

Climatic disequilibrium of recruit communities across a drought-induced die-off gradient in Mediterranean shrubland

Abstract

Positive plant-plant interactions (facilitation) could enhance recruitment and establishment of species less adapted to local macroclimatic conditions. A major cause of such effect is climatic buffering, which would imply an increase in the mismatch between the macroclimatic conditions and the climatic requirements of the existing community – climatic disequilibrium - of plants living under canopies. Here we explore the effect of drought-induced defoliation of Mediterranean shrubland canopy on the recruitment of woody species. We analyzed the differences in the climatic disequilibrium across different categories of canopy defoliation and plant-plant interactions - facilitation, neutral and inhibition -. Climatic disequilibrium was estimated as the Euclidean distance in the multivariate environmental space between observed macroclimate and community inferred climate. The inferred climate was calculated by averaging the coordinates of the species' climatic niches centroids -obtained from species distribution -, weighted by the species' relative abundances in each community. We found that the recruiting community growing under canopy showed higher climatic disequilibrium than in gaps. The facilitated recruiting community growing under dead and alive canopy showed the highest disequilibrium, followed by the one growing under mid-affected canopy. The climatic disequilibrium of the recruiting communities experiencing neutral and inhibited interaction was not affected by canopy defoliation. These findings point out that the climatic disequilibrium of the recruiting community is determined by the facilitation-competition balance. Alive canopy provides climatic buffering, but it also implies competition, while dead canopy may provide some structural climatic buffering, without implying competition for resources. These results highlight the relevance of incorporating plant-plant interactions, particularly facilitation, to better forecast plant community responses to extreme climate events and climate change.

Keywords: Facilitation, Plant recruitment, Species climatic niche, Drought induced die-off, Climatic disequilibrium, Climatic debt, Plant–plant interactions, Global change ecology, Plant population and community dynamics.

1. Introduction

Extreme climatic events (ECEs) - drought, heatwaves, cold snaps, windstorms, flooding - are expected to increase in the next future due to climate change, deeply altering abiotic and biotic conditions of ecosystems (IPCC, 2014). Among them, the impacts of severe droughts are expected to increase in magnitude, frequency and length in many regions (Ploughe *et al.*, 2019; Smith, 2011). In fact, die-off and mortality due to extreme drought episodes have already been reported on forests (Allen *et al.*, 2010; Breshears *et al.*, 2005) and shrublands (Jacobsen *et al.*, 2018; Pérez-Navarro *et al.*, 2021; Sapes *et al.*, 2017) around the world. This new scenario of raising aridity would produce strong impacts on the biodiversity and ecosystem functioning in different ways, even leading to vegetation shifts (Anderegg *et al.*, 2012; Martínez-Vilalta & Lloret, 2016).

The capacity of systems to avoid abrupt shifts (i.e., resilience in a broad sense) constitutes a major object of research, particularly in a climate change context (Davis & Shaw, 2001; Batllori *et al.*, 2020; Geng *et al.*, 2019;). Indeed, vegetation shifts are not as common as could be expected. For instance, at demographic level, it is required a mismatch between recruitment and mortality in the medium-term (Lloret *et al.*, 2012; Martínez-Vilalta & Lloret, 2016). Therefore, processes that balance this recruitment-mortality ratio after ECEs can be considered stabilizing mechanisms (Bertrand *et al.*, 2011; Lloret *et al.*, 2012), and they include: population tolerance or adaptability -related to phenotypic variability or plasticity-, release of competition and antagonisms, reinforcement of positive interactions, and/or presence of favorable microclimatic conditions (Benito Garzón *et al.*, 2011; Lloret *et al.*, 2012). Plant-plant interactions, and particularly positive ones, may play a vital role in these mechanisms, thus in ecological stability (Brooker, 2006; Michalet & Pugnaire, 2016). Interactions between recruiting plants and canopy - recruit-canopy, hereafter - modulate community demography by enhancing the recruitment and establishment - facilitation -, thus, counterbalancing competition (Alcántara *et al.*, 2019; Brooker, 2006; Ploughe *et al.*, 2019; Michalet & Pugnaire, 2016). Therefore, facilitation would promote the persistence of species prone to be absent according to macroclimatic conditions.

