p<0.001; \*\* p<0.01; \*p<0.05.



<b>Predictors</b>	<b>PC1</b>	<b>WI</b>	<b>WUD</b>
GW depth	<b>16.1%</b>	<b>27.8%</b>	<b>13.40%</b>
log(SWCs10)	<b>18.9%</b>	7.75%	<i>ns</i>
Sea Distance	9.11%	3.74%	5.58%
GW diff	3.32%	<i>ns</i>	9.01%
SWCsp10	<i>ns</i>	<i>ns</i>	3.70%
<i>Deviance explained</i>	47.4% <sup>a</sup>	39.3% <sup>b</sup>	31.7% <sup>c</sup>
<i>adjusted R<sup>2</sup></i>	0.463***	0.384***	0.301***
<i>F</i>	41.96	40.43	18.72

<sup>a</sup>  $PC1=3.74-0.21GW+1.30SWCs-1.74GWdiff+0.4e^{-4}SeaDist$

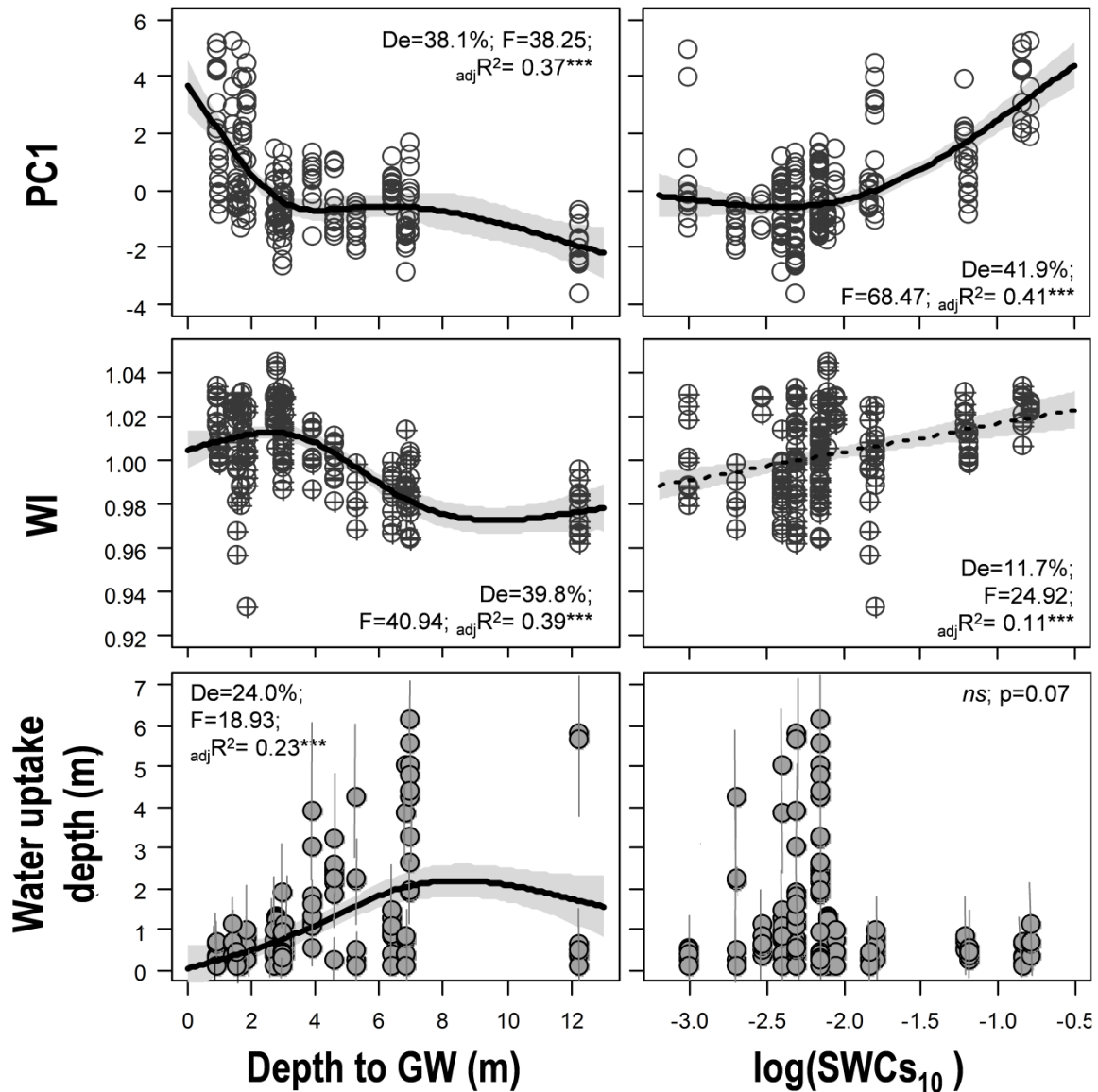
<sup>b</sup>  $WI=1.05-3.79e^{-3}GW+7.8e^{-3}SWCs-6.38e^{-6}SeaDist$

