

RESEARCH ARTICLE

The main factors that drive plant dieback under extreme drought differ among Mediterranean shrubland plant biotypes

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Abstract

Questions: Knowledge of how extreme drought events induce plant dieback and, eventually, plant mortality, may improve our forecasting of ecosystem change according to future climate projections, especially in Mediterranean drylands. In them, shrublands are the main vegetation communities in transition areas from a subhumid to semi-arid climate. This study analyzed differences in plant dieback after an unusual drought in 2014 and identified their main underlying factors in relation to three groups of explanatory variables: water availability, soil properties and vegetation structure attributes.

Location: Four Mediterranean shrublands along a climatic gradient in SE Spain.

Methods: At each experimental field site, we sampled a pool of vegetation structure characteristics, soil depth and soil surface properties, and we also determined water availability by continuously monitoring soil moisture and the microclimate conditions.

Results: The climatic analysis showed that there was an extreme drought event in 2014, which was below the first percentile of the driest years. Under such conditions, vegetation dieback occurred at all the study sites. However, plant dieback differed between sites and plant biotypes. Subshrubs were the main affected biotype, with diebacks close to 60% at the driest sites, and up to 40% dieback for shrubs depending on their vertical development. Relative extractable water and bare soil surface cover were the best explanatory variables of plant community dieback but changed between plant biotypes. Vegetation structure variables related to plant vertical development (leaf area index [LAI], plant height, phytovolume) were significant explanatory variables of plant dieback in shrubs, subshrubs and grasses. Consecutive dry days fitted the best model to explain subshrub dieback.

Conclusions: We found that rainfall pattern rather than total annual rainfall was the climatic factor that best determined water availability for plants in Mediterranean drylands. These results also pointed out the relevance of plant structure and soil properties for explaining ecosystem responses to extreme drought.

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KEYWORDS

climate change, consecutive dry days, grass, rainfall pattern, shrub, soil surface properties, subshrub, vegetation structure, water availability

1 | INTRODUCTION

“Ecological drought” is defined as an episodic water availability deficit that drives ecosystems beyond tipping points of vulnerability and impacts ecosystem health (Crausbay et al., 2017; Trambly et al., 2020). Unusual intense or extensive climatic events, such as extreme drought, may exceed ecological tipping points and trigger critical shifts in ecosystems with impacts on ecosystem integrity and functioning, which hamper their resilience and ability to provide ecosystem services (Scheffer et al., 2001). However, extreme drought events rarely elicit extreme ecological responses (Smith, 2011a, 2011b; Zhang et al., 2019). Worldwide there are several pieces of evidence for ecosystem critical responses to drought, such as large vegetation die-off events (Donaldson, 1967; Faber-Langendoen & Tester, 1993; Van Mantgem et al., 2009; Lloret et al., 2015; Anderegg et al., 2016; Greenwood et al., 2017). Nevertheless, our mechanistic understanding of these phenomena is still scarce due to the marked complexity of ecosystem responses to drought, which leads to a lack of consistence between experimental and observational studies (Leuzinger et al., 2011; Knapp et al., 2017; Yuan et al., 2017). It is, therefore, necessary to better characterize and monitor the ecological responses triggered by natural extreme drought events to validate experimental findings, and to help to disentangle these complex ecological processes.

Water availability is the underlying driver of ecosystem responsiveness to drought, which has been widely associated with drought intensity (Dracup et al., 1980; Slette et al., 2019). However, the process is a complex one. Responses to real water availability are determined mainly by regional climate features, local geophysical aspects like soil properties, and particular ecosystem sensitivity to water resources, as determined basically by plant and soil biotic communities and the way they use water. Thus, rainfall patterns rather than the total amounts of annual rainfall have been able to determine water availability in water-limited ecosystems (Le Houerou et al., 1988; Knapp & Smith, 2001; Felton et al., 2020). The timing and intensity of rainfall events are key aspects of the rainfall that drive ecological responses in arid ecosystems by conditioning the pulsed dynamics of soil moisture (Collins et al., 2014). Soil moisture is the most direct water source for plants and soil microbes, and has been widely used as an indicator of water availability and drought intensity (Zargar et al., 2011). In this regard, soil properties and microtopography features may also largely determine soil water availability by driving the infiltration and retention of rainfall water in soils. Soil surface properties, such as stoniness or litterfall cover, are key features of controlling rainfall water passing into soil by enabling its infiltration with increasing soil surface roughness and porosity, but by also providing protection from evaporative loss (Tongway & Ludwig, 1997; Read et al., 2016). Soil depth, stoniness and rocky outcrops as a counterpart determine

total soil water storage capability, water exposure to evapotranspiration, and soil water losses by deep percolation and runoff (Seligman et al., 1992; Hopp & McDonnell, 2009; Mei et al., 2018).

Shrublands are one of the main plant communities in Mediterranean drylands. In these water-limited ecosystems dominated by shrubs and grasses, vegetation shows a patched spatial arrangement by determining a source–sink pattern that influences water and nutrient dynamics (Ludwig et al., 2005; Bautista et al., 2007; Vásquez-Méndez et al., 2010). Functional traits of dominant plant species also determine changes in community sensitivity to water availability, such as plants' ability to withstand extreme drought events (Vilagrosa et al., 2014; Rosas et al., 2019; Peguero-Pina et al., 2020). The rooting depth and leaf area index (LAI) of dominant plant species may be two relevant morphological functional traits to explain ecosystem responsiveness to drought because most processes at the ecosystem level (e.g. net primary productivity and nutrient cycling) rely on these dominant plant species (Felton & Smith, 2017; Smith et al., 2020). A diminishing “mass ratio effect” of dominant plant traits, and the likely increase in plant–plant interactions, may lead to even more complex ecosystem responses to drought (Felton & Smith, 2017). Indeed, non-linear responses to drought have been reported when plant species and functional richness increase in drylands (Gherardi & Sala, 2015; Rodríguez-Ramírez et al., 2017), and biodiversity can increase the complexity of the biotic aspect of water availability control in dryland ecosystems.

