

The importance of functional diversity in the stability of Mediterranean shrubland communities after the impact of extreme climatic events

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Abstract

Aims

Extreme climatic events may have important consequences for plant community structure and composition. In 2005, a severe drought together with a cold winter promoted extensive damage and mortality in shrubland communities of southwest Spain (Doñana National Park). Here, we aim to identify the mechanisms underlying community stability (resistance and resilience) in response to this extreme climatic event, considering changes in the functional structure of these communities.

Methods

We used a trait-based approach, quantifying variations in 10 functional traits at the community level (community weighted means, CWM) and the functional diversity (functional richness, evenness and divergence) in 18 plots at three different times: predating the climatic event (estimated from the sum of the live and dead volume of each species in 2007), and 2 and 8 years after the 2005 episode. We also quantified the differences in functional traits and functional diversity between adult and recruit stages, which allowed us to better understand the contribution of the recruitment to the maintenance of the functional structure and diversity of the community.

Important Findings

Communities with higher functional divergence before the climatic event maintained nearly constant their levels of functional

divergence 8 years after, but they were more prone to changes in species composition. Community resistance in terms of vegetation cover was positively correlated with root dry matter content, whereas community resilience was positively correlated with leaf chlorophyll (LChl). We also found that some values (weighted means) of functional community traits (such as root dry matter content and LChl) had increased 2 years after the event, returning to the pre-event conditions after 8 years. In addition, there was hardly any establishment of new species in the community and the recruits did not make substantial differences to the community functional structure. Only seed mass differed significantly between the adult and seedling stages. In summary, the extreme climatic event induced rapid vegetation changes, modifying several functional properties of the community, but, in spite of the occurrence of changes in species composition, a rapid convergence of these shrubland communities took place due to the replacement of species with functional redundancy, thus recovering the initial conditions and supporting the existence of strong mechanisms of functional resilience.

Keywords: climate change, Doñana, drought, functional trait, recruitment, resilience, resistance

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INTRODUCTION

The occurrence of extreme climatic events, resulting from a high variability in temperature and precipitation, has received increased attention in the last few years (Easterling *et al.* 2000; Jentsch *et al.* 2011; Kreyling *et al.* 2008). The expected increase in climatic variability would involve more frequent extreme climatic events in the near future (IPCC 2013), in spite of the uncertainty when considering small temporal and spatial scales (Kao and Ganguly 2011). These extreme climatic events are likely to trigger ecosystem disturbances that may affect plant species composition (Lloret and Granzow-de la Cerda 2013) and, thus, the functional attributes of communities.

After climate event disturbances, rapid changes in plant communities can be hypothesized as a result of increased differential mortality in some species and their potential replacement by other species better adapted to the new climatic conditions (Lloret 2012). Alternatively, species can be replaced by others with similar functional attributes ('functional redundancy' hypothesis, e.g. Naeem 1998). Most research has focused on analysing the effect of extreme climatic events on: (i) variations in species and individual responses, mainly trees (Breshears *et al.* 2005; Gillespie and Loik 2004; Sangüesa-Barreda *et al.* 2012); (ii) changes in productivity and species composition (Grime *et al.* 2000; Jentsch *et al.* 2011; Sternberg *et al.* 1999; White *et al.* 2000) or (iii) recruitment processes (Lloret *et al.* 2005; Lloret and Granzow-de la Cerda 2013). Nonetheless, there is a lack of studies that evaluate the impact of climatic events on the functional structure of communities (but see Majekova *et al.* 2014; Polley *et al.* 2013) and, especially, that consider also different life-history stages (e.g. adult and recruitment stages).

The ecosystem response to disturbances (such as an extreme climatic event) comprises two main aspects related to stability: resistance, which can be defined as the tendency of the ecosystem to remain in a reference state despite perturbation; and resilience, which can be described as the ability of a particular ecosystem or community to return to a reference state prior to the disturbance (Potts *et al.* 2006 and references therein). At the community level, these processes are determined by the balance through time between demographic processes (recruitment and mortality rates) of the different coexisting species (Lloret *et al.* 2012). These processes may produce temporary changes in vegetation, although in many cases plant populations exhibit remarkable inertia (Lloret and Zedler 2009; Lloret *et al.* 2012).

The effects of climatic events on plant community stability (resistance and resilience) can be analysed also by exploring temporal changes in the functional structure and diversity of the community (Díaz and Cabido 2001; Hooper *et al.* 2005). Two widely recognized and complementary indicators can be used to explain how species traits within a community may influence these ecosystem properties (de Bello *et al.* 2010): (i) community weighted means (CWM), based on the biomass ratio hypothesis (Grime 1998), where the mean trait

values of the species present in a community are weighted by their relative abundances (Garnier *et al.* 2004) and (ii) functional diversity, defined as the degree to which coexisting species vary in terms of their functional traits (Weiher 2010). More diverse communities, in terms of species or functional groups, are theoretically expected to be more resistant and resilient against environmental perturbations (Grime 2001; Yachi and Loreau 1999), as has been reported for temperate grasslands (van Ruijven and Berendse 2010; Tilman *et al.* 2006). Although more diverse communities generally have higher stability (Bastolla *et al.* 2009; Díaz and Cabido 2001), there is considerable uncertainty about which components of diversity (i.e. species richness, functional group richness or the presence of some key species) determine this relationship (Kreyling *et al.* 2011). This conceptual framework has stimulated research aiming to functionally interpret the relationships between community composition, environmental changes and ecosystem processes (Dias *et al.* 2013; Lavorel *et al.* 2008; Mason *et al.* 2012; Villéger *et al.* 2010). However, the role of functional diversity in the vegetation responses to extreme climatic events remains poorly understood.