<sup>c</sup>  $WUD=2.46+0.16GW+4.28SWCsp-1.56GWdiff-4e^{-4}SeaDist$

361

362 Overall, the most important explanatory variables of ecophysiological variation were GW  
363 depth and summer SWC<sub>10</sub> (Table 3). Therefore, these were the predictors considered for  
364 further detailed relationships analysis. Both PC1 and WI were significantly, and non-  
365 linearly, affected by the selected predictors: negatively by GW depth and positively by  
366 summer SWC<sub>10</sub> (Fig. 2). WUD was weakly correlated with GW depth, and not  
367 significantly influenced by summer SWC<sub>10</sub> (Fig. 2). The significant non-linear relationship  
368 between both PC1 and WI and GW depth presented two inflection points: at ~3 m and ~7.5  
369 m groundwater depth (Fig. 2).

370



371

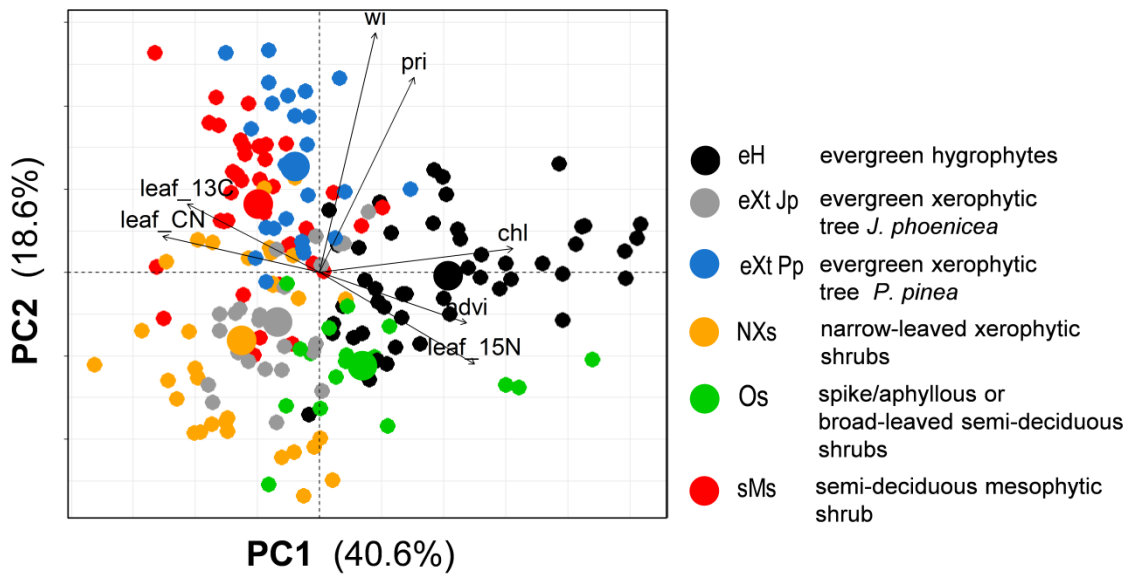
372 **Fig. 2** Relationships between the selected (most important) environmental variables [depth to  
 373 groundwater, ‘Depth to GW’, and soil water content in summer at 10 cm, ‘log(SWCs<sub>10</sub>)’] and plant  
 374 ecophysiological variables [the first axis of the PCA (PC1), Water Index (WI) and Potential water  
 375 uptake depth (Water uptake depth)]. *PC1* represents a proxy of C and N acquisition and *WI* the  
 376 plants’ water status. Solid and dashed lines represent the main trend of a Generalized Additive  
 377 Model (GAM) explaining more than 15 % of the variance and less than 15%, respectively. Grey  
 378 bands represent 95 % confidence intervals of a GAM. From left to right the effective degrees of  
 379 freedom for each GAM models are: k=2.96, k=1.97, k=2.97, k=1, k=2.66. Further statistical  
 380 information are shown in the figure: deviance explained (De), F- value (F), adjusted R<sup>2</sup> and p-value  
 381 (\*\*\* p<0.001; \*\* p<0.01; \*p<0.05’). Grey vertical bars in water-uptake depth panels represent the  
 382 standard deviation. n=191.