Climate change projections point out that a significant decrease in annual rainfall and a higher mean annual air temperature are expected in these Mediterranean zones (IPCC, 2021). By the end of the 21st century, the semiarid climate ($200\text{--}350\text{Lm}^{-2}\text{year}^{-1}$) is expected to shift to the north, replacing the dry–subhumid ($400\text{--}600\text{Lm}^{-2}\text{year}^{-1}$) with frequent years with annual rainfall below $200\text{Lm}^{-2}\text{year}^{-1}$ in these transition areas (Touhami et al., 2015; Moutahir, 2016). Such changes may increase the frequency and intensity of drought events, with impacts on soil water availability to plants (Dai, 2011; Trenberth et al., 2014; Sala et al., 2015), which would increase the desertification processes that already impact these ecosystems (Puigdefábregas & Mendizabal, 1998; Huang et al., 2016; Práválie, 2016). Therefore, Mediterranean drylands can serve as a model region to study climate change impacts, especially because of the close relations linking vegetation structure, water availability and ecosystem health (Lavorel et al., 1998; Trambly et al., 2020).

In this context, we analyzed the effect of an intense drought that occurred in the 2014 hydrological year on some Mediterranean areas of SE Spain. Annual rainfall was less than 50% of the long-term average, which caused notable tree mortality in several zones (García de la Serrana et al., 2015; Morcillo et al., 2022). Spread plant dieback and mortality were detected in four monitored Mediterranean shrublands. Our main objectives were to: (i) assess

vegetation dieback due to the 2014 drought and observe the differences between the main plant biotypes of these shrublands; (ii) identify the main factors from three groups of explanatory variables (water availability, soil properties, vegetation structure attributes) related to plant dieback in these Mediterranean shrublands.

2 | METHODS

2.1 | Study site

The present study was performed at four experimental field sites selected along a climatic gradient in the Alicante Province (SE Spain) from subhumid to semi-arid stands in three hydrological years: Predrought 2013 (Oct. 2012 to Sept. 2013), Drought 2014 (Oct. 2013 to Sep. 2014) and Postdrought 2015 (Oct. 2014 to Sep. 2015). From south to north, the experimental sites were “Serra de

les Àguiles” (SAG), “Serra del Ventós” (VEN), “El Cabeçó d’Or” (CAB) and “La Mela” (MEL) (Manrique-Alba et al., 2017) (Figure 1). The mean annual rainfall and the mean annual temperature are 300 mm and 17°C at the semi-arid end, and 650 mm and 14°C at the subhumid end, respectively (Table 1). At sites MEL and CAB, water deficit (Walter & Lieth, 1967) occurs in three months, from June to August. For sites SAG and VEN, water deficit occurs in five months, from May to September (Appendix S1). The studied vegetation type consists of shrublands with low–medium density plant patches composed of sclerophyllous shrubs and subshrubs mixed with grasses.

2.2 | Climate and drought characterization

We monitored the rainfall and environmental data during the study period (2012–2015) at each experimental field site, with a 0.2 mm resolution Rain Collector (II, Davis Instruments Corp., Hayward,

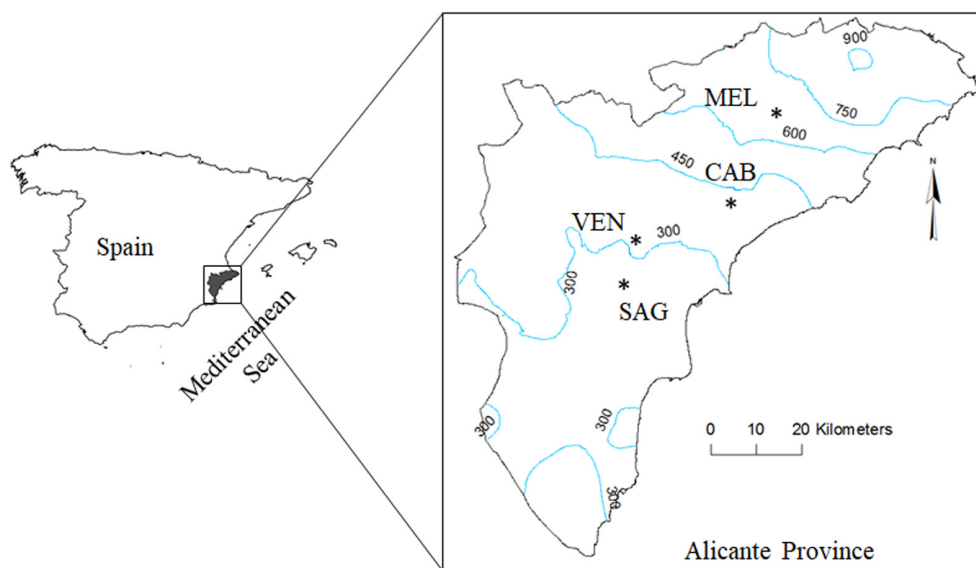


FIGURE 1 Location map of the studied sites in SE Spain. Blue lines denote isohyets every 100 mm. “Serra de les Àguiles” (SAG), “Serra del Ventós” (VEN), “El Cabeçó d’Or” (CAB) and “La Mela” (MEL).

TABLE 1 Geographical data, mean annual rainfall, mean annual temperature and climate classification according to Rivas-Martínez (1983) per studied site.

Geographical data	SAG	VEN	CAB	MEL
Latitude (N)	38°23′	38°28′	38°30′	38°42′
Longitude (W)	0°38′	0°36′	0°24′	0°16′
Elevation (ma.s.l.)	450	550	600	1050
Slope (%)	33.84 ± 2.44	30.50 ± 1.36	31.14 ± 1.73	28.94 ± 1.38
Aspect	NE	NO	NE	SE
Climate data				
Mean annual rainfall (mm)	299 ± 13.1	311 ± 14.2	397 ± 17.6	651 ± 31.0
Mean annual temperature (C°)	17.1 ± 0.09	17.5 ± 0.09	14.3 ± 0.1	12.4 ± 0.1
Climate classification	Semi-arid	Semi-arid	Dry	Subhumid

Abbreviations: CAB, El Cabeçó d’Or; MEL, La Mela; SAG, Serra de les Àguiles; VEN, Serra del Ventós.

CA, USA) connected to a datalogger (HOBO pendant event Onset Computer Corp., Inc., Southern MA, USA). The hourly air temperature (°C) was recorded with two sensors per site (HOBO datalogger U23 Pro v2, Onset Computer Corp.).

In order to compare the climate conditions during our study period to the long-term conditions, we used the long-term rainfall and temperature time series for the 1953–2012 period. They were obtained from the Spanish Meteorological Agency (AEMET) network (Moutahir et al., 2014). To compare the rainfall during the study period to the long-term values, we calculated the range of rainfall percentiles of the long-term rainfall per site (from monthly to annually accumulated) and estimated the percentile level for the 2014 (and seven previous years) hydrological year accumulated rainfall.

