

1 **Climatic events inducing die-off in Mediterranean**
2 **shrublands: Are species responses related to their**
3 **functional traits?**

4

5 Francisco Lloret^{1*}, Enrique G. de la Riva², Ignacio M. Pérez-Ramos³, Teodoro
6 Marañón³, Sandra Saura-Mas¹, Ricardo Díaz-Delgado⁴, Rafael Villar².

7

8 ¹ *CREAF i Unitat d'Ecologia, Dept. Biologia Animal, Biologia Vegetal i Ecologia,*
9 *Universitat Autònoma Barcelona, Edifici C, Campus UAB, 08193, Cerdanyola*
10 *del Vallès, Barcelona, Spain*

11 ² *Área de Ecología, Facultad de Ciencias, Universidad de Córdoba. 14071*
12 *Córdoba, Spain*

13 ³ *IRNAS, CSIC, Av. Reina Mercedes, 10. 41012 Sevilla, Spain*

14 ⁴ *EBD, CSIC. c/ Americo Vesputio, s/n, Isla de la Cartuja. 41092 Sevilla, Spain*

15

16 * corresponding author (francisco.lloret@uab.cat)

17

Post-print of: Lloret, F. et al., "Climatic events inducing die-off in Mediterranean shrublands : are species' responses related to their functional traits?" in *Oecologia* (Springer), vol.180, issue 4 (April 2016), p. 961-973. The final versión is available at DOI 10.1007/s00442-016-3550-4

18 **Abstract**

19 Extreme climatic episodes, likely those associated to climate change, often
20 result in profound alterations of ecosystems and, particularly, in drastic events
21 of vegetation die-off. Species attributes are expected to explain different
22 biological responses to these environmental alterations. Here we explored how
23 changes in plant cover and recruitment in response to an extreme climatic
24 episode of drought and low temperatures were related with a set of functional
25 traits (of leaves, roots and seeds) in Mediterranean shrubland species of SW
26 Spain. Remaining aerial green cover (RAGC) two years after the climatic event
27 was positively related with specific leaf area (SLA) and leaf proline content, and
28 negatively with leaf water potential and $\delta^{13}\text{C}$. Plant cover resilience – i. e. the
29 ability to attain pre-event values - was positively related to a syndrome of traits
30 characterized by a higher efficiency in water use and uptake. Higher SLA and
31 lower WUE characterized other species that were able to maintain green
32 biomass for a longer time period but they were less resilient at a medium term.
33 Seedling emergence was negatively associated with such syndrome, with
34 small-sized species being able to produce a large number of seedlings per
35 adult. Overall, recruitment was positively correlated with species die-off. This
36 study demonstrates the relationship between plant traits and strong
37 environmental pulses related to climatic change, providing a functional
38 interpretation of the recently reported episodes of climate-induced vegetation
39 die-off. Our findings also reveal the importance of selecting meaningful traits to
40 interpret post-event resilience processes, particularly when combined with
41 demographic attributes.

42

43 **Keywords:** climate change, drought, extreme climate episode, plant functional
44 traits, recruitment, resilience, seed mass, specific leaf area, root traits, water-
45 use strategies.

46

47 **Introduction**

48 Plant functional traits reflect the outcome of the interactions between plant
49 species and environment as a result of selection processes (Westoby et al.
50 2002; Reich et al. 2003). Accordingly, trait composition in coexisting species
51 would be the consequence of the biogeographical and ecological contexts (Díaz
52 and Cabido 1998; Ackerly 2004). Particularly, species responses to climate
53 change are expected to obey at some extent to the traits that they exhibit (e.g.
54 Esther et al., 2010; Lloret et al. 2103). Some attempts have been made at the
55 regional scale to relate functional traits either with species demographic rates
56 (Martínez-Vilalta et al. 2011) or with expected changes of the species' climatic
57 suitability (Thuillier et al. 2006; Lloret et al. 2013). But there is still scarce
58 information on the role of plant functional traits as drivers of population-level
59 responses to climatic extreme events.

60 There are evidences that climate change is involving an increase of
61 climatic variability (IPCC, 2013), although some uncertainties remain at small
62 spatial scales (Shih-Chieh and Auroop, 2011). This climatic variability implies a
63 higher frequency and intensity of extreme climate episodes - including heat
64 waves, cold snaps, droughts and floods - which can produce fast
65 transformations in the structure, composition and functioning of ecosystems
66 (Easterling et al. 2000). However, more detailed information on the relationships
67 between biotic processes and these climatic disturbances is needed to better

68 understand the impact of future climatic changes on vegetation dynamics
69 (Reyer et al. 2013). Specifically, drought events have been identified as
70 responsible in some measure for some recently reported episodes of vegetation
71 die-off worldwide (Allen et al., 2010; Martínez-Vilalta et al. 2012). Then,
72 changes in the functional characteristics of plant communities are likely to
73 occur, given the remarkable differences in species sensitivity to these climate-
74 driven disturbances (Lloret et al. 2012). Nevertheless, the different responses of
75 coexisting species to these climate extreme events and their relationships with
76 key functional traits remain poorly known (Koepke et al. 2010). These trait-
77 based studies might be particularly relevant for a better understanding of the
78 role of plant traits on community dynamics in a context of transformations of
79 ecosystems due to climate change (Chapin 2003; Suding et al. 2008).

80 The demographic responses to climatic extreme episodes are expected
81 to reflect the functional significance of traits in correspondence with such
82 environmental stresses. Particularly, conditions derived from extreme drought
83 conditions could be faced with mechanisms optimizing water acquisition, for
84 instance those involving more efficient root systems. In spite of its relevance to
85 understand plant strategies of resource use, root traits have been rarely
86 analysed within communities (but see Pérez-Ramos et al. 2012; Prieto et al.
87 2015), particularly in the context of natural pulses of water scarcity (McCormak
88 2012; Saura-Mas and Lloret 2013). Analogously, traits associated to the control
89 of water loss, such as water use efficiency (estimated indirectly by carbon
90 isotopic discrimination) or evaporative surface reduction might be more likely
91 present in those species better adapted to these drought conditions. Also, it has
92 been proposed that species prone to establish in stressful, dry environments

93 will probably develop a more conservative resource-use strategy characterized
94 by low values of specific leaf area (SLA), high-density tissues, low leaf-N
95 concentration and long leaf-life span (Reich et al. 1998; Díaz et al. 2004; Villar
96 et al. 2006). Finally, regenerative traits related to plant establishment, such as
97 seed mass (Westoby et al. 2001), may help to understand population recovery
98 after climatic extreme episodes. Then, species resilience, which measures the
99 capacity of populations to recover their pre-event state, can estimate the
100 delayed response to extreme drought events (Lloret et al. 2011).

101 In this study we use a demographic, trait-based approach to explore how
102 coexisting woody plant species respond to a climatic extreme event, and to
103 evaluate whether these species-specific responses are related to particular
104 plant functional traits. The study system is a Mediterranean shrubland located in
105 South Spain that suffered a strong die-off as a consequence of an anomalous
106 period of low precipitation and severe cold winter (Díaz-Delgado 2006). We
107 monitored remaining green aboveground cover, adult survival and new
108 recruitment of the main species of the community, two and eight years after the
109 climatic episode. We measured traits related to light and carbon acquisition
110 (plant height, SLA, leaf chlorophyll), water acquisition and use (leaf and root dry
111 matter content, tissue mass root density, leaf water potential, carbon isotopic
112 discrimination), nutrient acquisition and use (nitrogen leaf concentration) and
113 recruitment (seed mass). Specifically, we addressed the following questions: Do
114 plant functional traits of coexisting species explain: (i) differences among
115 species die-off resulting from the climatic extreme episode? (ii) the different
116 species resilience, in terms of plant cover, eight years after the climatic

117 episode? and (iii) differences in recruitment of seedlings and juveniles among
118 species after the climatic episode?

119

120

121 **Methods**

122 Study site and die-off episode

123 The study was carried on in the Doñana National Park (south-western Spain,
124 38°13' N, 48°10' W), at approximately 3 km far from the Atlantic Ocean, over a
125 large Quaternary eolic dune field that became stabilized during the Holocene.

126 The vegetation is a mosaic of wetlands, annual grasslands, shrublands and
127 woodlands dominated by *Juniperus phoenicea* L. subsp. *turbinata* (Guss.)