383

384 **Adjustments of plant functional types along a gradient of depths to groundwater and**  
385 **to top-soil water content**

386 We first tested if the vegetation physiological performance was different among water-use  
387 functional types (see Table 1). We found significant differences in physiology between the  
388 plant functional types ( $F=69.411$ ,  $p<0.001$ ; and  $F=22.104$ ,  $p<0.001$ , respectively) (Fig. S3,  
389 S4ac). We further realized that *J. phoenicea* and *P. pinea*, although considered to be from  
390 the same functional type, showed a different physiological pattern, especially on water  
391 status (Fig. S2, S3, S4bd). Thus, we subdivided this functional type, and considered these  
392 species separately in the following analysis. The six plant functional types clustered in the  
393 PCA, showing different summer physiological patterns (Fig. 3).

394



395 **Fig. 3** Principal component analysis (PCA) based on physiological measurements ( $n=191$ ), showing  
396 the individual scores and the water-use functional types. Functional types are represented by  
397 different colors as shown in the inner legend. The mean value of each functional type is represented  
398 by a bigger symbol. For functional classification based on summer water-use, and its effects on  
399 PC1, see Table 1 and Table S2. For physiological parameters considered see Methods section.

400

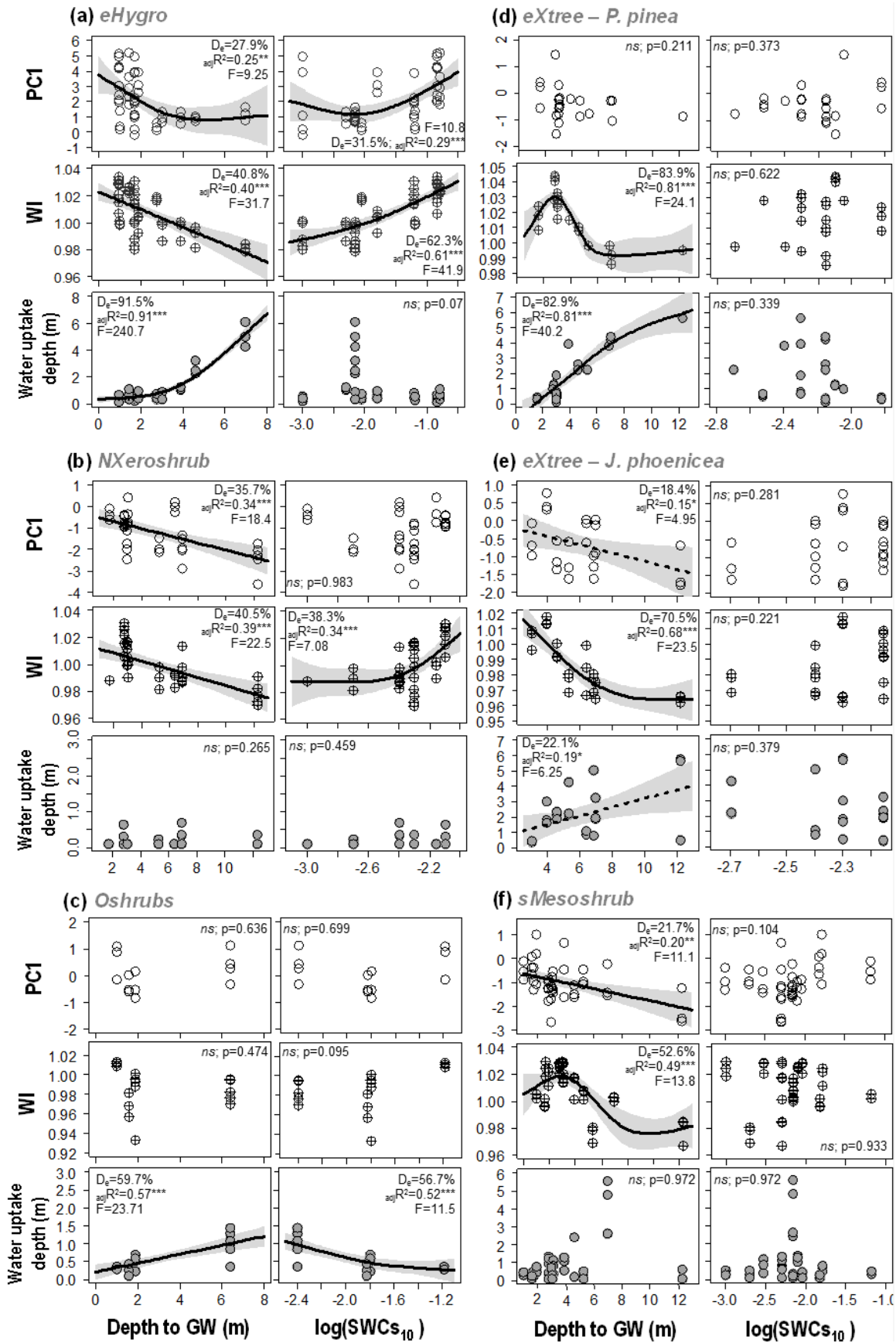
401

402

403 The evergreen hygrophytic species (that generally explore deeper soil layers and showed  
404 higher reliance on groundwater) showed the higher PC1 scores (i.e. higher photosynthetic  
405 capacity and both carbon and nitrogen acquisition), while narrow-leaved xerophytic shrubs  