We also estimated the accumulated rainfall and three rainfall pattern attributes in 2014 as water availability variables. We defined a rainfall event as a day with rainfall higher than 3 L m^{-2} . Then following Knapp et al. (2015), we calculated the rainfall pattern attributes: (i) number of rainfall events (NRE); (ii) average rainfall events size (AES) as the average rainfall volume (L m^{-2}) of the rainfall events; and (iii) consecutive dry days (CDD) as the average number of days between rainfall events. Air temperature (°C) was corrected by the mean elevation (m.a.s.l.) of each study site and by applying a monthly lapse rate calculated for the whole region by Moutahir (2016). Finally, we also estimated the Standardized Precipitation–Evapotranspiration Index (SPEI) of the 2014 hydrological year (12-month SPEI) as an integrated indicator of water deficit, which includes rainfall and air temperature (Vicente-Serrano et al., 2010).

2.3 | Vegetation structure characterization

In order to determine the effect of the 2014 drought on the shrubland plant community, we measured plant cover, structure and composition early in spring 2015 at each study site. We followed the point intercept method with vertical stratification (Fayle, 1959) to measure plant cover and the overlap of different plant species. We extended three independent 35-m-long transects per site following the line of slope, and recorded the contacts of all the different plant species every 50 cm along each transect within 25-cm height intervals with a vertical graduated rod. We distinguished between contacts of alive and dead plants (i.e., contacts with a completely dead stem).

Species were classified and grouped per plant biotype (Raunkjær, 1934; Mateo & Crespo, 2009): shrubs (phanerophytes, higher than 0.5 m); subshrubs (hemicryptophytes and chamaephytes, shorter than 0.5 m, with lignified stems); grasses (herbaceous species with no ligneous tissues in the hemicryptophyte and chamaephyte groups) (Appendix S2). We estimated the total cover of both the plant community and each plant biotype by integrating the plant cover of all the species into each biotype, and separating dead and alive plant cover. Using the vertically-stratified data

information, we estimated the following vegetation structure attributes: plant height (maximum height of the vertical plant contact at each transect point); leaf area index (number of vertical layers with plant contacts at each transect point; Heslehurst, 1971); plant volume (the product of plant cover and height); size of plant patches and interpatches (plantless areas). We considered plant patch areas to have two consecutive plant contacts or more along the transect. Likewise, interpatch areas were those with two or more consecutive points without plant contacts. We used species-specific cover data to calculate plant species richness, and the diversity and dominance indices. We estimated diversity with the Shannon Diversity Index (Shannon & Weaver, 1964; Hill, 1973), and evenness of plant community composition with the Simpson Index (Simpson, 1949).

Finally, we assessed drought effects on vegetation cover by estimating plant dieback from dead plant contacts. This accumulation of dead material in plants is the consequence of the partial mortality that affects Mediterranean shrubs as an adaptation strategy when conditions are limiting (Bellot & Escarré, 1980). To do so, we estimated the plant dieback level as the volumetric dead fraction to total plant volume ratio expressed as a percentage.

2.4 | Soil properties and soil water content

In order to characterize soil properties, soil depths (cm) were measured at three points per transect by inserting a metal bar into soil. Soil surface cover types were recorded at all the sampled points of each transect by identifying if litter, bare soil, stoniness and rocky outcrops were present. For the soil texture characterization, porosity and soil field capacity, we randomly took nine mixed subsamples at a soil depth from 10 cm to 30 cm at each experimental site. Soil analyses were carried out in an external laboratory (Laboratoris Escuredo®, Reus, Spain) (Appendix S3).

At each experimental field site, we monitored soil water content (SWC) ($\text{cm}^3 \text{ cm}^{-3}$) from 0 to 20 cm of soil depth by periodic measuring following the time domain reflectometry method (TDR) by using 18 TDR (20 cm long) probes per shrubland community. We measured SWC from May 2013 to October 2015. We calculated relative extractable water (REW, Granier, 1987; Bréda et al., 1995) from the SWC data as (1):

$$\text{REW} = \frac{\theta_t - \theta_{\min}}{\theta_{\text{FC}} - \theta_{\min}} \quad (1)$$

where: θ_t is the actual SWC ($\text{m}^3 \text{ m}^{-3}$), θ_{\min} represents the minimum SWC observed during the study period, and θ_{FC} denotes SWC at field capacity.

2.5 | Statistical analysis

We characterized shrublands by comparing vegetation structure and soil properties among study sites by a one-way ANOVA

(Tukey's HSD [honestly significant difference] post-hoc test). Data were transformed (logarithm and square root) whenever necessary to meet the ANOVA assumptions. After initially exploring the data distribution of our response variables (Appendix S4), we compared plant dieback among shrubland transects ($n = 12$, i.e., three transects by four sites) using a generalized linear model with beta distribution, and with Site as the fixed factor (Cullen & Frey, 1999; Delignette-Muller & Dutang, 2015).

We quantified the influences of the main explanatory factors on plant dieback with beta regressions in generalized linear mixed models by including Site as the random factor (Damgaard & Irvine, 2019). We grouped the possible explanatory factors into three groups: water availability variables (mean annual temperature, accumulated rainfall, SPEI, rainfall pattern variables NRE, AES and CDD, and soil moisture variables SWC and REW), soil properties (depth, bare cover, surface stoniness, litter cover and rocky outcrops) and vegetation structure variables (plant volume, plant height, LAI, plant patch size, interpatch size, plant richness, diversity and evenness). For each type of explanatory factor (water availability, soil properties and vegetation structure), we selected as the best explanatory variable of dieback those that produced models with lower Akaike Information Criterion corrected for small sample size (AICc; Hurvich & Tsai, 1991) and were not autocorrelated (correlation < 0.6). We first selected the best beta regression model with a lower AICc from all the explanatory variables. Then we explored other possible models with explanatory variables that were not autocorrelated (Appendix S5). In all cases, the models with only one explanatory variable obtained lower AICc values than the models with more than one explanatory variable. All the statistical analyses were conducted using the R statistical software (R Core Team, 2022, version 4.2.1).

3 | RESULTS

3.1 | Extreme drought event intensity

The 2014 drought episode drastically lowered the total annual rainfall between 33% and 48% compared to the long-term average. This reduction reached extremely low levels of rainfall, beyond the first of the long-term driest years at all the sites (Figure 2). The intensity of this drought event contrasted with the relatively wet conditions of the previous hydrological year (2013), when the total annual rainfall values were above the 70th percentile of the long-term series at all the sites, except at CAB, which reached the 40th percentile. Furthermore, five of the seven previous years were above the 60th long-term percentile (four years for CAB and MEL), and were always above the 20th percentile (Appendix S6).