128 Nyman (*Juniperus phoenicea* hereafter) and *Pinus pinea* L. The study was

129 performed in shrublands (locally named 'monte blanco'), which are considered

130 to be a serial stage of *J. phoenicea* woodlands (García Murillo and Sousa

131 Martín, 1999). The studied sites of 'monte blanco' shrublands are dominated by

132 medium-sized (1-3 m high) shrubs such as *Halimium halimifolium* (L.) Willk and

133 *Rosmarinus officinalis* L.. Other common shrubs are the tall (2-4 m high) shrub

134 *Erica scoparia* L., the medium-sized shrubs *Halimium commutatum* Pau, *Cistus*

135 *libanotis* L., *Stauracanthus genistoides* (Brot.) Samp. and *Ulex australis*

136 Clemente, and the small-sized shrubs (0.5-1 m high) *Lavandula stoechas* L.,

137 *Thymus mastichina* L., and *Helichrysum pichardii* Boiss. & Reuter.

138 The climate is sub-humid Mediterranean with oceanic influence. Mean

139 annual rainfall is 560 mm, with considerable between-year variability, ranging

140 from less than 300 mm to almost 1000 mm. Mean annual temperature is 16.5

141 °C, with mean monthly values ranging from 10.0 °C in January to 24.7 °C in

142 July. An episode of extreme drought occurred in the hydrological year 2004-
143 2005 (October 2004 to September 2005), when total rainfall was only 173 mm,
144 being the second driest recorded year since 1859. Winter rainfall was 58.9 mm,
145 less than one third of the historical average, while mean minimum temperatures
146 in January and February 2005 were respectively 1.1°C and 0.9°C, substantially
147 lower than the average values (5.0°C for January and 6.1°C for February). This
148 episode resulted in a general die-off of the shrubland populations (Díaz-
149 Delgado 2006, Appendix 1, 2, Electronic Supplemental Material). Annual rainfall
150 recovered in the years following the episode, ranging from 468.3 mm in the
151 2005-2006 hydrological year to 784.2 mm in 2009-2010 (Fig. 1).

152

153 Estimations of resilience and remaining green aerial biomass

154 Eighteen 25-m² (5 x 5 m) plots were established in November 2007, 2 years
155 after the drought episode, covering the range of die-off, from 14% to 88% of
156 green plant cover. NDVI from Landsat imagery (30 x 30 m² pixels, n = 21)
157 obtained for the site of the sampled plots did not show significant differences on
158 NDVI between November 2007 (sampling data) and 2005 (data of the end of
159 the climatic episode). These images showed a significant NDVI diminution in
160 2005 when comparing to previous years, as well as canopy recovery after 2007
161 (see Appendix 3, Electronic Supplemental Material). These data support the
162 adequacy of sampling in November 2007 to assess the effect of the climatic
163 event.

164 The plots were distributed across an area of approximately 10 km²,
165 separated by at least 50 m from each other. In November 2007 and July 2013
166 we carried out two plant surveys recording the number of adults (including alive

167 and dead plants), juveniles (plants established at least one year ago, but
168 without achieving the reproductive stage) and seedlings (less than one year old)
169 of all woody species present in each of the 18 plots. Species plant cover
170 (expressed as percentage) was estimated from contacts with branches
171 (excluding leaves and recent shoots) at 0.5 m intervals along ten 5 m long
172 transects, regularly distributed within the plot. Contacts were divided in two
173 categories corresponding to living (branches supporting leaves or green shoots)
174 or dead canopy (branches corresponding to recently defoliated organs,
175 recognized because they bore remaining thin tips of branches and there were
176 un-decomposed leaves on the ground beneath the contact). Dry organs with
177 signs of old decay (stumps, decomposed stems, branches without thin tips)
178 were excluded. By this sampling we could calculate an estimator of plant cover
179 suitable to compare canopy state before and after the climatic episode. Thus,
180 canopy prior to the episode was considered as the sum of living and dry plant
181 canopy in 2007. The increase of green canopy by growth of new shoots and
182 leaves between 2005 and 2007 should be considered as irrelevant with our
183 sampling, which focused on branches. Also, NDVI measures did not support a
184 strong canopy recover between these dates.

185 We calculated the remaining aerial green cover (RAGC hereafter) as the
186 percentage of living canopy in transect contacts in the 2007 survey respective
187 to the total of contacts of each species, including both living and dead canopy.
188 Although our sampling in 2007 was not simultaneous to the climate extreme
189 event, we consider that our estimation is a representative measurement of the
190 impact of the climatic episode on vegetation cover. In fact, given that delayed
191 canopy decay is common after drought episodes and disturbances, our survey

192 allowed integrate this phenomenon without overestimating regrowth, as
193 explained above. Average RAGC values for each species were obtained
194 combining the data of the eighteen plots. We used this calculation instead of the
195 mean value of plant contacts in the eighteen plots to minimize the stochasticity
196 associated to the low abundance of certain species in some plots.

197 Species resilience to the die-off episode was estimated in 2013 from
198 plant contacts measurements. We used the relative resilience index (RR
199 hereafter) (Lloret et al. 2011), which estimates plant recovery to the state
200 previous of a given disturbance, weighting by the impact of such disturbance:

201

$$202 \text{ Relative Resilience} = (Post-Dist) / Pre$$

203

204 where *Pre*, *Dist* and *Post* indicate performance previous (*Pre*), immediately
205 following disturbance (*Dist*) and after disturbance (*Post*). In our case the
206 disturbance was the climate-induced die-off episode, and the respective values
207 corresponded to species plant cover (contacts) prior to the climatic episode
208 (*Pre*), just after the episode (2007, *Dist*) and eight years later (2013, *Post*).

209

210 Measurements of Plant Functional Traits

211 In late spring 2013, during the maximum peak of plant growth, healthy adults of
212 the most abundant species were randomly selected (outside the plots to avoid
213 disruptions) for measuring ten above-ground and four below-ground functional
214 traits related with morphology, physiology, reproduction and plant chemical
215 composition (Table 1). All trait measurements were carried out according with
216 the criteria defined by Pérez-Harguindeguy et al. (2013).

217 Plant height (Phg) measurements were made on ten individuals using a
218 metric tape. Leaf traits, in particular specific leaf area (SLA; leaf area per unit of
219 dry leaf mass), leaf dry matter content (LDMC; dry mass per unit of water-
220 saturated fresh mass), leaf thickness (Lthick), leaf nitrogen concentration (LN)
221 and leaf chlorophyll (LChl; concentration of chlorophyll per unit of leaf fresh
222 mass) were measured in six individuals per species (see details about leaf traits
223 measures in Appendix 4, Electronic Supplemental Material). Carbon isotopic
224 ratio ($\delta^{13}\text{C}$; ‰, precision of ca. 0.2‰), which is related with plant water use
225 efficiency (Farquhar et al. 1982), was obtained from a mixture of leaves
226 collected from six different individuals.

227 In addition we used two physiological traits, leaf water potential (Ψ) and
228 leaf proline content (Prol), which are considered as an estimation of drought
229 stress in plants, from the values measured by Zunzunegui et al. (2005) for most
230 species (except *H. picardii* and *T. mastichina*) in the same study area.

231 Roots were sampled at the individual level by excavating the first 20-30
232 cm of the soil layer nearby the plant basal stem for four individuals per species.
233 We selected this specific soil depth based on other studies in Doñana National
234 Park (Martínez et al. 1998) that demonstrated that the largest fraction (70%) of
235 fine roots appears in the first 25 cm of soil depth. These root samples were
236 used to measure below-ground traits of fine roots (< 2 mm in diameter) related
237 with water and nutrient uptake (McCormak 2012): specific root area (SRA, root
238 area per unit of dry root mass), root dry matter content (RDMC, root dry mass
239 per unit of root fresh mass), root diameter (Rdiam, mean diameter), and tissue
240 mass root density (TMDr, root mass per unit of root volume). These data were

241 obtained by analyzing the scanned root samples with WinRHIZO 2009 (Regent
242 Instruments Inc., Quebec, Canada) and further weighing the dry root mass.

243 Data of seed mass (S_{mass}) was provided by the Seed Bank in the
244 Córdoba Botanical Garden.

245

246 Statistical analyses

247 We performed linear and quadratic polynomial fits of RAGC and RR in relation
248 with the 14 plant functional traits of the eleven dominant species of the 'monte
249 blanco' shrubland (*H. halimifolium*, *H. commutatum*, *C. libanotis*, *S. genistoides*,
250 *U. australis*, *R. officinalis*, *L. stoechas*, *T. mastichina*, *E scoparia*, *H. pichardii*
251 and *J. phoenicea*). We applied logarithmic (for SLA, L_{thick}, Prol, Phg and
252 S_{mass}) or reciprocal transformation (for LN) when needed to attain normality
253 criteria.