406 (that rely on water from shallower soil layers) showed the lower PC1 values (Fig. 3). The  
407 evergreen conifer tree *P. pinea* (dimorphic rooted species that are able to explore deeper  
408 soil layers) showed the highest values of water status (PC2, WI), while xerophytic shrubs  
409 the lowest ones (Fig. 3, Fig. S3, Fig. S4d).

410 Secondly, we explored the responses to the identified most important environmental  
411 drivers, i.e. summer depth to groundwater (GW depth) and top-soil water content (SWC<sub>10</sub>),  
412 among the water-use functional types. For that, we used the PC1 factor scores of each  
413 functional type as a proxy of the variation of C and N acquisition within functional type  
414 (and considering their relative physiological position within the community). The  
415 significant positive correlation observed between C and N acquisition and SWC<sub>10</sub>  
416 considering the overall woody vegetation (Fig. 2, Fig. S5) did not hold up when  
417 considering different functional types (Fig. 4). Evergreen hygrophytic species was the only  
418 group that showed a significant positive trend (Fig. 4). Conversely, we found a significant  
419 decrease of C and N acquisition (PC1) with increasing depths to groundwater among  
420 several functional types (Fig. 4, Fig. S6). Nevertheless, the photosynthetic conditions of the  
421 xerophytic tree *P. pinea* were not affected by greater GW depth (Fig. 4d, Table S4).  
422 Although hygrophytic species also made water uptake adjustments towards deeper soil  
423 layers when groundwater was deeper, unlike *P. pinea*, their PC1 values declined (Fig. 4a,  
424 Table S4). This decline was not linear, showing an inflection at ~ 3m of depth to  
425 groundwater, after which the PC1 values don't change.