The temperatures during the 2014 drought were also hotter than the long-term averages at all the sites, with increments of about 1–4°C in spring and autumn, and an exceptional increment that was 2–5°C higher than the long-term average in April (Figure 2). This month went above the 95th percentile of the hotter long-term values for

all the sites. At VEN, only three months (October, April, June) had higher temperatures in the 2014 hydrological year than in the long-term series.

3.2 | Impact of extreme drought on water availability

The low annual rainfall recorded for drought year 2014 was reflected as not only notable changes in the rainfall pattern attributes, but also as a drop in soil moisture at all the sites (Figure 3, Appendix S7). The main affected rainfall pattern attribute was CDD, with threefold longer dry periods than in 2013 (twofold at MEL). At SAG, VEN and CAB, the average dry periods spanned more than one month (38–48 days) in hydrological year 2014. NRE lowered at the same ratio as the annual total rainfall reduction did (ca. 65% less than in 2013 at all the sites). Reduction in AES led to similar values in 2014 at all the sites ($10 \pm 1 \text{ L m}^{-2}$), which contrasts with the higher variance observed in 2013 ($14 \pm 2.5 \text{ L m}^{-2}$) and means that the AES decrease was asymmetrical between sites. In SPEI terms, drought hit harder at CAB and MEL than at VEN and SAG, which was the opposite trend shown in the rainfall pattern attributes, especially in CDD.

Subhumid site MEL had higher REW values than the other sites in autumn and spring, but the mid-summer values were similar for all the sites (Figure 3). For hydrological year 2014, the REW values were below 0.4 for eight continuous months at SAG, VEN and CAB (from February to September) and for five continuous months (from May to September) at MEL. This low REW may be taken as a tipping point of soil water deficit for Mediterranean species (Granier, 1987; Bréda et al., 1995). Indeed, REW dropped below 0.2 at SAG and CAB for six and seven continuous months, respectively, while sites VEN and MEL presented REW values below 0.2 only for summer months. In contrast, the REW values for 2015 were below the 0.4 tipping point for 3–4 months, and lower than 0.2 for 1–2 months depending on the site and for the late spring and mid-summer seasons (we have no REW data for the whole of 2013).

3.3 | Shrubland characterization: Vegetation structure and soil properties

Shrubland structure varied between sites due to differences in the dominance of grass and shrub biotypes, differences in the plant patch pattern, and distinct vertical shrub development (Figure 4). Dry-subhumid sites (CAB and MEL) showed more plant abundance, with larger plant patches (i.e., smaller bare-soil patches) than at semi-arid sites SAG and VEN (Figure 4a,m). CAB had a bigger grass phytovolume with larger grass patches than the other sites (Figure 4d,p). VEN had the clumpiest and most vertically developed vegetation, with the tallest shrubs and the highest LAI (Figure 4e,f,i,j). The shrub phytovolume was lower at VEN than at the other sites despite it having larger (and taller) shrub patches. However, the size of shrub

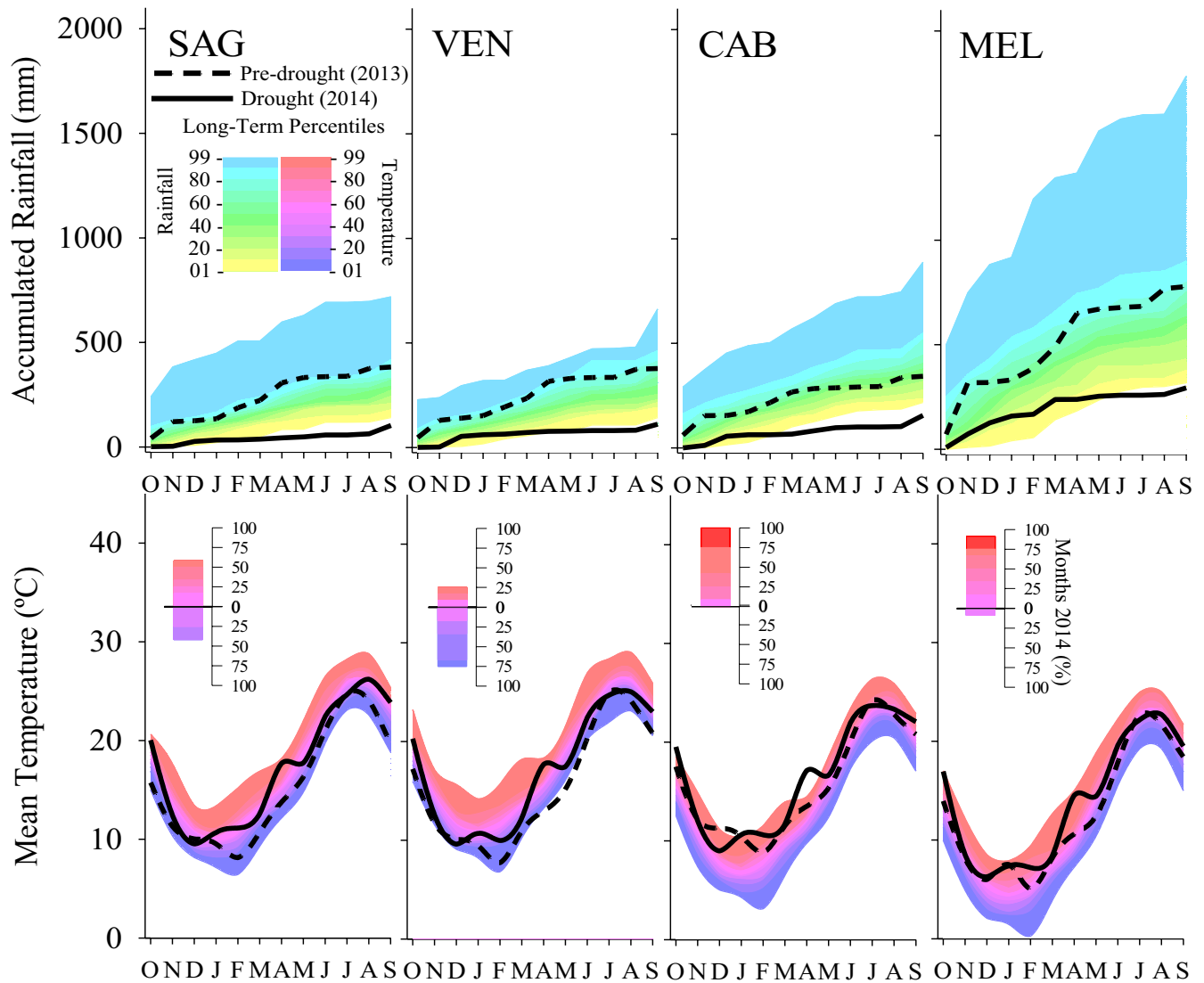


FIGURE 2 Monthly accumulated rainfall (top) and mean temperature (bottom) of hydrological years (October to September) 2013 (dashed line), 2014 (continuous line) and the range of rainfall percentiles of the long-term rainfall series (colored areas for the 10 percentile ranks). Inset in the bottom graphs: time above and under the long-term average temperature during the 2014 drought.