Among the extreme climatic events, severe drought and anomalous temperatures can have great effects on vegetation composition and productivity (Breshears *et al.* 2005). Water availability is a key factor for plant survival and growth in arid and semi-arid regions (Padilla and Pugnaire 2007). Therefore, functional traits related to drought resistance or resilience may be related to demographic performance after disturbance (Saura-Mas *et al.* 2009) and thus contribute to the species response to climatic events. In this sense, several functional traits have been used to assess the level of drought resistance shown by plants: e.g. those related with water use efficiency (represented by carbon isotopic discrimination, $\delta^{13}\text{C}$; Farquhar *et al.* 1982) or those associated with a more conservative resource-use strategy, such as low values of specific leaf and/or root area or higher tissue dry matter content (Hernández *et al.* 2010; Poorter and Markejstein 2008; Pérez-Ramos *et al.* 2013). In addition, some traits related with drought resilience may help to understand community recovery after extreme climatic episodes (Lloret *et al.* 2016), such as regenerative traits related to plant establishment (e.g. higher seed mass; Pérez-Ramos *et al.* 2010), or higher photosynthetic potential (e.g. higher leaf nitrogen and chlorophyll concentrations)—which allows plants to reach high rates of growth and foliage production after drought (Eamus and Prior 2001).

In 2005, two simultaneous extreme climatic events, a severe drought and a very cold winter, took place in Doñana National Park (southwest Spain), and were followed by extensive shrubland damage and mortality (Díaz-Delgado 2006; Díaz-Delgado *et al.* 2014, see aerial photographs in supplementary Fig. 1). These climatic events could have promoted differential die-off among coexisting species, modifying the functional structure of the community. Consequently, we hypothesise that these events could have had a filtering effect increasing the functional homogeneity (favouring tolerant

species) during a first stage and recovering the functional heterogeneity afterwards.

In this study, our main objective was to identify possible mechanisms of stability (resistance and resilience) of shrubland communities following an extreme climatic event of severe drought and a cold winter, using a trait-based approach. For this purpose, we explored temporal changes in the community functional structure: trait composition at the community level and functional diversity (of both adults and recruits) in response to those climatic events. For this, we surveyed the species composition after the event and some years later, estimating the pre-event composition by adding together the live and dead volume of each species. We also measured a broad set of functional traits (including leaf, stem, root, seed and whole-plant traits) that could be related with plant survival after drought and/or low temperatures. Then, we quantified relevant indexes of functional diversity. Specifically, we studied three main topics with the final aim of answering the following questions: (i) regarding changes in the functional diversity of plant communities: was there a decrease in functional diversity after the climatic event? Were communities harbouring higher initial functional diversity more resistant or resilient to these climatic disturbances? (ii) Regarding changes in community functional traits: can we predict the functional traits contributing most to the community resistance and resilience to extreme climatic events? Which functional traits were affected (positively or negatively) by the climatic event? And (iii) regarding the regeneration patterns: was the community functional diversity of the plants at the recruit stage a reflection of the adult stage? Alternatively, are they biased towards certain functional traits associated with colonisers after disturbance?

MATERIALS AND METHODS

Study area

The study was carried out in Doñana (southwest Spain), which was declared a National Park (1969), Biosphere Reserve (1981) and World Heritage site (1994). The climate is Mediterranean-type with an oceanic influence; mean annual rainfall is 560 mm, albeit with considerable interannual variations, ranging from <300 mm in dry years to 1000 mm in extremely wet years. The mean annual temperature is 16.5°C, with mean temperatures of 24.7°C in the hottest month (July) and 10.0°C in the coldest month (January). According to the Global-Aridity index (Trabucco and Zomer 2009) the study area is classified as semiarid. The site is ca. 3 km from the Atlantic Ocean, on a large Quaternary eolic dune field that was stabilized during the Holocene (Muñoz-Reinoso and Garcia-Novo 2005). The vegetation of the Doñana paleodunes is a mosaic of wetlands and extensive shrublands, with locally dense stands of juniper (*Juniperus phoenicea* ssp. *turbinata*) that are often mixed with *Pinus pinea* (originally planted), remnant individuals of *Quercus suber*, small patches of *Pistacia lentiscus* and grassland areas dominated by annual plants.

Specifically, the study was carried out in a xeric shrubland type locally known as ‘monte blanco’, with a large abundance of shrub species such as *Cistus libanotis*, *Halimium halimifolium*, *Helichrysum pichardii*, *Lavandula stoechas*, *Rosmarinus officinalis*, *Thymus mastichina* and *Ulex australis*. The ‘monte blanco’ is considered to be a seral stage of juniper woodlands (García-Murillo and Sousa-Martín 1999). The abundance of herbaceous species, in terms of plant biomass, is marginal in the ‘monte blanco’ shrublands; therefore, they were not considered in this study.

An event of extreme drought occurred during the hydrological year 2004–2005, when total rainfall only reached 173 mm (69% less than the average). This drought was combined with a very cold winter, with absolute minimum temperatures of –5°C and –4°C and mean minimum temperatures of 1.1°C and 0.9°C for January and February, respectively, which were much lower than the mean minimum values registered for the last 35 years (4.7°C for January and 5.8°C for February; see supplementary Fig. S2). This climatic event was rapidly followed by a general die-off of green tissue on the dominant shrubland vegetation that reached 75% of the plant cover in some stands (Lloret et al. 2015) and produced a significant drop in the Normalized Difference Vegetation Index (NDVI) during the year of the event (Díaz-Delgado 2006; supplementary Figs S1 and S3). In the years following the event, the annual rainfall ranged from 468 mm (in the 2005–2006 hydrological year) to 713 mm (in 2010–2011).

Sampling of vegetation and estimation of resistance and resilience

Eighteen permanent plots of 25 m² (5 × 5 m) were established in November 2007 (2 years after the drought). The reliability of surveying the impact on the vegetation 2 years after the extreme climatic event was supported by NDVI values obtained from Landsat imagery for 30 × 30 m pixels ($n = 21$) corresponding to the locations of the sampled plots. The comparative analyses of these images between different years did not detect significant differences in plant canopy greenness between November 2005 and 2007, while there was a significant decrease in 2005 in relation to the previous years as well as a slight recovery after 2007 (see supplementary Fig. S3).