254 Plant functional trait syndromes (patterns of the whole set of traits)
255 across species were assessed by a PCA considering the average values of
256 traits for the different species. Leaf water potential (Ψ) and Leaf proline content
257 (Prol) were not included in this analysis since the information was not available
258 for some species. Then, we also performed linear fits of species RAGC and RR
259 with the respective coordinates of the first PCA component.

260 We analysed the relationships between recruitment after the die-off
261 episode and functional traits by GLMs, in which the main factor was the total
262 number of seedlings recorded in 2007 or the total number of juveniles recorded
263 in 2013 per species. In the 2013 survey, the number of seedlings was scarce
264 due to seed bank depletion (del Cacho and Lloret 2012), and was not included
265 in these analyses. We performed a GLM separately for each selected trait and

266 for coordinates of the first PCA component describing trait syndromes as the
267 main explicative variable, and in each model we included species adult
268 abundance prior to the die-off episode (considering the sum of species
269 transects contacts from all plots) and species defoliation (estimated as the
270 difference of living and dry plant organs in transects contacts from all plots) as
271 covariates. We included these two covariates to control for the abundance of
272 species on the number of recruits and to assess the effect of the loss of canopy
273 cover on recruitment, respectively. We applied log-transformations to the
274 number of seedlings and juveniles, as well as to adult abundance (previous to
275 the die-off). We performed a step-wise selection procedure using the Akaike
276 information criterion (AIC) to select the best-fitted models.

277 All the analyses were performed using JMP 10.0 (SAS Institute Inc.).

278

279 **Results**

280 The climatic extreme event reduced more that 50% of aerial green cover in
281 three of the most common species (*R. officinalis*, *C. libanotis*, *H. commutatum*)
282 by 2007 (Fig. 2). Canopy of the most abundant species (*H. halimifolius*) was
283 reduced around 25%, while loss of green canopy in other large shrubs (*U.*
284 *australis*, *S. genistorides*, *E. scoparia* and *J. phoenicea*) ranged between 10
285 and 40%. Smaller shrubs, such as *L. stoechas*, *T. mastichina* and *H. picardii*
286 tended to be less affected, with canopy loss below 20%. In 2013, most species
287 still remained with reduced canopies compared to their state before the event,
288 ranging this value around 40-60% in *H. halimifolium*, *H. commutatum*, *R.*
289 *officinalis*, *L. stoechas*, *U. australis*, *H. picardii* and *E. scoparia*.

290 The first and second axes of the PCA ordination describing trait
291 syndromes in the studied species accounted for the 45.4 and 22.0 % of the
292 variability, respectively. The first axis was positively related to Lthick, $\delta^{13}\text{C}$,
293 Rdiam, Smass and negatively related to SLA, SRA, and TMDr (Fig. 3).

294 Remaining aerial green cover (RAGC) was linearly and positively related
295 with SLA ($r^2 = 0.47$, $P = 0.02$) and leaf proline content ($r^2 = 0.56$, $P = 0.02$), but
296 negatively with leaf water potential ($r^2 = 0.46$, $P = 0.04$) and $\delta^{13}\text{C}$ ($r^2 = 0.38$, $P =$
297 0.04) (Fig. 4). RAGC showed a significant linear negative relationship with
298 RDMC, after excluding *R. officinalis* ($r^2 = 0.58$, $P = 0.01$) (Fig. 4).

299 Relative resilience (RR) was linearly, positively related with $\delta^{13}\text{C}$ ($r^2 =$
300 0.43 , $P = 0.03$), Smass ($r^2 = 0.53$, $P = 0.01$), Rdiam ($r^2 = 0.39$, $P = 0.04$) and the
301 first PCA axis ($r^2 = 0.44$, $P = 0.03$), while it was negatively with TMDr ($r^2 = 0.38$,
302 $P = 0.04$) (Fig. 5). Quadratic polynomial fits did not improve linear ones in the
303 RAGC and RR analyses.

304 The number of seedlings in 2007 for each species was positively related
305 with SLA and LN and negatively with LDMC, Lthick, $\delta^{13}\text{C}$, Smass and the score
306 in the first PCA axis (Table 2). The number of seedlings was also positively
307 related to the species defoliation, except for the model analysing LN (Table 2).
308 Adult abundance prior die-off was not significantly related with the number of
309 seedlings and, therefore, it was removed from the models.

310 The number of juveniles in 2013 was negatively related to the first PCA
311 axis ($r^2 = 0.91$, $F = 28.32$, $P = 0.003$, estimate = -0.702). But we failed to find
312 significant relationships when analysing the functional traits separately, except
313 for LDMC, which also exhibited a negative relationship ($r^2 = 0.77$, $F = 11.4$, $P =$
314 0.01 , estimate = -20.8). The number of juveniles was again positively related

315 with species defoliation ($F = 17.0$, $P = 0.009$, estimate = 2.12 and $F = 9.43$, $P =$
316 0.022, estimate = 0.408, for the first PCA axis and the LDMC models,
317 respectively), while adult abundance prior die-off was not.

318

319 **Discussion**

320 *Plant functional traits as drivers of response to the extreme climatic episode*

321 Results from this study demonstrated that some key functional traits of plant
322 species are able to explain a relevant part of the between-species variability in
323 the response to climatic extreme events. Plant functional groups based on
324 certain key traits have been largely used to describe community patterns along
325 ecological and biogeographical gradients (e.g. Diaz and Cabido 1998; Thuillier
326 et al. 2006; Esther et al. 2010). Previous studies have analysed how key
327 functional traits strongly change across local environmental gradients (e.g.
328 Ackerley 2004; Pérez-Ramos et al. 2012; de la Riva et al. 2015; all of them
329 under Mediterranean conditions). Our results expand these approaches by
330 demonstrating that several key traits may also explain species responses to
331 sporadic pulses of strong environmental stress – in our case, extreme
332 conditions of drought and cold –, and might be thus act as drivers of a
333 succeeding resilience.

334 The observed loss of green canopy was consistent with damage caused
335 by the drought in the 2004-2005 hydrological year, but also with the extreme
336 cold occurring in the 2005 winter. Low temperature is a limiting factor in
337 Mediterranean Basin ecosystems (Mitrakos 1980; Larcher 1981), as evidenced
338 by field physiological measurements (Karavatas and Manetas 1999; Granda et
339 al. 2014) and experiments under controlled conditions (Logullo and Salleo

1993; Oliveira and Peñuelas 2004; Cavender-Bares et al. 2005). Symptoms of cold-induced impact include foliage damage (Oliveira and Peñuelas 2004), and the involved physiological mechanisms comprise xylem cavitation, loss of leaf stomatal conductance to water vapour and decline of photochemical efficiency of photosystem II (Granda et al. 2014). In fact, we are not able to disentangle the effects of the two climatic stressors (extreme drought and cold), indeed a synergistic effect between them is likely to have occurred (see other examples in Willson and Jackson 2006; Granda et al 2014).

348

The role of water-use traits.- In general, the studied woody plant species showed a predominant conservative resource-use strategy (Reich et al. 1998; Díaz et al. 2004; Villar et al. 2006), likely due to the homogeneous stressful Mediterranean environment (with a strong seasonal water deficit) where they inhabit. Within this functional context, we found that several plant traits correlating to die-off response and their resilience after disturbance were related to their water acquisition strategies. Species with higher rates of defoliation (low RAGC) exhibited lower SLA (which indicates a lower assimilation rate per unit mass; Reich et al. 1997), higher $\delta^{13}\text{C}$ (which is related with higher water use efficiency and stomatic control; Farquhar et al. 1982; Domínguez et al. 2012), and higher leaf water potential (Ψ). These results suggest that some dominant shrub species, such as *R. officinalis* and *C. libanotis*, in addition to stomatic control, massively shed their leaves to cope the extreme conditions of water deficit, probably as a mechanism for reducing the transpiring leaf surface and thereby the rate of water loss (Pérez-Ramos et al. 2013). The existence of this syndrome of semideciduous shrubs which drop their leaves and show very low

365 values of leaf water potential under high water deficit has been previously
366 described in this community (Zunzunegui et al. 2005) and concurs with
367 observations in Mediterranean species (Saura-Mas and Lloret 2007) and desert
368 shrub communities (Smith et al.1995). The positive relationship between leaf
369 proline content and green cover (RAGC) would illustrate the stress associated
370 to the strategy of retaining green leaves, which in fact was negatively correlated
371 with leaf water potential (Zunzunegui et al. 2005). These species with high
372 defoliation and $\delta^{13}\text{C}$ differs from those (*L. stoechas*, *T. mastichina* or *H.*
373 *halimifolium*) showing higher SLA and lower water use efficiency (WUE), which
374 were be able to maintain green biomass for a longer time period but were less
375 resilient at the medium term.