426



428 **Fig. 4** Relationships between the abiotic variables Depth to groundwater (Depth to GW) and Soil  
429 water content in summer at 10 cm [ $\log(\text{SWC}_{10})$ ] and plant ecophysiological variables [the first  
430 axis of the PCA (PC1), Water Index (WI) and Potential water uptake depth (m)], per water-use  
431 functional type. (a) eHygro (n=48), (b) NXeroshrub (n=35), (c), Oshrubs (n=18), (d) eXtree Pp  
432 (n=24), (e), eXtree Jp (n=24), (f) sMesoshrub(n=42); see Table 1 for details on plant functional  
433 types. Y-axis of the different functional types can present different scales. Solid and dashed lines  
434 represent the main trend of a Generalized Additive Model (GAM) explaining more than 10 % of the  
435 variance and less than 10%, respectively. Grey bands represent 95 % confidence intervals of a  
436 GAM. From left to right the effective degrees of freedom for each significant GAM models are: (a)  
437  $k=1.84$ ,  $k=1.88$ , null,  $k=1.67$ ,  $k=1.99$ , null; (b)  $k=1$ , null,  $k=1$ ,  $k=2.24$ , null, null; (c) null, null, null,  
438 null,  $k=1$ ,  $k=1.91$ ; (d) null, null,  $k=3.88$ ,  $k=2.08$ , null; (e)  $k=1$ , null,  $k=1.91$ , null,  $k=1$ , null; (f)  $k=1$ ,  
439 null,  $k=2.88$ , null, null, null. Further statistical information of GAM (deviance explained 'De', F-  
440 value, adjusted  $R^2$  and p-value) are shown in the figure.  
441

442 Shrubby species that did not adjust their water uptake depth towards deeper soil layers with  
443 increasing depths to groundwater, linearly declined their PC1 (Fig. 4 b,f).

444 We further confirmed the high variation in water-uptake depth responses and water-  
445 sources-use strategies among the different functional types (Fig. 4, Fig. S3). The relevant  
446 water-source-use adjustments observed in both evergreen xerophytic trees and hygrophytic  
447 species were driven by GW depth, but not  $\text{SWC}_{10}$  (Fig. 4a, d, e).

448 We found a significant decrease of WI with increasing depths to groundwater among all  
449 functional types (except for aphyllous species) (Fig. 4). Because this common trend was  
450 shared by plant functional types differing in water-sources-use, and no significant  
451 correlations were found between WI and water-uptake depth in five functional types (Table  
452 S3), WI changes seem to be independent of water sources used by plants. The only plant  
453 types that additionally changed their WI in function of  $\text{SWC}_{10}$ , were narrow-leaved  
454 xerophytic shrubs and hygrophytic species (Fig. 4 a, b).

455 A summary of how hydrological changes affected the woody vegetation and the different  
456 functional types (i.e. their ecophysiological responses to depth to groundwater) is shown in  
457 Table 4.

458 **Table 4.** Functional responses to increasing depths to groundwater of woody community (woody  
 459 species) and of the different functional types in the dry season. The plant functional types  
 460 considered were: narrow-leaved xerophytic shrubs (NXs), semi-deciduous mesophytic shrub (sMs),  
 461 evergreen hygrophytic shrubs and trees (eH), evergreen xerophytic tree *P. pinea* (eXt Pp) and  
 462 evergreen xerophytic tree *J. phoenicea* (eXt Jp). The functional type that included aphyllous/spike  
 463 species ('Os', see Table 1) was excluded from the table, since there was no significant correlations  
 464 in either PC1 or WI. The responses to depth to groundwater considered were: C and N acquisition  
 465 (using PC1, as a proxy of photosynthetic capacity and nitrogen acquisition), Water status (through  
 466 Water index) and Potential water uptake depth. Additional responses of plants considering top-soil  
 467 moisture (SWC<sub>10</sub>) are denoted with asterisks. Direction of the relationships between functional traits  
 468 and depth to groundwater are denoted as arrows: down if negative (↓), up if positive (↑); null  
 469 symbol if no significant correlation occurs (∅).

	<b>C and N acquisition</b>	<b>Water status</b>	<b>Water-uptake depth</b>	
<b>Woody species</b>	↓	↓	∅	*
<b>NXs</b>	↓	↓	∅	*
<b>sMs</b>	↓	↓	∅	
<b>eH</b>	↓	↓	↑	*
<b>eXt Jp</b>	↓	↓	↑	
<b>eXt Pp</b>	∅	↓	↑	

\* significant effect of SWC<sub>10</sub>

470

## 471 **Discussion**

472 Our results showed that increasing depth to groundwater does negatively affect the  
 473 ecophysiological performance of woody vegetation in the dry season. We found that,  
 474 regardless their distinct water-uptake depth responses, there was a convergence of  
 475 physiological responses among various plant functional types. This indicates that this  
 476 hydrological factor significantly, either direct or indirectly, influenced functional traits  
 477 related to both water status and photosynthetic capacity of woody plants, irrespective of  
 478 their water-sources-use strategy. We found non-linear relationships which imply the  
 479 existence of a groundwater table depth threshold from which there is a steep physiological