The plots were separated by at least 50 m from each other and were distributed in three sites (six plots per site) within an area of approximately 10 km²: Raposo (N 37°0′2″, W 6°30′20″), Ojillo (N 36°59′40″, W 6°30′50″) and Marqués (N 37°0′45″, W 6°31′50″). The three sites slightly differed in their elevation with respect to the dune field (Raposo was located at the bottom, at 18 m a.s.l., Marqués on the top, at 30 m a.s.l. and Ojillo in an intermediate position, close to the top, at 21 m a.s.l.), which likely resulted in potential differences in their height above the water table (García et al. 2014).

The composition and abundance of the shrub species (see supplementary Table S1) were measured in each plot by estimation of the volume (from the product of the height and mean canopy diameter), as determined by the extreme of

branches, excluding leaves and recent shoots of all living and dead adult shrubs. This procedure made the estimated volume comparable for living and dead plants, as shown by the lack of significant difference in the volume between dead and living individuals for all species (t -values ranging from 0.08 to 1.79, $P > 0.05$ in all cases). The only exception was the small-sized *Thymus mastichina*, for which the dead plants were smaller ($t = 3.18$, $P = 0.004$); however, this species contributed little to the overall community due to its low abundance. Dead individuals were identified to the species level by their morphological traits (bark, branch ramification, dry leaves on the ground). We ensured that plants considered as dead had recently lost their foliage (presumably as a consequence of the recent climatic event) by only including plants having branches with thin tips and non-decomposed leaves on the ground beneath the plant canopy, while excluding old stumps and plants constituted only by shoots without thin tips on the branches. The species relative abundance per plot 2 years after the event (named hereafter '+2 years') was calculated as the live volume in the 2007 survey relative to the sum of the live volume of all species.

The species relative abundance per plot previous to the climatic event (named 'pre-event') was calculated as the sum of the live and dead volume of 2007 of each species relative to the sum of the live and dead volume of 2007 for all species. This assumption was supported by the fact that: (i) plants considered as dead were recently defoliated, as indicated by the presence of non-decomposed leaves on the ground beneath plant canopies, as well as by the presence of standing thin branches on plants; (ii) there was no decrease in the volume of plants considered as dead, in comparison to living plants, as explained in detail above; (iii) the increase in the green parts of living plants due to regrowth in 2007 can be considered negligible, as supported by non-significant differences in NDVI measurements between 2005 and 2007 (more details in supplementary Fig. S3). In June 2013 (8 years after the event; named '+8 years'), we measured again the plant species composition and relative abundance of all shrub species (from their plant volumes).

We consider that the 2007 survey—2 years after the event—is a valuable measure of the vegetation response to the climatic episode. Although our estimation of the resistance to the 2005 event merges the damage suffered during that period with delayed mortality (Lloret and López-Soria 1993) and fast recovery until 2007, we consider that these two later effects were relatively low and compensated each other. In fact, in disturbance studies it is recommendable to evaluate the impact of the extreme climatic event considering a short lag after the event, because this allows integration of the delayed decay and regrowth directly related to the studied event.

All these measurements were performed with the main aim of determining the community resistance and resilience after the extreme climatic events. The resistance index (Rt-cover) was defined for each plot as the state of the vegetation 2 years

after the climatic event relative to the pre-event state (Lloret *et al.* 2011). It was calculated as the sum of the resistance of each species i , estimated as $[(V_{i+2\text{ years}} - V_{i\text{ pre-event}})/V_{i\text{ pre-event}}]$, for all the species of the community, V_i being the volume estimated for species i in a particular time period.

Similarly, the resilience index (Rs-cover) was estimated for each plot as the relative recovery rate of the vegetation 8 years after the climatic event. It was calculated as the sum of the resilience of each species i , estimated as $[(V_{i+8\text{ years}} - V_{i\text{ pre-event}})/V_{i\text{ pre-event}}]$, for all the species of the community, V_i being the volume estimated for species i in a particular time period.

We also estimated the resistance and resilience of the species composition (Rt-comp and Rs-comp, respectively), defined as the temporal changes in species composition and abundance (Kreyling *et al.* 2011). They were quantified by using the similarity quantitative index (Bray and Curtis 1957; Faith *et al.* 1987) between the values measured pre-event and 2 years after the episode [Rt-comp; $(\sum |V_{i\text{ pre-event}} - V_{i+2\text{ years}}|)/(\sum |V_{i\text{ pre-event}} + V_{i+2\text{ years}}|)$] as well as between the pre-event conditions and 8 years after the climatic episode [Rs-comp; $(\sum |V_{i\text{ pre-event}} - V_{i+8\text{ years}}|)/(\sum |V_{i\text{ pre-event}} + V_{i+8\text{ years}}|)$].

The recruitment of 1-year-old seedlings was estimated in November 2007 by recording all the seedlings of shrub species that emerged within each of the 18 plots. The existence of cotyledon scars was considered as evidence that they had recently emerged after the extreme climatic episode. In June 2013, we recorded all juveniles of these shrub species; i.e. plants more than 1-year-old but which had not reached the reproductive stage.

Measurement of plant traits

In late spring 2013, during the peak of plant growth, healthy adults of 16 species were randomly selected (outside the plots, to avoid disruption of the vegetation monitoring) for the measurement of eight aboveground and two belowground functional traits related with morphology, physiology, chemical composition and reproduction (Table 1). The species were selected according to their abundance in the community (supplementary Table S1) and, thereby, their potential relevance to the process of community assembly (Carlucci *et al.* 2012; Garnier *et al.* 2004; Pérez-Ramos *et al.* 2012). All trait measurements were carried out according to the criteria and methodology defined by Pérez-Harguindeguy *et al.* (2013); chlorophyll concentration was measured by the Wintermans and de Mots method (1965). For more methodological details, see de la Riva *et al.* (2016a).