interpatches was also notably larger at VEN than at the other sites (Figure 4b,n). SAG was the shrubland with a smaller phytovolume, mainly because of short vegetation height and a smaller amount of grasses. Subshrub structure and abundance were similar between sites (Figure 4c,g,k,o). The composition of plant communities (species richness, plant diversity, plant evenness) was also similar at all four sites (Appendix S8).

The main differences between shrubland soils were due to the presence of rocky outcrops, while other factors like soil depth, litter cover and soil surface stoniness were relatively even between shrublands (Appendix S9). Shrubbylands showed a latitudinal trend of rocky outcrops, from a smaller amount of rocky outcrop at SAG (~1%), medium at VEN and CAB (~10%) and bigger at MEL (~25%). The opposite trend was observed in the amount of bare soil. However, in this case, differences between sites were not significant. The soil depth of shrubbylands was the same (~40 cm), except for VEN with

shallower soil (~16 cm). The soil surface cover was different between MEL, where it consisted mainly of litter (~53%), and the other sites, where soil was mostly covered by stones (~45%).

3.4 | Extreme drought effects on vegetation dieback

After the 2014 drought, visual observations indicated that plants underwent decaying processes because whole individuals had died, and also due to partial canopies in multistemmed species. In this context, plant dieback varied among sites by ranging from $12.5 \pm 3\%$ at VEN and MEL, to $26\% \pm 3\%$ at CAB, with the highest dieback levels, $38\% \pm 2\%$, at SAG (Appendix S10, Figure 5a). Shrub dieback was $26\% \pm 4\%$ for SAG, CAB and MEL, and was almost negligible for VEN (<1%) (Figure 5b). Subshrub dieback reached $49\% \pm 6\%$ at SAG, CAB

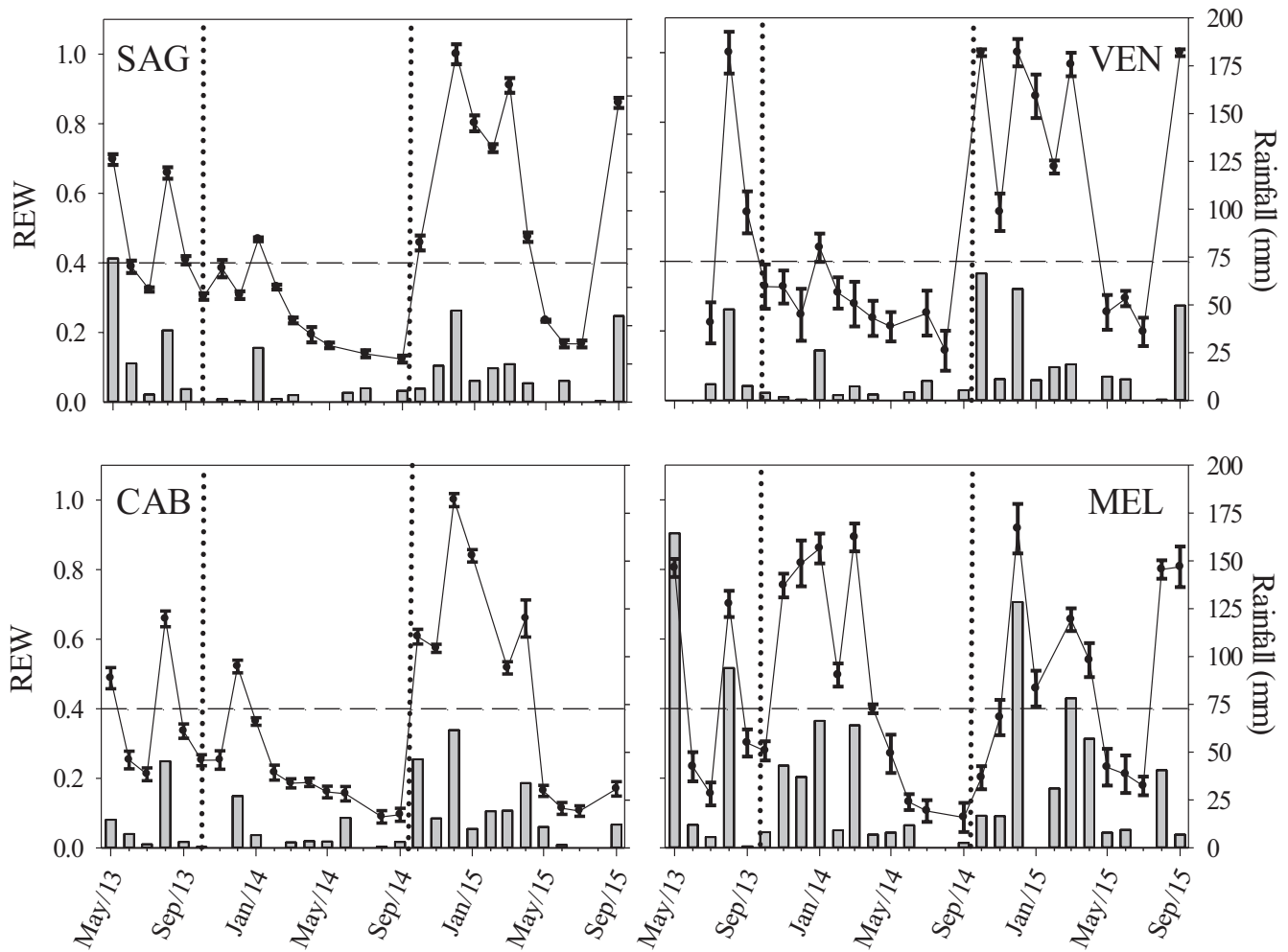


FIGURE 3 Monthly relative extractable water (REW) from May 2013 to September 2015 vs monthly rainfall at each study site. The straight line represents $REW = 0.4$, which is the tipping point of soil water deficit for Mediterranean species according to Granier (1987) and Bréda et al. (1995). The vertical dotted line shows the beginning and end of the 2014 hydrological year.

and VEN, with no subshrub dieback evidence for MEL (Figure 5c). Grass dieback was higher at SAG with 23% and only $2.5\% \pm 1\%$ at the other sites (Figure 5d).