480 response in the vegetation. We also revealed that pre-determined functional groups did sort  
481 along a physiological trait axis. Accordingly, they showed distinct operating physiological  
482 ranges, but common physiological responses to increasing depth to groundwater. They  
483 consistently declined their water content and generally reduced carbon and nitrogen  
484 acquisition with falling water table (Table 4). These results strongly suggest that  
485 groundwater drawdown have an impact on physiological fundamental processes,  
486 constraining the physiology of woody vegetation in this semi-arid ecosystem.

### 487 **Woody vegetation physiological responses to increasing depth to groundwater**

488 Through a multivariate approach we integrated into one single dimension, traits related to  
489 photosynthetic activity and nitrogen assimilation and consequently obtained a proxy of the  
490 vegetation's carbon and nitrogen acquisition (Fig. 1). Considering this proxy and the  
491 reflectance water index (related to plant *water status*), we revealed that the woody  
492 vegetation's physiology was strongly affected by groundwater table depth during the dry  
493 season (Table 3). Under greater depth to groundwater and lower top-soil moisture, plants  
494 decreased their C and N acquisition, regulating water loss through stomata control  
495 (indicated by increasing  $\delta^{13}\text{C}$ ), while reducing chlorophyll content and NDVI (Fig. 2). Also  
496 linked to increasing depths to groundwater we found both an increase in leaf C/N and a  
497 decrease in  $\delta^{15}\text{N}$ , reflecting the varying nitrogen acquisition along the gradient of depth to  
498 groundwater. The impossibility of taking up nutrients can be caused by the low soil  
499 moisture, as soil water content below wilting point significantly constrains plant capacity to  
500 take up nutrients. This is strongly experienced by plants that depend on shallow water  
501 layers and where water table is deeper. Moreover, nutrient availability is known to change  
502 along soil moisture gradients, with a maximum in mesic soils and minimum in very dry



503 conditions (Saha *et al.*, 2009; Araya *et al.*, 2013). Thus, the fine-scale hydrological gradient  
504 present in our study area can be also linked to nitrogen conditions (Serrano *et al.*, 2003;  
505 Gallardo & Merino, 1993; Bedard-Haughn *et al.*, 2003), which plant  $\delta^{15}\text{N}$  could reflect  
506 (Handley *et al.*, 1999). As we observed an intraspecific variation in leaf  $\delta^{15}\text{N}$  linked to  
507 groundwater table depth (i.e. within species with the same nitrogen strategy) we suspect  
508 that soil water and nitrogen availability are the main causes of the  $\delta^{15}\text{N}$  changes (and not  
509 mycorrhizal associations (Hobbie & Högberg, 2012)). Thus, in addition to the intrinsic  
510 limitation of nutrient acquisition under low water availability, by low water and nitrogen  
511 uptake, the decline in soil nutrients availability can be additionally promoting the decline in  
512 nitrogen content and  $\delta^{15}\text{N}$  along the groundwater table depth gradient (Kulmatiski *et al.*,  
513 2017). Furthermore, we observed a strong link between the water status of the woody  
514 community and variations in depths to groundwater. This extends the patterns previously  
515 observed for some woody species (Antunes *et al.*, 2018a). Interestingly, we observed a non-  
516 linear physiological pattern along the groundwater table depth gradient. At the community  
517 level, from 0 to 3 m water table depths there is a steep decrease in C and N acquisition and  
518 at 3 m water table depth there is a sharp decrease in plant water content. In this threshold  
519 responses, trade-offs seem to occur: once the C and N acquisition decreases, the water  
520 status is maintained; while when photosynthetic activity is maintained (through probably  
521 maintenance of stomatal conductance) water status declines (through possibly both water  
522 loss and low water uptake, at places where groundwater is deeper than 3 m).