Aboveground functional traits

Plant height (Phg) measurements were made on 10 individuals per species. Leaf and stem traits-specific leaf area (SLA; leaf area per unit of leaf dry mass), leaf dry matter content (LDMC; leaf dry mass per unit of leaf water-saturated fresh mass; mg g^{-1}), leaf nitrogen concentration (LNC; %), leaf chlorophyll (LCh); concentration of chlorophyll per unit of fresh leaf mass; $\mu\text{g g}^{-1}$) and stem dry matter content (SDMC;

Table 1: the functional traits studied, their abbreviations, units and their main role in plant functioning

Trait	Abbreviation	Unit	Functional role
Specific leaf area	SLA	m ² kg ⁻¹	Light capture and growth rate
Leaf dry matter content	LDMC	mg g ⁻¹	Physical resistance and stress tolerance
Stem dry matter content	SDMC	mg g ⁻¹	Resistance to physical hazards
Specific root area	SRA	m ² kg ⁻¹	Water and nutrients acquisition
Root dry matter content	RDMC	mg g ⁻¹	Resistance to physical hazards
Leaf nitrogen concentration	LN	%	Light capture and photosynthetic rate
Leaf chlorophyll ^a	LChl	µg g ⁻¹	Light capture and photosynthetic rate
Isotopic carbon fraction	δ ¹³ C	‰	Gas exchange and water-use efficiency
Plant height	Phg	m	Light capture, above-ground competition
Seed mass	S _{mass}	mg	Dispersal capability and seedling survivorship

^aBased on fresh mass.

stem dry mass per unit of stem water-saturated fresh mass; mg g⁻¹) were measured in six individuals per species. A mixture of leaves from six different individuals was collected for measurement, at the species level, of the carbon isotopic ratio (δ¹³C; ‰), a trait directly related with plant water use efficiency (Farquhar et al. 1982). The average seed mass (*S_{mass}*) for each species was compiled from a local data-set (Cordoba Botanical Garden).

Belowground functional traits

The roots of four individuals per species were sampled by excavating the first 20–30 cm of the soil layer near to each plant basal stem. We selected this specific soil depth based on other studies of Mediterranean woody vegetation in Doñana National Park (Martínez et al. 1998) that demonstrated that the largest fraction (70%) of fine roots appears in the first 25 cm of soil depth. These root samples were used to measure two belowground traits of fine roots (<2 mm in diameter) related to water and nutrient uptake (Jackson et al. 1997): specific root area (SRA, root area per unit of root dry mass) and root dry matter content (RDMC, root dry mass per unit of root water-saturated fresh mass). These data were obtained by analysing the scanned root samples with WinRHIZO 2009 (Regent Instruments Inc., Quebec, Canada) and weighing the root water-saturated and dry masses.

Measurement of community variables

The CWM for each trait and community sample were calculated as $\sum P_i \times \text{Trait}_i$, where P_i is the relative abundance of species '*i*' in the community sample and Trait_i is the average trait value obtained for species '*i*' (Garnier et al. 2004).

The functional diversity of each community sample was summarized by means of three different and complementary indexes: functional richness (F_{Rich}), which is determined by species occurrence (i.e. independently of their abundances) and reflects the amount (the difference between the maximum and minimum values) of functional trait variability in a given community, reflecting how much of the niche space is occupied by the species present; functional evenness

(F_{Eve}), which quantifies the evenness of abundance distribution across species trait values, measuring the regularity of spacing between species along a functional trait gradient and evenness in the distribution of abundance across species; and functional divergence (F_{Div}), which captures the degree of divergence in the abundance distribution of species functional traits and represents how abundance is spread along a functional trait axis, being low when the functional traits of the most abundant species are close to the centre of the functional trait range (for more details see Mason et al. 2005 and Villéger et al. 2008). These independent metrics express different facets of functional diversity by which the community affects ecosystem processes through the functional traits of its species (Mason et al. 2005; Mouchet et al. 2010). In addition, these indexes may reveal the impact of perturbations, such as climatic changes, on community composition and functioning (Villéger et al. 2010). For the purpose of estimating functional diversity, the species occurrence and abundance were estimated from measurements of plant volumes at each sampling time (pre-event, +2 years, +8 years).

Data analyses

To understand the multidimensional relationships among functional traits and detect a possible redundancy, we conducted exploratory principal components analysis (PCA) based on a correlation matrix of the 10 functional traits in the 16 species sampled. Seed mass (*S_{mass}*) was log-transformed prior to the analyses to fulfil assumptions of normality.

To explore the influence of the initial functional diversity on community resistance and resilience after the event we conducted two complementary analyses. First, we explored the relationships between the pre-event FD indexes (F_{Rich} , F_{Eve} and F_{Div}) and the different indexes of community resistance and resilience in order to test our initial hypothesis that communities harbouring higher initial functional diversity are more resistant or resilient to a climatic disturbance. Second, we explored the relationships between each functional diversity index in the pre-event and +8 years surveys, to determine if the functional diversity remains constant or not with time.

In addition, we tested whether the resistance and resilience of the community were related with certain initial community functional traits (pre-event CWMs). All these tests were conducted with linear mixed models, considering the predictor variable as the fixed effect and site as the random effect.

Temporal changes in the community functional structure were analysed by using one-way repeated measures ANOVA. Differences between sites (six plots per site) and with time (pre-event, +2 years, +8 years) for each of the 10 community functional traits (CWM) and the three functional diversity indexes were tested. Planned comparisons (least significant difference, LSD) were used to test, *post hoc*, for differences implicit in the experimental design (Sokal and Rohlf 1995). The probability values of within-subject factors were analysed with Wilk's lambda multivariate test.

In order to determine the differences in the functional traits and FD indexes between the communities of adults and recruits, we performed a stepwise discriminant analysis for the different surveys, with community functional traits and FD indexes used as independent variables and the groups of adults (+2 years and +8 years surveys) and recruits (+2 years seedlings, +8 years juveniles) to be discriminated. In these analyses, the species abundances of adults and recruits were estimated from the number of individuals per plot. This analysis allows us to understand the contribution of the recruitment to the maintenance of the functional structure and diversity of the community.