376

377 *The role of root traits.-* Our results also showed a relevant role of root traits in
378 species resistance to die-off. The sandy nature of the soil system facilitated the
379 interpretation of the root features due to an unusually homogeneous soil
380 environment. Accordingly, the most affected species by die-off (lower RGAC) in
381 our study site were those having higher RDMC. Thus, we found some
382 parallelism between root and above-ground traits for water-use; species with
383 both high values of SLA and low of RDMC would experience relative low
384 construction costs and would show a more exploitative resource-use strategy
385 (Villar and Merino 2001), presented a successful strategy to withstand extreme
386 climatic episodes. Also, species with higher resilience were those with wider
387 roots and lower root tissue density (TMDr), indicating a likely higher efficiency of
388 water uptake. Conversely, plants with high values of root tissue density are
389 commonly associated to a strategy characterized by a large investment in the

390 structural features of roots and a limited capacity to acquire water in the upper
391 soil layer (Wahl and Ryser 2000).

392

393 *The role of seed mass.*- Resilience of species after the climatic event was also
394 positively related to their seed mass, likely because this trait determined the
395 success of seedling establishment and new recruits that achieved enough size
396 to account for community plant cover eight years after the climatic episode.
397 These successful recruits corresponded mainly to species with relatively large
398 seeds (*C. libanotis* and *R. officinalis*, and to a lesser extent *H. commutatum* and
399 *H. halimifolium*), which were able to remain abundantly in the soil bank and to
400 produce new cohorts of seedlings after the canopy opening resulting from die-
401 off (del Cacho and Lloret 2012). However, other species such as *J. phoenicea*,
402 with large-sized seeds and high rates of seedling survival, produced small seed
403 banks and few recruits, relying its recovery on adult performance, at least at the
404 considered temporal scale (García et al. 2014). Conversely, species that
405 produced a large number of very small seeds (*H. picardii* and *E. scoparia*)
406 showed a low resilience after die-off.

407 Overall, the observed relationship between seed mass and resilience
408 agrees with the role of seed mass for enhancing seedling survival (Moles and
409 Westoby 2006), particularly under drought stressful conditions (Westoby et al.
410 2002). This relationship supports the hypothesis of trade-off between stress
411 tolerance and fecundity proposing that in more stressful conditions, species with
412 large seeds tend to be favoured thanks to their advantage during the
413 establishment stage (Muller-Landau 2010). In the Doñana shrublands, the
414 increase of light and soil resources associated to the process of gap opening in

415 the years after defoliation would produce a competition release that could
416 promote the successful recruitment of these particular species with larger
417 seeds, as supported by the positive effect of die-off on the number of seedlings.
418 Thus, species filling the soil bank with abundant, relatively large seeds would be
419 better suited to obtain advantage of this opportunity window, and thus
420 promoting community cover resilience.

421

422 *Recruitment strategies after an extreme climatic event*

423 Overall, the most affected plant species were those producing a higher number
424 of seedlings after the climatic episode, a feature observed in other
425 Mediterranean communities after natural disturbances such as fire (Lloret
426 1998). In fact, many of the species of this community exhibiting high recruitment
427 rates can be considered to show also a post-fire seeder strategy (Verdú and
428 Pausas 2007), indicating a possible convergence of responses following
429 different types of disturbances. The number of seedlings was negatively related
430 to seed size, as expected according to the classical trade-off between size and
431 number of seeds (Leishman 2001). However, seedlings from species producing
432 abundant, small seeds will eventually exhibit high mortality rates (Lloret et al.
433 1999), being other species with larger seeds such as *C. libanotis* and *R.*
434 *officinalis* the main contributors of the recovery of the community cover from
435 new recruits.

436 The species that showed a higher number of seedlings (after controlling
437 by the effect of canopy loss or die-off) were those having low-density, thinner
438 and N-rich leaves, lower stomata control (i.e. less $\delta^{13}\text{C}$). This syndrome is
439 commonly associated with an acquisitive resource-use strategy. This is the

440 case of the short-lived shrubs *L. stoechas*, *T. mastichina* and *H. picardii*. In spite
441 of their greater ability to establish as seedlings, these species showed a low
442 resilience and eventually they did not achieve dominance in the canopy,
443 probably as a result of their smaller size and their tendency to loss the canopy
444 cover even several years after the climatic event.

445 The significant relationship between recruitment and the main trend of
446 trait variation (first PCA axis) persisted for the juvenile stage. However, when
447 considering separately the different traits, it tended to disappear. Seedling
448 mortality in these Mediterranean environments is high during the first seasons
449 after emergence and it is subjected to a high stochasticity associated to
450 microhabitats (Lloret 1998). In fact, some species (such as *R. officinalis* and *C.*
451 *libanotis*) with intermediate scores in the first trait PCA axis were heavily
452 affected by die-off but reached to produce a large number of juveniles, which
453 will likely replace the damaged populations. This contrasts with species that
454 experienced similar cover losses but with less capacity to establish new
455 seedlings (*E. scoparia* and *U. australis*) or with high rates of seedling mortality
456 (*H. commutatum*). Other species (*S. genistoides* and *J. phoenicea*) were more
457 resistant thanks to moderate cover losses, in spite of producing few recruits.
458 The case of *H. halimifolium* seems different because they are relatively large
459 shrubs finding difficulties to restore the canopy after die-off while their quite
460 abundant number of seedlings experienced high mortality rates. These patterns
461 highlight the difficulties to scale-up broad species functional characterizations to
462 particular demographic processes.

463

464 *Limitations of the trait-based approach*

465 In spite of the contrasted patterns obtained in this study, we found that the
466 relationships between species functional traits and die-off responses were
467 limited to a relatively low number of functional attributes. There are several
468 reasons to interpret this limited ability of the species functional traits as
469 predictors of population-level processes. At the species level, within-species
470 variability of functional trait values may be equally important for interpreting
471 population responses to a particular environmental factor than species-
472 averaged values (Albert et al. 2011; Kichenin et al. 2013). Also, functional traits
473 often exhibit trade-offs between them due to functional, structural or
474 phylogenetic constraints (Reich et al. 2003; Cavender-Bares et al. 2009). Thus,
475 the effect of environmental drivers on a single attribute may be masked if traits
476 respond differently to co-occurring environmental factors. Finally, many
477 functional traits simultaneously obey to different environmental factors and they
478 may hardly show strong relationships with a single one – in our case, extreme
479 water deficit-. Overall, species may have similar traits but differ in others,
480 allowing diverse trait combinations that may promote species coexistence, for
481 instance under periods of low water availability (Pivovarovoff et al. 2014). In fact,
482 correlations between plant functional traits and environmental factors have
483 been mainly found across wide abiotic or successional gradients or at regional
484 scale (Díaz et al 2004; Wright et al. 2004). Noticeably, the studied community
485 exhibited a quite homogeneous pattern of functional diversity when considered
486 in the context of the plant communities of the area (de la Riva et al. 2015).

487

488 *Conclusions*

489 Our study provides a functional interpretation of the responses performed by
490 coexisting species to a climatic extreme episode causing vegetation die-off.
491 Current climatic tendencies of increasing climatic variability in some regions,
492 such as the Mediterranean basin, reinforce the relevance of studying the impact
493 of these climatic anomalies on community dynamics and ecosystem processes.
494 Although drought-induced die-off has caused great concern because of its large
495 impact on forests, it also affects other woody plant communities, such as
496 Mediterranean and semi-arid woodlands (Lloret and Granzow-de la Cerda
497 2013; Breshears et al. 2005), where it produces important changes on
498 ecosystem biodiversity and functioning (Royer et al. 2011). Similarly to other
499 drivers of global change, here we highlight the utility of using a trait-based
500 approach to assess ecosystem responses – changes in vegetation cover in this
501 case -. Nevertheless, the impact on ecosystem functioning would eventually
502 depend on the degree of coupling between traits sensitive to the environmental
503 change and traits with relevance on ecosystem functioning (Suding et al 2008).
504 Our study reveals the importance of selecting appropriate meaningful traits that
505 are as directly linked as possible with the specific environmental stressor. We
506 finally remark that functional traits can provide relevant insights to interpret post-
507 event resilience that can contribute to stabilize plant community after extreme
508 climatic events, particularly when combined with demographic attributes (Lloret
509 et al. 2012).