### 523 **Physiological adjustments to falling water table among plant functional types**

524 Exploring the ecophysiological differences among water-use functional types we have  
525 found that they separated according to different physiological status (Fig. 3). Their relative

526 position along the C and N acquisition and water status axes reflected the inter-specific  
527 variability of the woody community. These results are in accordance with the differential  
528 water-use strategies and distinct responses and adaptations to summer drought among  
529 coexisting semi-arid Mediterranean species (Filella & Peñuelas, 2003; Veneklaas & Poot,  
530 2003; Peñuelas *et al.*, 2011; Zunzunegui *et al.*, 2011; West *et al.*, 2012). Nevertheless, the  
531 individuals within each functional type varied in their ecophysiological performance,  
532 resulting in a considerable intra-specific variation. This variation within functional type was  
533 strongly associated with the depth of the water table (Fig. 4). Unlike top-soil water content,  
534 increasing depth to groundwater negatively affected all studied plant functional types.  
535 Particularly, the impact of falling water-table on water status was consistent throughout the  
536 different functional types studied. Thus, regardless their water-sources-use strategy and  
537 different leaf-level drought strategies, plants experienced a decline in their water content  
538 where groundwater is deeper and therefore less available to plants. This convergent result  
539 strongly suggest that there are a limited number of physiological responses to extremely  
540 low availability of groundwater and soil water in this woody community (Bucci *et al.*,  
541 2004).

542 There was also a generality of declines of the C and N acquisition, however particularly  
543 steep for those functional types that don't root more deeply. The groundwater table depth  
544 gradient produced clear root adjustments only in evergreen hygrophytic species and conifer  
545 tree *P. pinea*, an acclimation process especially relevant for species dependent in  
546 groundwater as a water source (Dawson & Pate, 1996; Zencich *et al.*, 2002; Naumburg *et*  
547 *al.*, 2005; Barbeta & Peñuelas 2017; Fan *et al.*, 2017). In comparison to shallow-rooted  
548 species, it seems that this strong water-source-use adjustment towards deeper soil layers  
549 compensates, although only partly, for water stress caused by decreasing groundwater

550 availability. In fact, this belowground changes are expected to buffer plants from drought  
551 stress (Nardini *et al.*, 2016; Johnson *et al.*, 2018). Accordingly, *P. pinea* showed no impact  
552 on photosynthetic activity along the groundwater gradient (in accordance with Antunes *et*  
553 *al.*, 2018a); and the hygrophytic species stops dropping their C and N acquisition, once an  
554 exponential rise in water uptake depth begins when groundwater was over 3 m deep.  
555 However, despite the evidence of use of deeper soil water across the range of water table  
556 depths, increasing depth to groundwater induced a significant decline in plant water content  
557 in these functional types. Thus, and similarly to other studies in dry areas (Horton *et al.*,  
558 2001; Zencich *et al.*, 2002; Gries *et al.*, 2003; Miller *et al.*, 2010), water uptake depth  
559 adjustments towards deeper soil layers allowed the woody vegetation to subsist during the  
560 dry summer but not to flourish. Comparatively, the similarly deep-rooted species *J.*  
561 *phoenicea*, showed a weaker response in water-uptake depth through the groundwater depth  
562 gradient. Apart from the possibility that the groundwater is not the main driver of  
563 adjustments in this species, this might be caused by physiological trade-offs resulting in  
564 more variable responses along the groundwater gradient. In fact, juniper species can show a  
565 high drought impact (West *et al.*, 2007, 2008b; Grossiord *et al.*, 2017; Johnson *et al.*,  
566 2018), but also great resistance (Zunzunegui *et al.*, 2011; Dickman *et al.*, 2015; Garcia-  
567 Forner *et al.*, 2016). Nevertheless, they did decline their water status likewise all other  
568 species.

569 Populations of the studied functional types might have survived across a wide range of  
570 depths to groundwater due to physiological and root trait plasticity. However, in a temporal  
571 perspective, as falling water-table continues (or became more pronounced) their  
572 ecophysiological conditions can reach limiting values, with great implications for the  
573 community. In general, the curves of response to groundwater depth are reflecting the