The PCA and linear mixed model analyses were conducted in the R 2.10.0 statistical platform, using the packages 'FactoMiner' (Lê *et al.* 2008) and 'nlme' (Pinheiro *et al.* 2015). The package 'FD' (Laliberté and Legendre 2010) was used to calculate the three functional diversity indexes considered in this study. The repeated measures ANOVA and discriminant analysis were performed with SPSS 17.0 (SPSS, Chicago, IL, USA).

RESULTS

The PCA analysis showed a high dispersion of the factors (functional traits) along the first and second axes (supplementary Fig. S4), indicating a low redundancy (i.e. a low number of significant correlations) among the traits. Although chlorophyll (LChl) and SDMC showed a high correlation (supplementary Fig. S4), both traits were maintained in the analysis of functional diversity because correlation between traits that do not have a functional link *a priori* may be considered a relevant aspect of species distribution in the functional trait space (Villéger *et al.* 2008). The traits related to water-use efficiency ($\delta^{13}\text{C}$), reproductive effort (S_{mass}), light capture (Phg) and SLA (in the opposite direction) exhibited the highest (absolute) scores for the first principal component, which accounted for 32% of the total variance. The second principal component (explaining 26% of the total variance) was related to the dry matter content of the different organs (LDMC, RDMC and SDMC) and to chlorophyll (LChl), while

SRA was on the opposite extreme of the axis (supplementary Fig. S4).

The functional richness (F_{Rich}) decreased after the event and subsequently increased to attain values similar to those in the pre-event conditions (Fig. 1), while functional evenness (F_{Eve}) and functional divergence (F_{Div}) did not change significantly with time (supplementary Table S2). In addition, F_{Div} and F_{Rich} in the +2 years and +8 years surveys showed positive relationships with their respective pre-event values ($P < 0.05$; Fig. 2a), indicating that plots with more functional diversity remained as the most functionally diverse after the climatic event. The F_{Div} of the pre-event communities was negatively related with the resilience composition (Rs-comp) ($P < 0.05$; Fig. 2b), meaning that the most functionally divergent communities exhibited the most significant changes in species composition in response to the climatic event. However, none of the FD indexes (F_{Rich} , F_{Eve} and F_{Div}) were significantly related to community resistance and resilience at the cover level or to Rt-comp (data not shown).

The resistance (Rt-cover) of the communities to the climatic event ranged from -0.88 to -0.11 and was related positively to RDMC_{CWM} ($P < 0.05$; Fig. 3a) and SDMC_{CWM} (marginally significant) and negatively to SRA_{CWM} ($P < 0.05$; Fig. 3b). On the other hand, the resilience (Rs-cover) of the communities to the climatic event (after 8 years) ranged from -0.83 to 2.13 and was related positively to LChl_{CWM} ($P < 0.05$; Fig. 3c).

Our results indicate that there were several significant changes in the community functional traits (3 out of 10 traits) with time, independent of the site (see supplementary Table S2). The community-weighted values of three traits (LChl_{CWM} , RDMC_{CWM} and Phg_{CWM} 'marginally significant') increased after the event (+2 years) but returned to pre-event values in the +8 years survey (Fig. 4). The community values (weighted means) of seed mass (S_{massCWM}) increased over time, with a significant change between pre-event and +8 years (Fig. 4c).

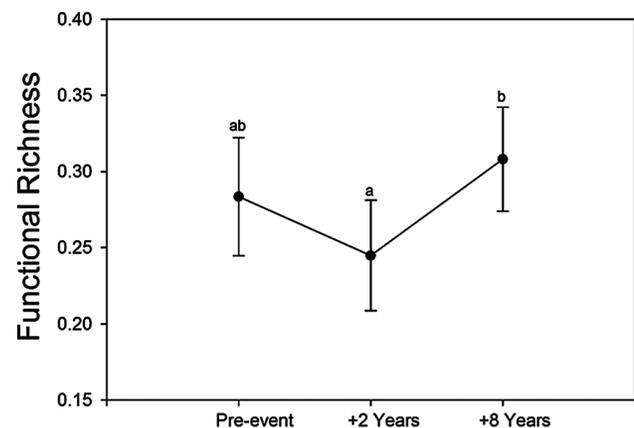


Figure 1: differences in the functional diversity index (functional richness) with time (pre-event, +2 years, +8 years). Different letters denote significant differences between groups (repeated-measures ANOVA, least significant difference *post hoc* test).

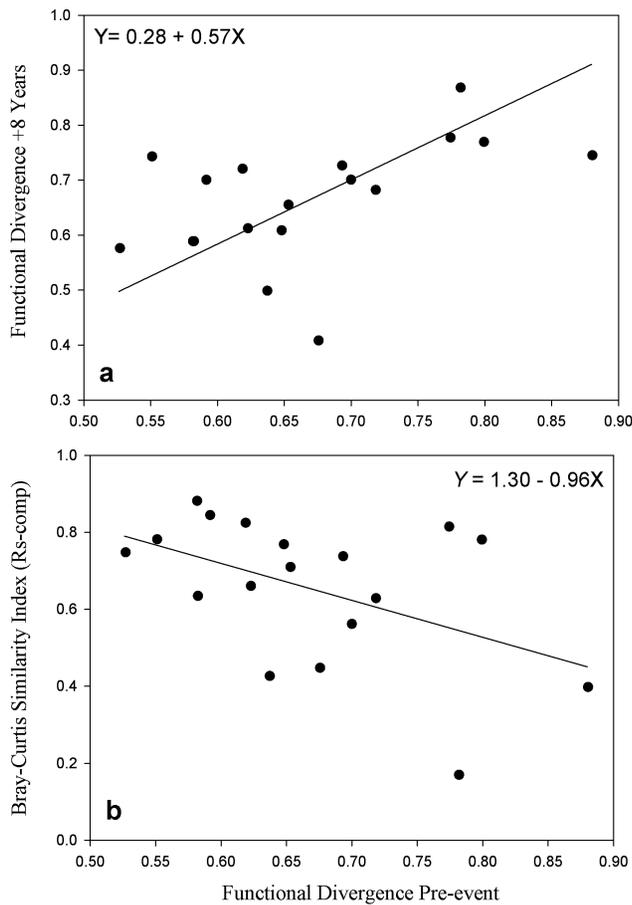


Figure 2: relationship between the functional divergence (pre-event) and (a) the functional divergence after 8 years and (b) the Bray-Curtis similarity index. The significance level was $P < 0.05$ for the two cases.