510

511 **Acknowledgements**

512 This study was supported by the projects CGL2009-08101, CGL2010-16373,
513 CGL2012-32965, DIVERBOS (CGL2011-30285-C02-01 and C02-02), AGAUR

514 2009-SGR-00247 and 2014-SGR-00453, ICTS-RBD 38/2007, 27/2009 and
515 11/2013, and by European FEDER funds. Personnel from the ICTS-RBD kindly
516 supported the fieldwork. We thank the help of C. Padilla, C. Navarro and M.
517 Olmo during field sampling and trait measurements. Data of seed mass was
518 kindly provided by Jardín Botánico de Córdoba (Francisca Herrera). Isotopic
519 analysis was carried out in the LIE of EBD, CSIC, and N of leaves in the SCAI
520 of University of Córdoba.

521

522

523

524

525 **References**

526

527 Ackerly DD (2004) Functional strategies of chaparral shrubs in relation to
528 seasonal water deficit and disturbance. *Ecol Monogr* 74:25–44

529 Aerts R (1995) The advantages of being evergreen. *Trends Ecol Evol* 10:402–
530 407

531 Albert CH, Grassein F, Schurr FM, et al. (2011) When and how should
532 intraspecific variability be considered in trait-based plant ecology? *Pers
533 Plant Ecol Evol Syst* 13: 217-235

534 Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell, N, Vennetier M,
535 Kitzberger T, Rigling A, Breshears D, Hogg EH, Gonzalez P, Fensham
536 R, Zhang Z, Castro J, Demidova N, Limm JH, Allard G, Running SW,
537 Semerci A, Cobb N (2010) A global overview of drought and heat-
538 induced tree mortality reveals emerging climate change risks for forests.
539 *For Ecol Manage* 259:660–684

540 Breshears DD, Cobb, NS, Rich PM et al. (2005) Regional vegetation die-off in
541 response to global-change-type drought. *Proc Nat Acad Sci USA* 102:
542 15144-15148

543 Cavender-Bares J, Cortes P, Rambal S, Joffre R, Miles B, Rocheteau A (2005)
544 Summer and winter sensitivity of leaves and xylem to minimum freezing
545 temperatures: a comparison of cooccurring Mediterranean oaks that
546 differ in leaf lifespan. *New Phytol* 168: 597-612

547 Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of
548 community ecology and phylogenetic biology. *Ecol Lett* 12: 693-715

549 Chapin FS III (2003) Effects of plant traits on ecosystem and regional
550 processes: a conceptual framework for predicting the consequences of
551 global change. *Ann Bot* 91:455-463

552 del Cacho M, Lloret F (2012) Resilience of Mediterranean shrubland to severe
553 drought episode: the role of seed bank and seedling establishment. *Plant*
554 *Biol* 14: 458–466

555 Diaz S, Cabido M, Casanoves F (1998) Plant functional traits and
556 environmental filters at a regional scale. *J. Veg Sci* 9:113-122

557 Diaz S, Hodgson JG, Thompson K (2014) The plant traits that drive
558 ecosystems: evidence from three continents. *J Veg Sci* 15: 295-304

559 Díaz-Delgado R (2006) Evento de mortalidad en la vegetación terrestre del
560 Parque Nacional de Doñana. Estación Biológica de Doñana, CSIC,
561 Sevilla

562 Domínguez MT, Aponte C, Pérez-Ramos IM, García LV, Villar R, Marañón T
563 (2012) Relationships between leaf morphological traits, nutrient
564 concentrations and isotopic signatures for Mediterranean woody plant
565 species and communities. *Plant Soil* 357:407-424

566 Easterling D, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO,
567 (2000) Climate extremes: Observations, modelling, and impacts. *Science*
568 289: 2068-2074

569 Esther A, Groeneveld J, Enright NJ, Miller BP, Lamont BB, Perry GLW, Blank
570 FB, Jeltsch F (2010) Sensitivity of plant functional types to climate
571 change: classification tree analysis of a simulation model. *J Veg Sci* 21:
572 447-461

573 Farquhar GD, Learyb MHO, Berry JA (1982) On the relationship between
574 Carbon isotope discrimination and the intercellular Carbon Dioxide
575 concentration in leaves. *Aust J Plant Physiol* 9:121–137

576 García Murillo P, Sousa Martín A (1999) El paisaje vegetal de la zona oeste del
577 Parque Natural de Doñana (Huelva). *Lagascalía* 21:11–132

578 Granda E, Scoffoni C, Rubio-Casal AE, Sack L, Valladares F (2014) Leaf and
579 stem physiological responses to summer and winter extremes of woody
580 species across temperate ecosystems. *Oikos* 123:1281-1290

581 García C, Moracho E, Díaz-Delgado R, Jordano P (2014) Long-term expansion
582 of juniper populations in managed landscapes: patterns in space and
583 time. *J Ecol* 102:1562–1571

584 IPCC (2013) Climate change 2013: The physical scientific basis. WMO, UNEP

585 Karavatas S, Manetas Y (1999) Seasonal patterns of photosystem II
586 photochemical efficiency in evergreen sclerophylls and drought semi-
587 deciduous shrubs under Mediterranean field conditions. *Photosynthetica*
588 36:41-49

589 Kichenin E, Wardle DA, Peltzer DA, Morse CW, Freschet GT (2013)
590 Contrasting effects of plant inter- and intraspecific variation on
591 community- level trait measures along and environmental gradient.
592 *Funct Ecol* 27:1254-1261

593 Koepke DF, Kolb TE, Adams HD (2010) Variation in woody plant mortality and
594 dieback from severe drought among soils, plant groups, and species
595 within a northern Arizona ecotone. *Oecologia* 163:1079-1090

596 Larcher W (1981) Low temperature effects on Mediterranean sclerophylls: an
597 unconventional viewpoint. In: Margaris NS, Mooney HA (eds)
598 Components of productivity of Mediterranean-climate regions – basic and
599 applied aspects. Dr W. Junk Publishers, The Hague, pp 259-266

600 Leishman MR (2001) Does the seed size/number trade-off model determine
601 plant community structure? An assessment of the model mechanisms
602 and their generality. *Oikos* 93: 294-302

603 Lloret F (1998) Fire, canopy cover and seedling dynamics in Mediterranean
604 shrubland of northeastern Spain. *J Veg Sci* 9:417-430

605 Lloret F, Casanovas C, Peñuelas J (1999) Seedling survival of Mediterranean
606 shrubland species in relation to root:shoot ratio, seed size and water and
607 nitrogen use. *Funct Ecol* 13:210-216

608 Lloret F, Keeling E, Sala A (2011) Components of tree resilience: effects of
609 successive low-growth episodes in old ponderosa pine forests. *Oikos*
610 120:1909-1920

611 Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F (2012)
612 Extreme climatic events and vegetation: the role of stabilizing
613 processes. *Glob Change Biol* 18: 797-805

- 614 Lloret F, Martínez-Vilalta J, Serra-Díaz J, Ninyerola M (2013) Relationship
615 between projected changes in climatic suitability and demographic and
616 functional traits of forest tree species in Spain. *Clim Change* 120: 449-
617 462
- 618 Lloret F, Granzow-de la Cerda I (2013) Plant competition and facilitation after
619 extreme drought episodes in Mediterranean shrubland: does damage to
620 vegetation cover trigger replacement by juniper woodland? *J. Veg Sci* 24:
621 1020-1032
- 622 Logullo MA, Salleo S (1993) Different vulnerabilities of *Quercus ilex* L. to
623 freeze - and summer drought - induced xylem embolism: an ecological
624 interpretation. *Plant Cell Environ* 16:511-519
- 625 Martínez F, Merino O, Martín A, García Martín D, Merino J (1998) Belowground
626 structure and production in a Mediterranean sand dune shrub community
627 *Plant Soil* 201:209-216
- 628 Martínez-Vilalta J, Mencuccini M, Vayreda J, Retana J (2010) Interspecific
629 variation in functional traits, not climatic differences among species
630 ranges, determines demographic rates across 44 temperate and
631 Mediterranean tree species. *J Ecol* 98:1462–1475
- 632 Martínez-Vilalta J, Breshears DD, Lloret F (2012) Drought-induced forest
633 decline: causes, scope and implications. *Biol Lett* 8:689-691
- 634 McCormack ML, Adams TS, Smithwick, EAH, Eissenstat, DM (2012) Predicting
635 fine root lifespan from plant functional traits in temperate trees. *New*
636 *Phytol* 195:823-831
- 637 Mitrakos K (1980) A theory for Mediterranean plant life. *Acta Oecol / Oecol*
638 *Plant* 1:245–252
- 639 Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life
640 cycle. *Oikos* 113:91-105
- 641 Muller-Landau HC (2010) The tolerance-fecundity trade-off and the
642 maintenance of diversity in seed size. *Proc Nat Acad Sci USA* 107:4242-
643 4247
- 644 Oliveira G, Peñuelas J (2004) Effects of winter cold stress on photosynthesis
645 and photochemical efficiency of PSII of the Mediterranean *Cistus albidus*
646 L. and *Quercus ilex* L. *Plant Ecol* 175:179-191