3.5 | Relation among explanatory factors and plant dieback

The explanatory variables that best correlated with plant dieback changed between plant biotypes (Figure 6). At the plant community level, water availability and soil properties, but not vegetation structure, showed significant correlations with plant dieback. However, at the plant biotype level, only the plant structure variables correlated significantly with dieback at all the different biotypes. Both REW and bare soil cover showed the highest correlations with plant community dieback, which indicates greater dieback events under extreme drought in barer soils with lower REW. For each plant biotype, the best correlated explanatory variable belonged to one group, which was different in each case: plant structure in shrubs, water availability in subshrubs and soil

properties in grasses. In shrubs, LAI correlated the best with dieback. The shrub communities with higher LAI showed less dieback under extreme drought conditions. Soil stone cover correlated negatively with shrub dieback, and no water availability factors were correlated. CDD was the main explanatory factor that correlated with subshrub dieback, which denotes greater subshrub dieback linked with an increase in dry spells during extreme drought. Other factors that also correlated with subshrub dieback were the phytovolume of the plant community and subshrubs. In this case, no soil property factor was significantly correlated. The shrublands with a bigger phytovolume of the plant community showed less subshrub dieback under extreme drought, and this trend was the same when only the subshrub phytovolume was taken into account. Bare soil was the best explanatory variable that correlated with grass dieback, which suggests greater grass dieback in barer soils under extreme drought. Furthermore, grass height correlated significantly with grass dieback, which indicates greater dieback in shorter grasses under extreme drought conditions. However, in this case, no water availability variables correlated significantly with grass dieback.

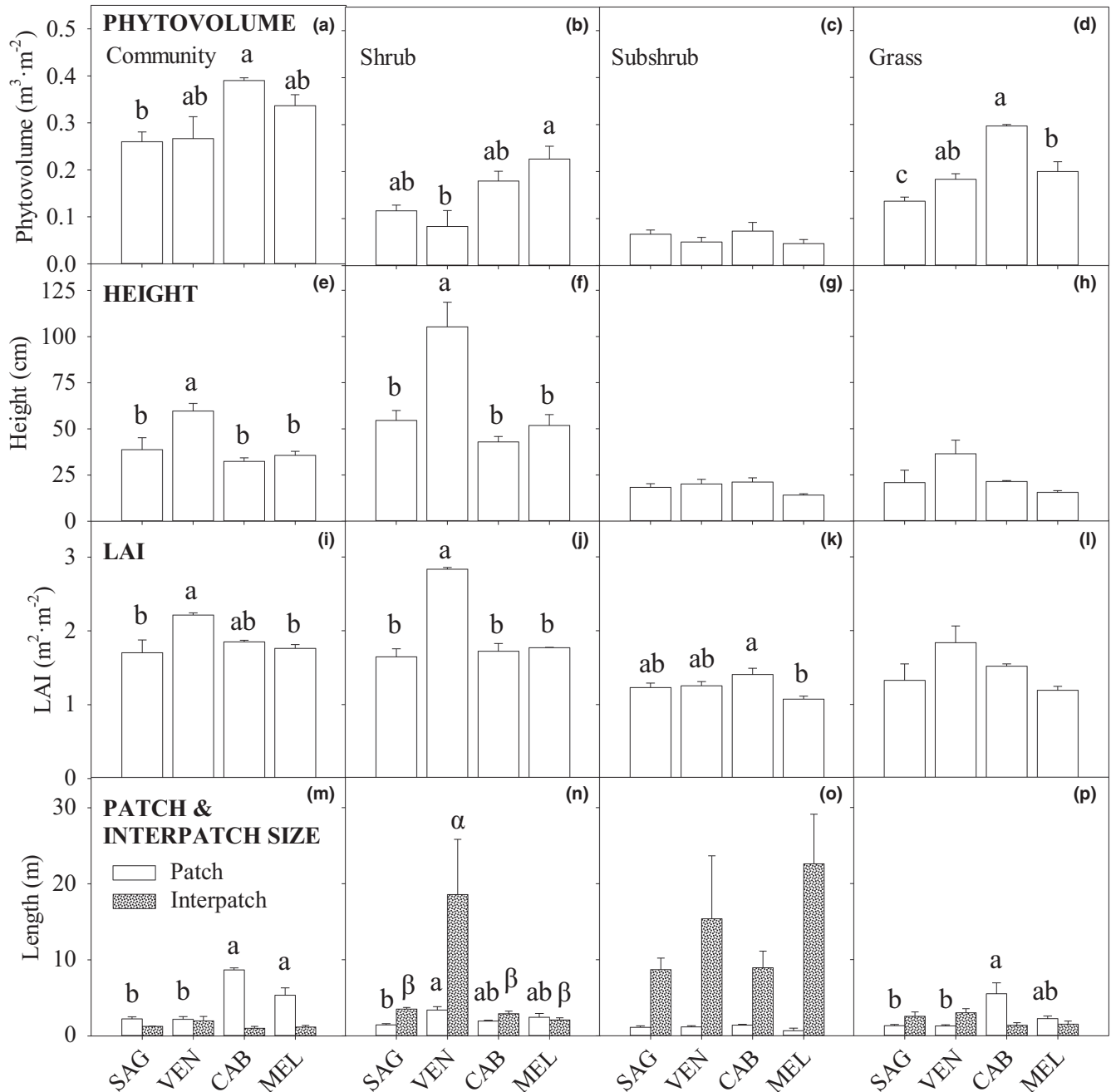


FIGURE 4 Vegetation structure in the four Mediterranean shrublands. Bars with different letters show statistically different values ($\alpha < 0.05$).