Stepwise discriminant analysis indicated that the adult and recruit groups differed in functional richness (F_{Rich}) and seed mass ($S_{massCWM}$), since these variables explained most variation in the analysis (Fig. 5). Only the first function of the discriminant analysis that corresponded to opposite values of F_{Rich} and $S_{massCWM}$ was significant ($P < 0.001$) and explained about 94% of total variance. All pairwise comparisons between groups had significantly different distances ($P < 0.005$, except +2 and +8 years adults which showed no differences). The communities of juveniles (+8 years) showed higher values of $S_{massCWM}$ and lower values of F_{Rich} than seedlings (+2 years). Also, seedlings had higher $S_{massCWM}$ and lower F_{Rich} values than adults (both +2 and +8 years) (Fig. 5).

DISCUSSION

This study supports the high functional resilience of Mediterranean shrubland communities to different disturbances, that has been widely reported after wildfires (Díaz-Delgado et al. 2002; Lloret and Zedler 2009), and expands its significance for other strong environmental fluctuations such

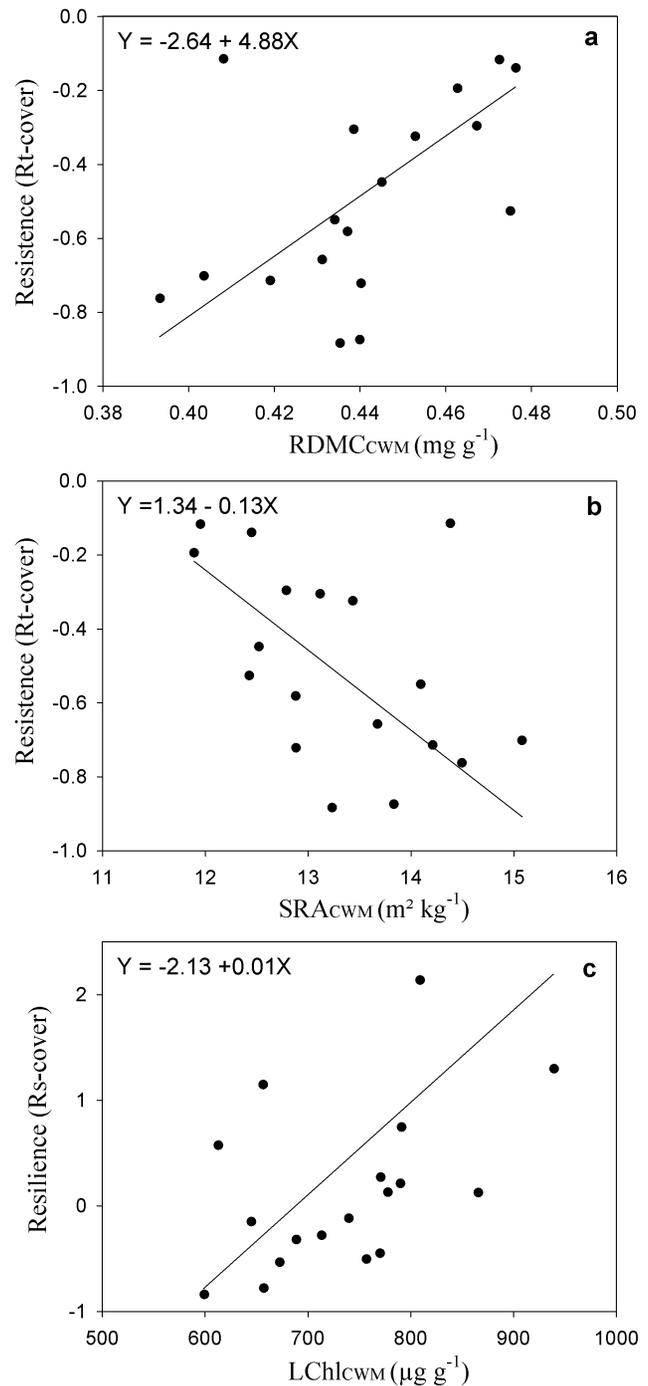


Figure 3: relationship between the community resistance and community functional traits: (a) root dry matter content (RDMC_{CWM}) and (b) specific root area (SRA_{CWM}); and between the community resilience and (c) community chlorophyll content (LChl_{CWM}). The significance level was $P < 0.05$ for all cases. See Table 1 for abbreviations.

as those derived from extreme climatic events. In addition, our findings reveal that these resilience mechanisms do not necessarily imply that the same species composition remains at a local scale. After an episodic disturbance plant competition could decrease, thus facilitating species replacement