647 Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry
648 P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C,
649 Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas
650 JL, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG,
651 Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L,
652 Bonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S,
653 Cornelissen JHC (2013) New handbook for standardised measurement
654 of plant functional traits worldwide. *Aust J Bot*:167–234

655 Pérez-Ramos IM, Roumet C, Cruz P, Blanchard A, Aufran P, Garnier E (2012)
656 Evidence for a “plant community economics spectrum” driven by nutrient
657 and water limitations in a Mediterranean rangeland of southern France. *J*
658 *Ecol* 100:1315–1327

659 Pérez-Ramos IM, Volaire F, Fattet M, Blanchard A, Roumet C (2013) Tradeoffs
660 between functional strategies for resource-use and drought-survival in
661 Mediterranean rangeland species. *Environ Exp Bot* 87:126-136

662 Pivovarov AL, Sack L, Santiago LS (2014) Coordination of stem and leaf
663 hydraulic conductance in southern California shrubs: a test of the
664 hydraulic segmentation hypothesis. *New Phytol* 302:842-850

665 Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and
666 consequences of variation in leaf mass per area (LMA): a meta-analysis.
667 *New Phytol* 182:565–588

668 Prieto I, Roumet C, Cardinael R, Dupraz C, Jourdan C, Kim JH, Maeght JL,
669 Mao Z, Pierret A, Portillo N, Rouspard O, Thammahacksa C, Stokes A
670 (2015) Root functional parameters along a land-use gradient: evidence of
671 a community-level economics spectrum. *J Ecol* 103:361-373

672 Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman
673 WD (1998) Relationships of leaf dark respiration to leaf nitrogen, specific
674 leaf area and leaf life-span: a test across biomes and functional groups.
675 *Oecologia* 114:471–482

676 Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M,
677 Walters MB (2003) The evolution of plant functional variation: traits,
678 spectra and strategy. *Int J Plant Sci* 164 S3: S143-S164

679 Reyer CPO, Leuzinger S, Rammig A, Wolf A, Bartholomeus RP, Bonfante A,
680 De Lorenzi F, Dury M, Glonig P, Jaoudé RA, Klein T, Kuster TM, Martins

681 M, Niedrist G, Riccardi M, Wohlfahrt G, De Angelis P, de Dato G,
682 François L, Menzel A, Pereira M (2013) A plant's perspective of
683 extremes: Terrestrial plant responses to changing climatic variability.
684 *Glob. Change Biol.* 19: 75-89

685 Royer PD, Cobb NS, Clifford MJ, Huang, CY, Breshears DD, Adams HD,
686 Villegas JC (2011) Extreme climatic event-triggered overstorey
687 vegetation loss increases understorey solar input regionally: primary and
688 secondary ecological implications. *J Ecol* 99:714-723

689 Ruíz-Robledo J, Villar R (2005) Relative growth rate and biomass allocation in
690 ten woody species with different leaf longevity using phylogenetic
691 independent contrasts (PICs). *Plant Biol* 7:484–494

692 Saura-Mas S, Lloret F (2007) Leaf and shoot water content and leaf dry matter
693 content of Mediterranean woody species with different post-fire
694 regenerative strategies. *An Bot* 99:545-554

695 Saura-Mas S, Lloret F (2014) Adult root structure of Mediterranean shrubs:
696 relationship with post-fire regenerative syndrome. *Plant Biol* 16:147-154

697 Shih-Chieh K, Ganguly Auroop R (2011) Intensity, duration, and frequency of
698 precipitation extremes under 21st-century warming scenarios. *J Geo*
699 *Res-Atmosph* 112:D16119

700 Smith SD, Herr CA, Leary KL, Piorkowski JM (1995) Soil-plant water relations in
701 a Mojave Desert mixed shrub community: a comparison of three
702 geomorphic surface. *J Arid Environ* 29:339–351

703 Suding KN, Lavorel S, Chapin FS, Cornelissen JHS, Diaz S, Garnier E,
704 Goldberg D, Hooper D, Jackson S, Navas ML (2008) Scaling
705 environmental change through the community-level: a trait-based
706 response and- effect framework for plants. *Glob Change Biol* 14:1125–
707 1140

708 Thuillier W, Lavorel S, Sykes MT, Araujo MB (2006) Using niche-based
709 modelling to assess the impact of climate change on tree functional
710 diversity in Europe. *Div Dist* 12:49-60

711 Verdú M, Pausas JG (2007) Fire drives phylogenetic clustering in
712 Mediterranean Basin woody plants communities. *J Ecol* 95:1316-1323

713 Villar R, Ruiz-Robledo J, de Yong Y, Poorter H (2006) Differences in
714 construction costs and chemical composition between deciduous and

715 evergreen woody species are small as compared to differences among
716 families. *Plant Cell Environ* 29:1629–1643

717 Villar R, Merino JA (2001) Comparison of leaf construction costs in woody
718 species with differing leaf life-spans in contrasting ecosystems. *New*
719 *Phytol* 151:213-226

720 Wahl S, Ryser P (2000) Root tissue structure is linked to ecological strategies of
721 grasses. *New Phytol* 148:459-471

722 Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological
723 strategies: some leading dimensions of variation between species. *Ann*
724 *Rev Ecol Syst* 33:125–159

725 Willson CJ Jackson RB (2006) Xylem cavitation caused by drought and freezing
726 stress in four co-occurring *Juniperus* species. *Physiol Plant* 127:374-382

727 Wright IJ, Westoby M (2002) Leaves at low versus high rainfall: coordination of
728 structure, lifespan and physiology. *New Phytol* 155:403–416

729 Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-
730 Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E,
731 Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C,
732 Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H,
733 Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG,
734 Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum.
735 *Nature* 428:821–827

736 Zunzunegui M, Barradas MD, Ain-Lhout F, Clavijo A, Novo FG (2005). To live or
737 to survive in Doñana dunes: adaptive responses of woody species under
738 a Mediterranean climate. *Plant Soil* 273:77-89

739

740 **Figure Legends**

741

742 Figure 1. Mean annual temperature and total precipitation in Doñana NP. Right,
743 upper corner: box indicating medians, 25 and 75% percentiles and extreme
744 values for the period 1978-2013. Data correspond to hydrological years (from
745 September until August). Arrows indicate the die-off year (2004-05).
746

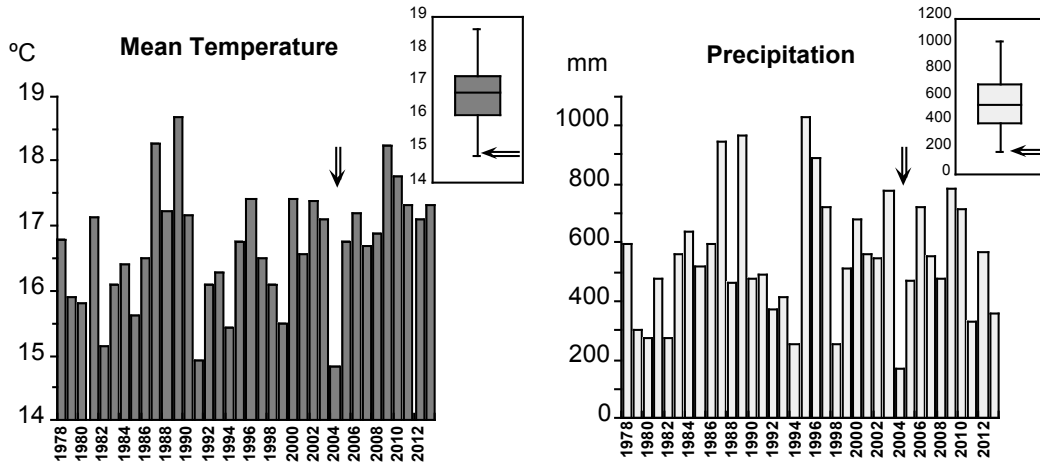
747 Figure 2. Species plant cover (%) estimated from transects contacts
748 intercepting plants of the plots sampled in 2007 and 2013. Values prior to the
749 event correspond to the sum of living and dead plants parts in 2007. Data
750 correspond to the pooled values of the eighteen surveyed plots.
751