4 | DISCUSSION

The structure and functioning of drylands are strongly influenced by precipitation patterns. In such environments, changes in rainfall frequency and annual quantity of rainfall may have profound effects on soil moisture and might, thus, affect plant communities (Pugnaire et al., 2004; Knapp et al., 2008; Roitberg et al., 2016). Present studies essentially need to incorporate data on drought-induced plant dieback and mortality to predict impacts on global and local scales (Allen et al., 2010, 2015; Greenwood et al., 2017; McDowell et al., 2018). Our results revealed an extremely dry year, with

precipitation recorded in the 2014 hydrological year going below the first percentile of the driest years. This low precipitation mainly influenced autumn and winter months when recovery from the summer drought spell is critical for plant functioning. Furthermore, the mean temperature showed a hot 2014 hydrological year principally in autumn, winter and spring, with growing evaporative demand (Moutahir, 2016) and, thus, increasing potential plant water stress (Tardieu & Simonneau, 1998).

Several studies have shown that the effect of drought episodes in SE Spain, such as those recorded in 1994, 2003 and 2014, has caused considerable damage to plant communities, along with

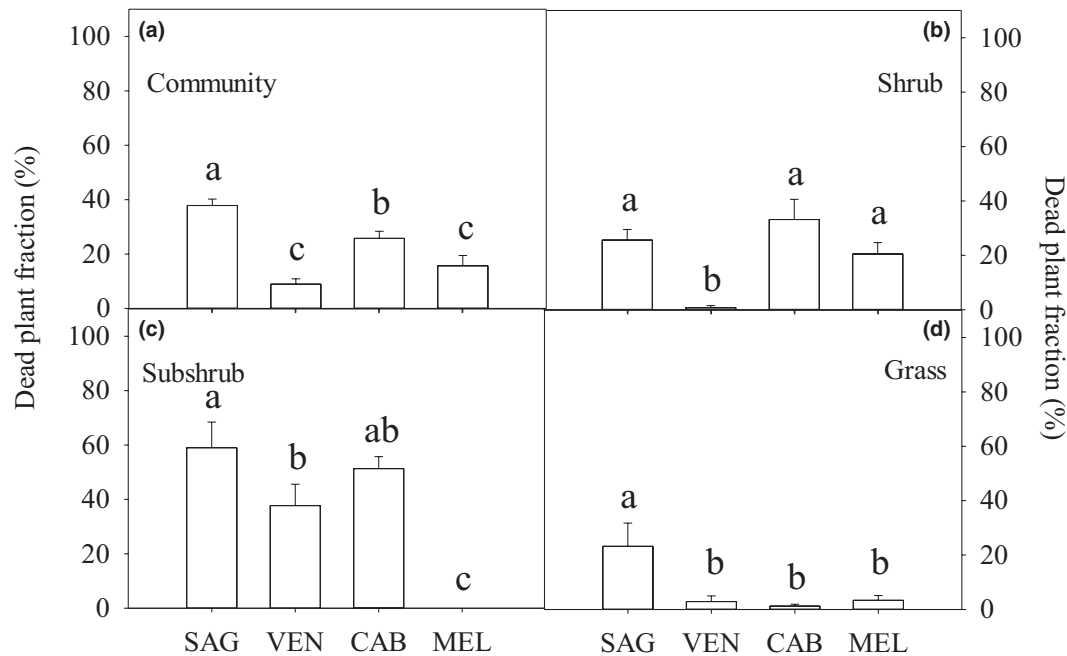


FIGURE 5 Plant dieback in the total plant community and plant biotypes after the 2014 drought in the four Mediterranean shrublands. Bars with different letters denote statistically different values ($\alpha < 0.05$).

decay processes and further generalized plant mortality (Peñuelas & Filella, 2001; Herrero et al., 2013; García de la Serrana et al., 2015; Morcillo et al., 2022). Mediterranean shrublands are quite vulnerable to rising temperatures and decreasing water availability (Bellot et al., 2004), and the expected increasing aridity in regions that are already dry in large areas of the Mediterranean Basin may have serious ecological and socio-economic consequences (IPCC, 2021). Our results showed that not only were water availability factors correlated with the observed plant dieback in response to extreme drought, but so were other factors related to soil properties, and vegetation structure played an important role. Soil moisture is a key parameter to determine how water availability correlates with plant community dieback. However, our results confirmed the relevance of available water (REW) rather than absolute water content (SWC) in the soil of drylands, which rely more on soil texture and composition, biological cover, rainfall pattern and soil moisture dynamics than on the amount of incoming rainfall (Noy-Meir, 1973; Ogle & Reynolds, 2004; Berdugo et al., 2014). Changes in rainfall pattern have been shown to affect plant functioning, productivity and survival (Fay, 2009; Heisler-White et al., 2009; Cherwin & Knapp, 2012; Reed et al., 2012; Felton et al., 2020) mainly because soil water availability depends more on the number and distribution of rainfall events than on the total rainfall amount in arid ecosystems (Hottenstein et al., 2015). In this study, we showed that CDD was the most significant explanatory factor to correlate with subshrub dieback. This highlights the timing of rainfall events regardless of the amount of rainfall as a main factor of decay in shallow-rooted plant species, which usually show the highest dieback and mortality ratios during extreme droughts (Jacobsen & Pratt, 2018).

Vegetation structure correlated with the dieback of all the plant biotypes, mainly through vertical plant development (height, LAI and phytovolume), while spatial distribution (patch and interpatch sizes) was less relevant. In plants with similar functional strategies (i.e., biotypes regarding potential plant growth and root development), short stature and low LAIs of plants suggest less developed or younger individuals than plant stands with a taller stature and higher LAIs of plants (Westoby, 1998; Reich et al., 2003). This could be due to lesser root system development in shorter than in taller shrub stands (Cornelissen et al., 2003; Christina et al., 2011). Drought usually affects short plants in shrublands of arid ecosystems, mainly because of the shallow root systems of this vegetation (Paddock III et al., 2013; Venturas et al., 2016; Jacobsen & Pratt, 2018). In this sense, we revealed that shrubs and grasses with lower LAI and height, and subshrubs, were the vegetation most affected by extreme drought. As extreme drought altered the rainfall pattern by becoming more irregular with higher CDD, the plants with more developed root systems could have been favored because of the gravimetric downward shifts of the soil water profile (Sala et al., 1992, 2015). Furthermore, the subshrubs in shrublands with a bigger phytovolume showed less dieback, which could be due to the facilitation of these short-statured plants by the rest of the plant community, especially taller shrubs and grasses under extreme drought conditions (Holzapfel & Mahall, 1999; Cortina et al., 2011; Soliveres & Maestre, 2014). For example, under extreme drought conditions, taller shrubs and grasses may buffer environmental conditions for the short-statured plants by mechanisms such as shading (i.e., reducing direct radiation, soil water evaporation and soil and air temperature) and increasing water availability through hydraulic lift (i.e., lift of water stored in deep soil layers and release in upper