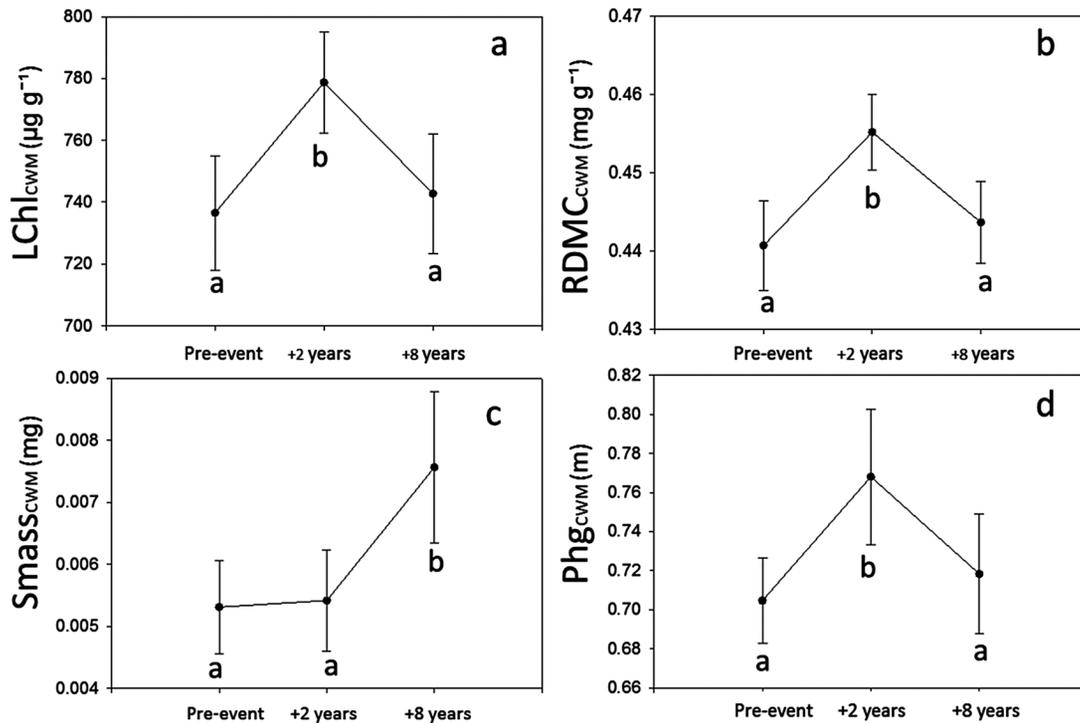


Figure 4: differences between community-weighted (CWMs) traits with time (pre-event, +2 years, +8 years). See abbreviations in Table 1. Different letters denote significant differences between groups (repeated measures ANOVA and least significant difference *post hoc* test).

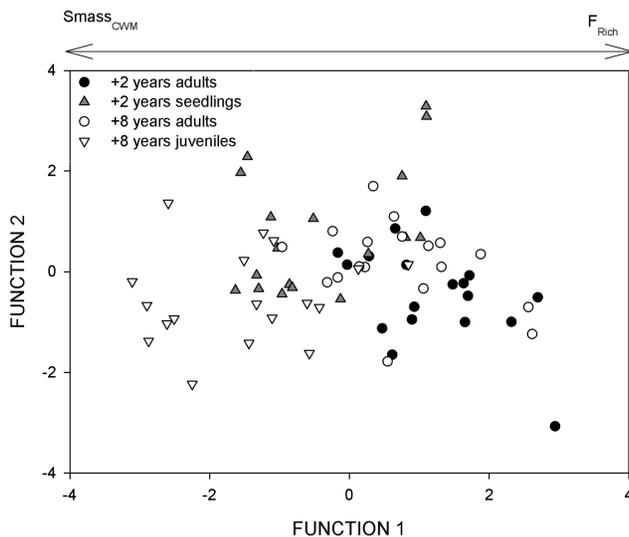


Figure 5: mean scores of the different vegetation communities on the two canonical discriminant functions obtained by stepwise discriminant analysis. Only the first function was significant ($P < 0.001$) and was determined by F_{Rich} and $S_{massCWM}$. Discriminant analysis was performed for the different surveys, with the functional community traits (CWM) and functional diversity indexes as independent variables and the groups of adults and recruits 2 and 8 years after the event (+2 years and +8 years adults, +2 years seedlings, +8 years juveniles) to be discriminated. See Table 1 for abbreviations.

(Fattorini and Halle 2004), but we did not observe major changes in the functional structure of the communities in the short-or medium-term.

Effects of the climatic event on the functional diversity

The functional diversity (measured as F_{Rich}) of the shrubland communities tended to diminish after the extreme climatic episode, but the initial diversity values had been restored after 8 years. This decrease in functional richness can be explained mostly by the response of some individual species (Mason *et al.* 2005), such as *Calluna vulgaris* which was not recorded 2 years after the event but had increased its abundance 8 years after (supplementary Table S1). This later increase could be attributable to the well-known resprouting ability of this species. However, a change in functional richness does not always imply a change in other functional indexes (F_{Eve} and F_{Div}), particularly when the abundance within the niche space remains invariable (Mason *et al.* 2005). The variation of functional richness indicates that the stressful environmental conditions of high water deficit and low temperature acted as a temporal filtering pulse on the vegetation. A higher functional diversity may imply a higher number of species groups living at the edge of their physiological tolerance thresholds. This, in turn, may mean that plants from a higher number of species will be stressed, damaged or dead (Parmesan *et al.* 2000) due to a variety of hazards and extreme climatic episodes, potentially promoting notable compositional changes (Stampfli and Zeiter 2004). Thus, as we hypothesised, the climatic episode that happened in 2005 induced high canopy losses in the Doñana shrubland, operating as an environmental filter that produced a remarkable loss of functional diversity, initially increasing the functional homogeneity.

The loss of plant cover of the dominant species allowed the establishment of others *via* sexual regeneration (del Cacho and Lloret 2012) or favoured their self-replacement due to the resprouting potential of some of these shrubs (Lloret and Zedler 2009). Such a high rate of community recovery might explain the subsequent increase detected in functional richness 8 years after the event, and hence the high recovery rate of the functional heterogeneity.

With regard to the functional divergence, which indicates the abundance of species with specialized functional trait values (Villegger et al. 2010), the communities with higher values of F_{Div} exhibited a lower resilience composition (R_{s-comp}) value with time (i.e. lower stability). Thus, a higher functional divergence was associated with a lower stability of species composition over time. However, these communities maintained higher values of functional divergence 8 years after the event. They did not suffer a significant loss of functional diversity in spite of experiencing higher rates of species replacement. This combination of high functional diversity and species turnover can be possible when changes in abundance occur in species that are functionally redundant, likely because their functional traits are related to the major drivers of ecosystem processes in our case response to water deficit (effect traits) or because it allows the maintenance of populations in our case mostly by seedling establishment (response traits) (Villéger 2010). In general, a disturbance in the ecosystem can promote the replacement of dominant species by other, less abundant competitors with similar functional properties (Naeem 1998; Walker et al. 1999), which does not induce strong changes in ecosystem functioning (Cingolani et al. 2005; Schindler 1990). In our case study, two of the most dominant species prior to the climatic event, *Halimium halimifolium* and *Rosmarinus officinalis* (supplementary Table S1), were partially replaced by other, functionally closer species such as *Cistus libanotis* and *Lavandula stoechas* after the climatic episode, as shown by their relative proximity in the PCA analysis (supplementary Fig. S4). Besides, communities with higher F_{Div} maintained their levels over time, suggesting that the most diverse communities have more variable niche widths and, thereby, higher functional stability (Tilman 2004).