752 Figure 3. Principal Component Analysis (PCA) biplot of functional traits
753 (abbreviations as in Table 1) and species (abbreviations, CL: *Cistus libanotis*,
754 HC: *Halimium commutatum*, HH: *Halimium halimifolium*, HP: *Helicrysum*
755 *picardii*, LS: *Lavandula stoechas*, RO: *Rosmarinus officinalis*, SG:
756 *Stauracanthus genistoides*, TM: *Thymus mastichina*, UA: *Ulex australis*, ES:
757 *Erica scoparia*, JP: *Juniperus phoenicea*).
758

759 Figure 4. Relationship between Remaining Aerial Green Cover (RAGC)
760 measured in 2007 and (a) Specific leaf area (SLA), (b) $\delta^{13}\text{C}$ (‰), (c) Leaf water
761 potential (Y) and (d) Root dry matter content (RDMC) of coexisting species in
762 Doñana NP shrubland affected by climatic-induced die-off in 2005. RDMC was
763 fitted to RAGC after excluding the outlier *Rosmarinus officinalis* (within a
764 square, see Results section).
765

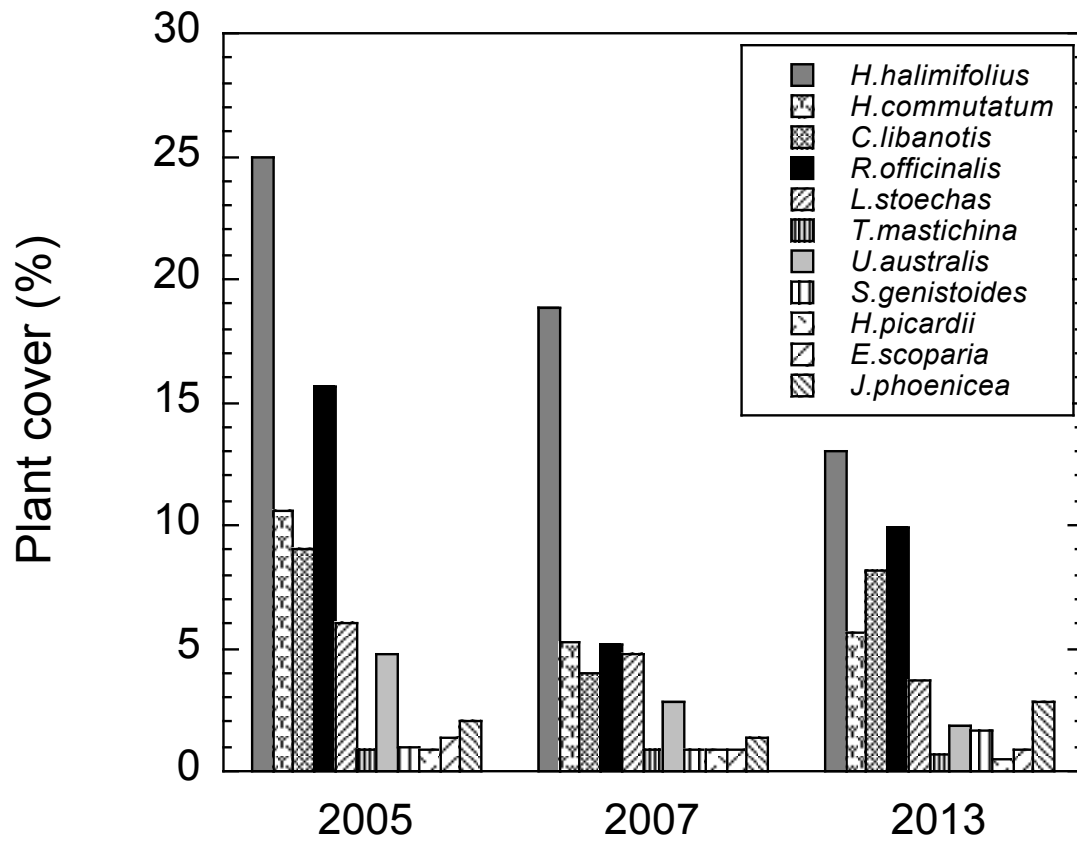
766 Figure 5. Relationship between Relative Resilience (RR) measured in 2013 and
767 (a) $\delta^{13}\text{C}$ (‰), (b) Seed mass (Smass), (c) Root diameter (Rdiam) and (d)
768 Tissue mass root density (TMDr) of coexisting species in Doñana NP shrubland
769 affected by climatic-induced die-off in 2005.
770