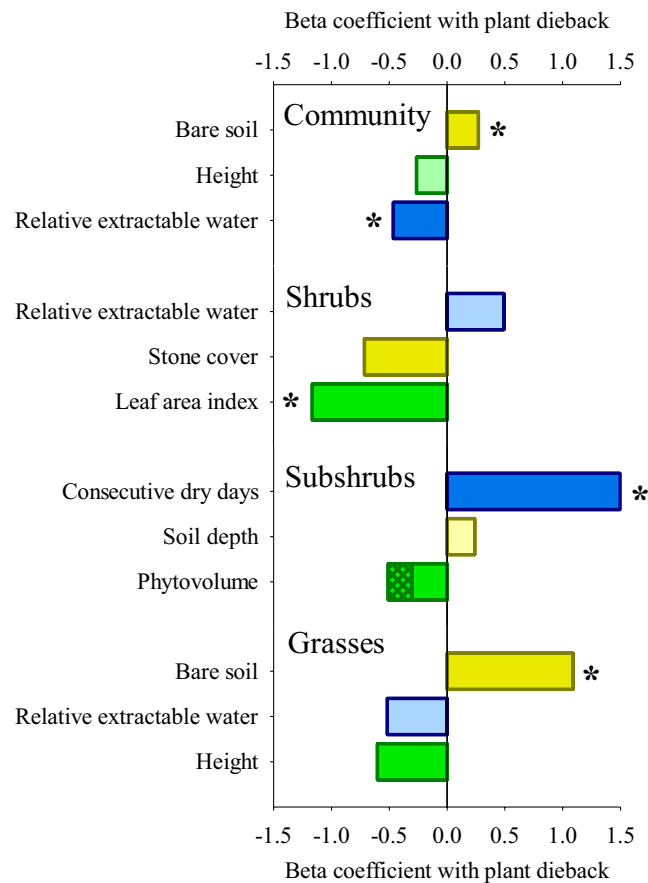


FIGURE 6 Correlation beta coefficients of the relations of the water availability variables (blue bars), soil properties (yellow bars), and vegetation structure (green bars) with plant dieback of the plant community and biotypes in the four Mediterranean shrublands ($n = 12$). Asterisks indicate the models with lowest Akaike Information Criterion corrected for small sample size (AICc) at each plant biotype (two models with $\Delta AICc < 2$ at the plant community level). Dark-colored bars show significant correlations. The bars with a double filled pattern denote the plant community level (filled pattern) and biotype level (non-patterned bar) of the explanatory variable.

soil layers by roots) (Padilla & Pugnaire, 2006; Prieto et al., 2010). Therefore, vertical vegetation development may be a better indicator of shrubland vulnerability to extreme drought than the spatial arrangement in Mediterranean drylands.

Soil properties were the main factors correlating with decaying grasses, and they also highly correlated with the dieback of the plant community and shrubs. Bare soil surface was the most relevant soil surface trait to explain plant dieback at both the plant community and grass levels. This could be due to the greater sensitivity of grass species to surface water loss by evaporation given their shallow root system. Surface stoniness has been related to higher infiltration rates under wet conditions (Mayor et al., 2009), which may explain the negative correlation that we found between shrub dieback and stone cover. However, the lack of correlation with grass and subshrub dieback could be explained by the opposite role of soil surface stoniness under extremely dry conditions, especially for shallow-rooted

plants. Stones on the soil surface might reduce water input to soil by intercepting the majority of less intense rainfall events (>80% of the rainfall events in 2014 were $< 3 \text{ L m}^{-2}$, which was twice that in an average year). Negative correlations have been shown between surface stoniness and the cover of short plant species in these ecosystems (Maestre & Cortina, 2002). Therefore, only deep-rooted plants (some shrubs) might have profited by high soil surface stoniness, while this benefit of increasing infiltration during high rainfall events for shallow-rooted plants (subshrubs and grasses) could have been masked by the interception of minor rainfall events during dry periods.

5 | CONCLUSIONS

The climate phenomenon observed in 2014 was an extreme drought that affected all four study sites. Subshrubs in semi-arid and dry ecosystems were the biotype most affected by drought, while the shrub and grass dieback differences among sites were likely due to different development stages (vertical development). The plant dieback-related factors vastly varied between plant biotypes, and vegetation structure for shrubs, water availability for subshrubs and soil properties for grasses were the most relevant ones. REW and rainfall pattern attributes (CDD) proved to be better explanatory variables of vegetation dieback than accumulated rainfall. Vertical development (LAI and height) drove shrub and grass resistance to extreme drought, while spatial arrangement did not seem to be related to plant dieback. Lack of soil surface cover was also relevant for explaining plant dieback, although surface stoniness seemed beneficial only for deep-rooted biotypes. These results highlight the relevance of plant structure and soil surface properties in Mediterranean drylands to withstand extreme drought events. They suggest that shrubland landscape architecture management is a suitable action for adaptation to climate change to increase the resilience of these ecosystems to climate change.

AUTHOR CONTRIBUTIONS

Juan F. Bellot and Adrián Maturano-Ruiz conceived the research idea; Samantha Ruiz-Yanetti, Àngela Manrique-Alba and Adrián Maturano-Ruiz collected the field data, Hassane Moutahir collected the climatic data; Adrián Maturano-Ruiz performed statistical analyses; Samantha Ruiz-Yanetti and Adrián Maturano-Ruiz wrote the original draft; all authors discussed the results and commented on the manuscript.

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DATA AVAILABILITY STATEMENT

The data are available in <https://doi.org/10.5281/zenodo.7794181>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Climate diagrams of each study site.

Appendix S2. Plant composition in the four Mediterranean shrublands.

Appendix S3. Soil properties per studied site.

Appendix S4. Distribution of exploratory data.

Appendix S5. Multicollinearity of exploratory data.

Appendix S6. Monthly accumulated rainfall of hydrological year 2014 and seven previous years.

Appendix S7. Water availability variables in the four Mediterranean shrublands during the 2014 drought.

Appendix S8. ANOVA results of vegetation structure variables at plant community level and the main plant biotypes.

Appendix S9. Soil properties of the four Mediterranean shrublands and the statistic parameters of differences between them.

Appendix S10. Results of generalized ANOVA with beta distribution for plant dieback of the different biotypes.

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