Functional traits and stability after the extreme climatic event

The most stable shrubland communities (with more resistance) were those dominated by species having traits more closely associated with drought resistance, such as higher values of root and stem dry matter ($RDMC_{CWM}$ and $SDMC_{CWM}$) and lower values of specific root area (SRA_{CWM}) (Poorter and Markesteijn 2008). A large thawing rate in drought-prone ecosystems increases the probability of xylem embolism, as a result of high daily temperature oscillations (Granda et al. 2014). Thus, higher values of $SDMC$ might confer an advantage because they reduce the plant vulnerability to xylem cavitation promoted by unusually low temperatures (Hacke

et al. 2001). Similarly, Polley et al. (2013) and Majekova et al. (2014) found, in grasslands communities, that LDMC was the best predictor associated with greater population temporal stability, the more conservative and slow-growing species being more stable over time.

In addition, the communities with higher rates of recovery of plant growth after the disturbance (higher resilience) were positively related to higher values of chlorophyll in their dominant species. A higher concentration of LChl is closely correlated with a higher mass-based maximum photosynthetic rate (Evans and Poorter 2001), and thus with faster plant growth (Poorter and Remkes 1990). Previous studies have also shown that ecosystems with a higher flux of energy are usually more resilient to disturbances, likely because they have the potential to exhibit rapid rates of vegetation recovery (Begon et al. 2006).

Our results are in accordance with previous studies suggesting that plants have developed mechanisms of stability to cope with adverse climatic stressors. Thus, whereas the ability to tolerate the climatic event is restricted to certain functional traits related with a resource-conservation strategy, we found that one trait of the plants which correlated with their resilience after disturbance was related to their acquisition strategies. However, in spite of the contrasting patterns obtained in this study, we found that the existence of relationships between community functional traits and resistance or resilience responses was limited to a relatively low number of functional attributes. There are several ways to interpret this limited ability of the community functional traits to act as predictors of community resistance/resilience to disturbances. On the one hand, the shrub species of 'monte blanco' share similar functional characteristics that should be well adapted to the dry environment and the great seasonal thermal amplitude of the Mediterranean environment that they inhabit (Diaz-Barradas et al. 1999; Granda et al. 2014; Zunzunegui et al. 2005). In this sense, when considering groups of species belonging to environmentally similar sites, the general trends (e.g. the axis of acquisition-conservation strategies; Wright et al. 2004) became weaker or disappear (de la Riva et al. 2016b). At a larger spatial scale, all the species studied tend to exhibit a more conservative strategy and are closely grouped in the same functional space within the regional species pool (de la Riva et al. 2016b; supplementary Fig. S5). On the other hand, the combination of different climatic stressors (low temperatures and water deficit) during the event, which could result in contrasting or even opposite relationships with certain functional traits (Dreesen et al. 2012; Granda et al. 2014), may be responsible for the limited relationships found between functional traits and stability indexes (resistance or resilience).

After the extreme climatic episode analysed in this study, the main change in the functional characteristics of the community was an increase in the relative abundance of dominant species with greater root dry matter content, LChl or plant height. Thus, the climatic event promoted rapid changes in

the structure and composition of the shrubland communities studied, with a massive dieback of canopies (del Cacho and Lloret 2012). This pattern is consistent with previous reports on changes at the regional scale in woodlands from SW North America (Breshears *et al.* 2005). However, the functional attributes of the communities of Doñana exhibited, overall, a remarkable resilience, as they tended to return quickly to their initial (pre-event) states.

Recruitment, community structure and functional diversity

The combination of demographic and functional attributes in our study enabled us to detect remarkable differences in the functional diversity of different demographic stages in the shrubland communities studied: it was higher for the adult than for the recruit stage. There was a lower number of species for the seedling and juvenile stages than for the adults, likely because not all the shrub species were successful recruiters. This uncoupling between the composition of the canopy and the community of seedlings and saplings has been observed in other Mediterranean forests (Pérez-Ramos and Marañón 2012), which supports the possibility of future shifts in species composition. We propose that the extreme drought event could also have resulted in lower functional diversity (F_{Rich}) in the recruits since it could have affected more severely the early life-history stages of some species (González-Rodríguez *et al.* 2011; Pratt *et al.* 2007; Vallejo *et al.* 1999). In addition, when exploring the more relevant traits of the recruits, we found higher community values of seed mass at the seedling and juvenile stages than at the adult stage. Seedlings which originate from larger seeds could have a competitive advantage to cope with drought, because they are able to develop deeper roots and forage for water in deep soil layers over the dry season (Quero *et al.* 2007; Westoby *et al.* 2002).

In conclusion, extreme climatic events can initiate stochastic succession, with more important effects over the first years (Kreyling *et al.* 2011). In this study, we show how these climatic events also have consequences for the functional properties of the community, with potential influences on ecosystem functioning (Grime 2001). However, the high recovery ability detected in these shrubland communities supports the existence of important mechanisms of resilience to extreme climatic episodes (Lloret *et al.* 2012). Our findings reveal that, in spite of the stability of the functional structure, replacement by species with similar traits exists. In addition, there was no colonisation by new species in the community and the recruits did not provide substantial differences to the community functional structure, seed mass being the only trait whose community values (weighted means) differed significantly between the adult and recruit stages.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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