771
772
773
774
775



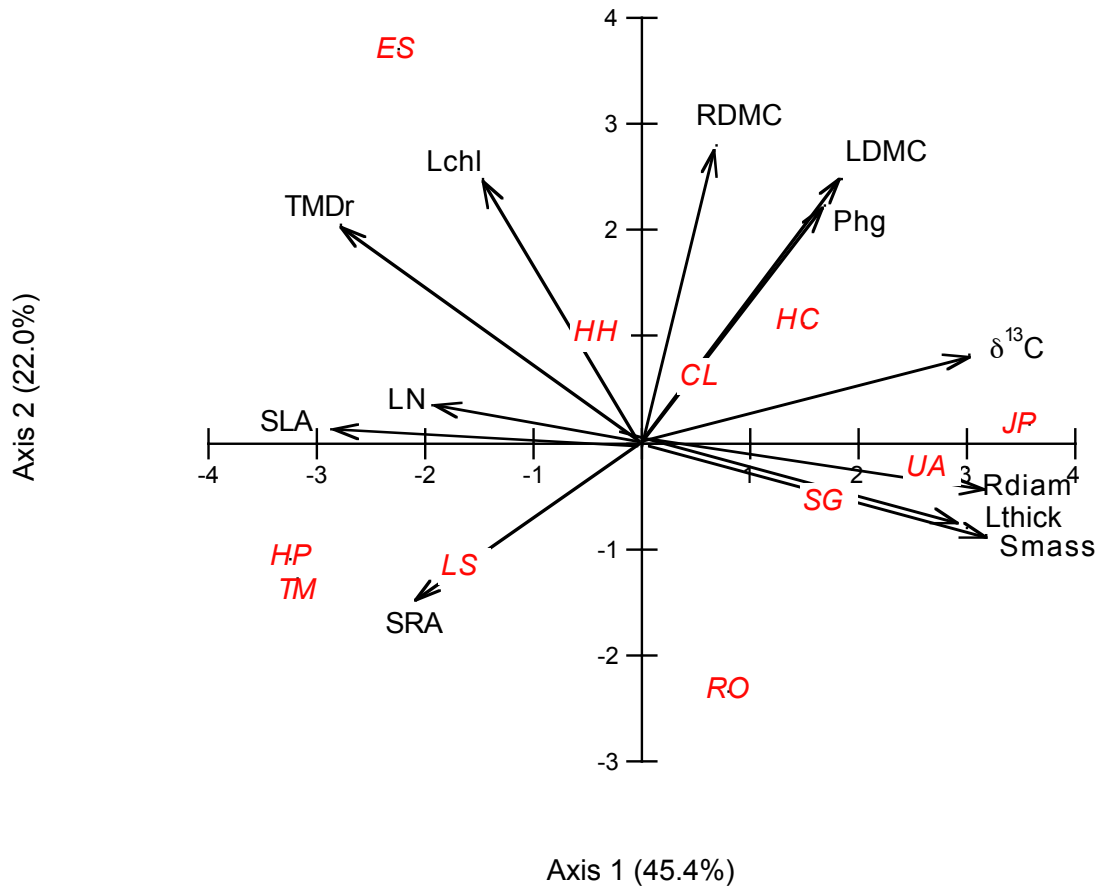
776
777
778
779
780
781
782

Figure 1



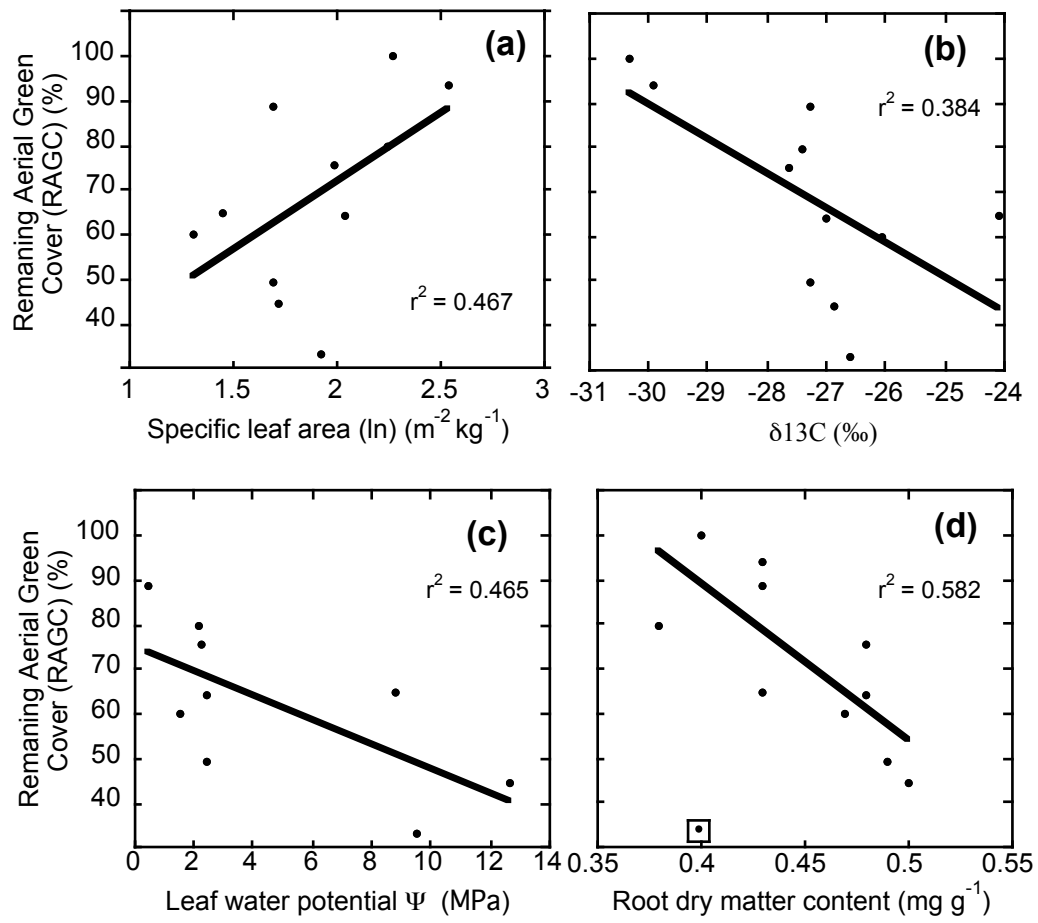
784
785
786
787

Figure 2



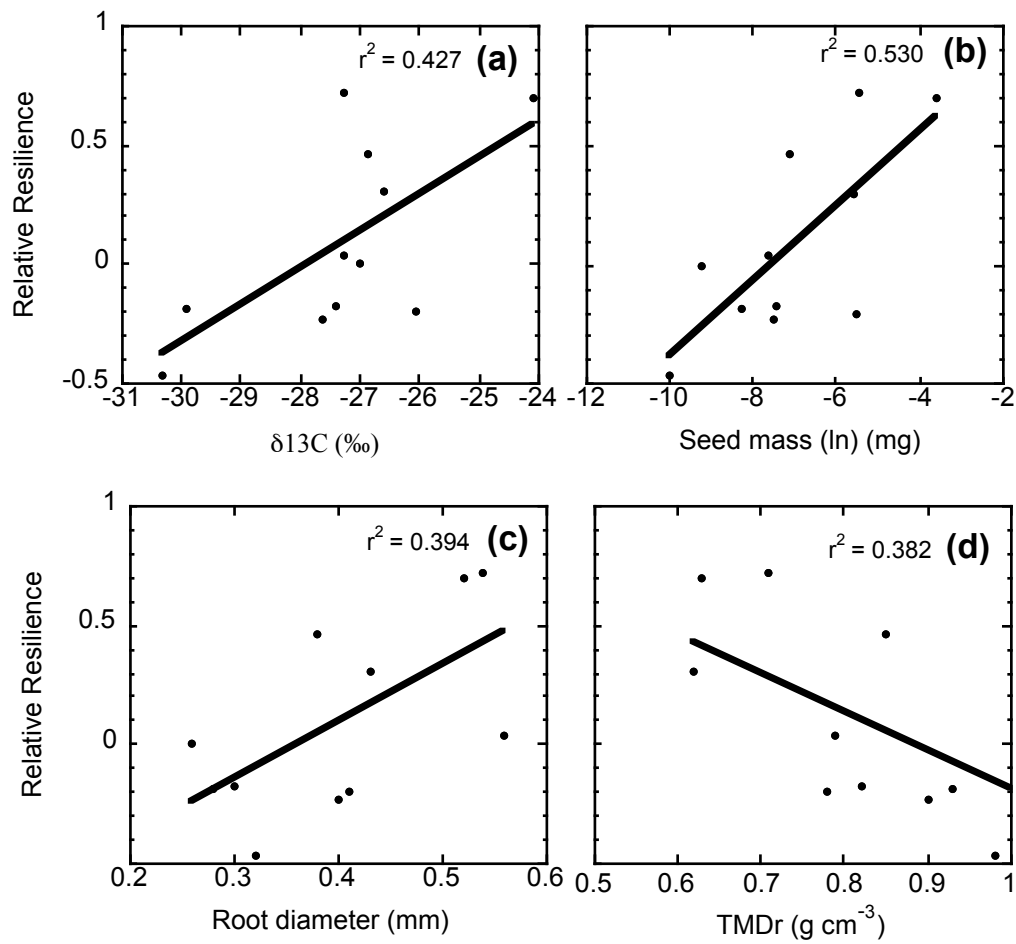
789
 790
 791
 792
 793

Figure 3.



795
796
797
798

Figure 4



799
800
801
802
803
804
805

Figure 5

806 **Table 1.** List of the functional traits considered in this study, their abbreviations,
 807 units and their main role in plant functioning.
 808
 809

Trait	Abbreviation	Unit	Functional role
Specific leaf area	SLA	m ² kg ⁻¹	Light and carbon acquisition and water use
Leaf dry matter content	LDMC	mg g ⁻¹	Carbon acquisition and water use
Leaf thickness	Lthick	mm	Light and carbon acquisition
Leaf nitrogen concentration	LN	%	Nutrient acquisition and use
Leaf chlorophyll	LChl	µg g ⁻¹	Light and carbon acquisition
Leaf proline content	Prol	µg g ⁻¹	Drought stress
Isotopic carbon fraction	δ ¹³ C	‰	Carbon acquisition and water use efficiency
Leaf water potential	Ψ	MPa	Water acquisition and use
Specific root area	SRA	m ² kg ⁻¹	Water and nutrient acquisition
Root diameter	Rdiam	mm	Water and nutrient acquisition
Tissue mass root density	TMDr	g cm ⁻¹	Water and nutrient acquisition
Root dry matter content	RDMC	mg g ⁻¹	Water and nutrient acquisition
Plant height	Phg	m	Light and carbon acquisition
Seed mass	Smass	mg	Recruitment

810
 811

812 **Table 2.** Results of GLMs describing the number of seedlings (log-transformed)
 813 recorded in 2007, two years after the die-off episode, in relation to different
 814 plant traits. Models included species defoliation, estimated from contacts
 815 transects (see Methods). Species die-off was not significant in the LN model
 816 and it was removed. Only traits exhibiting a significant relationship are shown.
 817

	Trait			Defoliation			Whole model
	estimate	F	p	estimate	F	p	r ²
SLA	5.60	6.03	0.049	1.12	10.67	0.017	0.638
LDMC	-28.63	10.43	0.018	0.50	6.53	0.043	0.735
Lthick	-2.74	19.93	0.004	0.62	15.18	0.08	0.832
δ ¹³ C	-0.82	11.16	0.016	0.74	12.87	0.012	0.746
LN	5.35	6.29	0.036	-	-	-	0.440
Smass	-0.86	21.32	0.004	0.46	9.09	0.024	0.841
First PCA axis	-0.66	35.38	0.001	0.69	29.29	0.002	0.895

818
 819
 820

Supplementary Material

[Click here to download Supplementary Material: Electronic Supplemental Material.pdf](#)