574 ecophysiological sensitivity of the vegetation. As such, higher correlation slopes between  
575 the hydrological driver and the response will imply a greater sensitivity and vulnerability,  
576 because small changes in the environment would represent bigger changes in the  
577 physiological condition (Esperón-Rodríguez & Barradas, 2015). In this perspective, woody  
578 vegetation of this semi-arid sandy ecosystem is expected to be more vulnerable to  
579 photosynthetic and nitrogen limitation until 3 m groundwater depth, and further vulnerable  
580 to water limitation at 3-8 m groundwater depth. Particularly, the narrow range of water  
581 table depths within which hygrophytes are in better physiological state suggests that future/  
582 further changes in the depth of water table could lead to very low levels of physiology and,  
583 ultimately, to transitions between vegetation states. Interestingly, this range is in agreement  
584 with Sommer and Froend's study (2014) thresholds of transition of hydrotypes (vegetation  
585 states): at 3 m groundwater depth they observed a transition from hygrophytic dominant  
586 community to a more meso-xerophytic one.

587 In conclusion, we found that, during the dry summer, depth to groundwater is highly  
588 important in physiological structuring woody community in a semi-arid sandy ecosystem.  
589 We have enlighten the impact of hydrological drought can have on plants' water-related  
590 fundamental processes in this semi-arid ecosystem. From all studied environmental factors,  
591 groundwater table depth was the most important driver of ecophysiological adjustments.  
592 Greater depths to groundwater affected all studied plant functional types, either on their  
593 photosynthetic related parameters, water status or water-uptake depth (or a combination of  
594 all). Under these hydrological changes, a general increase of ecophysiological vulnerability  
595 of woody vegetation occurs, which strengthens the generality of hydrological drought  
596 impact on these ecosystems, where water stress is the rule. Although differing in their  
597 physiological range and limitations, and in their water-sources-use strategy, our acute

598 physiological responses, especially in their water status, supports the existence of  
599 systematic physiological constraints at the community level. Thus, the different plant  
600 functional types appeared to have distinct operating ranges along common physiological  
601 response curves dictated by groundwater table depth. Their physiological responses, caused  
602 by differing long-term groundwater limitation, reveal that the water uptake depth  
603 adjustments are not enough to compensate the experienced water deficits. In a temporal  
604 perspective, it is expected that woody vegetation ecophysiology, and ultimately their  
605 survival will be greatly impacted by groundwater drawdown as water table drops more,  
606 depleted by prolonged drought and human consumption. We acknowledge that we do not  
607 know the ecophysiological limits of the studied species, but observations of high mortality  
608 of plants in the last years in this ecosystem (Zunzunegui *et al.*, 1998; Muñoz-Reinoso,  
609 2001; Muñoz-Reinoso & de Castro, 2005; Lloret & Granzow-de la Cerda, 2013; Lloret *et*  
610 *al.*, 2016) seem to support the undergoing vulnerability, and fitness loss of woody  
611 vegetation under groundwater limitation. Our study may contribute for predicting  
612 physiological performance changes and state of woody vegetation that results from ongoing  
613 increased groundwater drawdown. It has, therefore, evident implications for the  
614 conservation of plant communities that now face changing hydrological conditions caused  
615 by water extraction and climate change in this coastal ecosystem.

616

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849

850

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1080 **Supporting information**

1081 **Appendix 1** Bayesian stable isotope mixing models for quantification of water sources  
 1082 used by plants.

1083 **Appendix 2** Details on the estimation of potential water-uptake depth.

1084 **Figure S1** Study site and sampling points over summer groundwater table depth map.

1085 **Figure S2** PCA based on physiological measurements (n=191), showing species' individual  
 1086 scores.

1087 **Figure S3** Boxplots of physiological traits and water-uptake depth by functional types.

1088 **Figure S4** Boxplots of PCA factor scores of first and second dimension by functional type.

1089 **Figure S5.** Relationships between physiological traits and both groundwater depth and top-  
 1090 soil water content considering the overall woody vegetation.

1091 **Figure S6.** PCAs of physiological traits of each functional type and relationships between  
 1092 PCA axis and both groundwater depth and top-soil water content.

- 1093 **Table S1.** Pearson correlations between potential predictor variables.
- 1094 **Table S2.** Spearman correlations between the PCA axes (PC1 and PC2) and the leaf-level  
1095 physiological variables.
- 1096 **Table S3.** Spearman correlations between plant water-uptake depth, water index and PC1.
- 1097 **Table S4.** Spearman correlations between physiological traits measured and both  
1098 groundwater depth and top-soil water content, for the functional types: eH and eXt\_Pp.