The stress gradient hypothesis (SGH) proposes that the balance between facilitation and competition depends on the degree of environmental stress. Thus, facilitative interactions would prevail under high-stress conditions while competitive ones would do under low-stress conditions (Ploughe *et al.*, 2019; Michalet & Pugnaire, 2016). Consequently, under extreme drought episodes or gradual increments of dry periods, the facilitation effect on microclimate

conditions would appear enhanced as a stabilizing mechanism. This mechanism likely increases the system resistance and resilience by promoting the survival and recruitment of plants during and after ECEs (Lloret & Granzow-de la Cerda, 2013; Lloret *et al.*, 2012; Reyer *et al.*, 2015).

Under a climate change context, stabilizing mechanisms could also hinder the migration and colonization of species that are prone to live under new conditions emerging with climate-driven disturbances (Bertrand *et al.*, 2011; Svenning & Sandel, 2013; Urban *et al.*, 2012). So, stabilizing mechanisms would be translated into an increasing mismatch between the macroclimatic conditions and the climatic characterization of the existing community. This mismatch is known as climatic disequilibrium (CD, Blonder *et al.*, 2015; Duchenne *et al.*, 2021; Svenning & Sandel, 2013), and it would be higher in resilient communities as a consequence of the maintenance of the composition of the established community. In contrast, local extinctions or abundances changes triggered by climatic disturbances could lead to a CD reduction due to a raising selective pressure against less climatically suitable species (Dullinger *et al.*, 2012; Pérez-Navarro *et al.*, 2021).

Accordingly, if canopy-recruit interactions are driven by facilitation, the CD of the recruiting community is expected to be higher than non-facilitated ones, as climatic buffering promoted by canopies would allow the persistence of species less adapted to macroclimatic conditions. In contrast, if competitive interactions are dominant we can expect reduced values of CD of the recruiting community as plants farther from their climatic optimums tend to show poorer performance (Sapes *et al.*, 2017) and therefore are more likely to be excluded by competitive exclusion. Previous studies have found higher values of CD in plant communities growing under canopies, suggesting canopy-induced buffering of macroclimatic temperatures (Zellweger *et al.*, 2020), and manipulative experiments have reported differences in under-canopy microclimatic conditions according to the degree of canopy defoliation (Anic *et al.*, 2021). However, despite the relevance of plant canopies on buffering macroclimatic conditions, there is a gap in our knowledge of how canopy die-off could affect facilitation and recruiting capacities, thus modifying the CD of understory communities.

In this study we explore the effect of drought-induced defoliation of shrubland canopy on recruit-canopy interactions, analyzing changes in the community CD of the recruiting community of woody species. Specifically, we quantified the interactions between recruiting species and the state of the canopy in a Mediterranean shrubland which suffer recurring droughts, considering open gaps and canopies with different degrees of defoliation (die-off). This quantification will

likely allow detecting subsets of recruiting species (subcommunities) experiencing positive (i.e. facilitation), negative (i.e., inhibition) or neutral effects.

Specifically, we aim (i) to test the existence of a positive effect of the shrubland canopy on the overall recruitment of woody species; (ii) to compare the CD in the facilitated, neutral and inhibited recruit subsets of species, provided they exist; (iii) to test the effect of the canopy defoliation degree on the CD of the overall recruiting community; and (iv) to test the effect of canopy defoliation degree on the CD in the facilitated, neutral and inhibited recruiting subcommunities. We hypothesized that (i) canopy will have an overall positive effect on the recruitment; (ii) the facilitated subcommunity will present the highest CD due to the canopy effect on microclimate, while the inhibited subcommunity will present the lowest CD; (iii) defoliation would generally diminish the canopy buffering, so the CD will diminish with the degree of defoliation; (iv) particularly, the CD of the facilitated subcommunity will decrease as defoliation increases, while the CD of the inhibited subcommunity will increase, since drought affectation is also expected to diminish the competitive capabilities of adults.

2. Materials and methods

2.1. Description of the study area

The study area was the Doñana National Park, sited in southwest Spain. The climate is semiarid Mediterranean, characterized by the concurrence of the hottest and driest months. The mean annual temperature is 18.2 °C, reaching 32.7 °C on average in the hottest month (July) and 5.9 °C on average in the coldest one (January). Furthermore, the mean annual precipitation is 525 mm, with a great intra-annual variability (AEMET, 2021). The site suffered several severe droughts that affected the entire Iberian Peninsula between 1994 and 2019. Concretely, in 2010 decade the site suffered five drought periods (2011/12, 2013/14 y 2014/15 y 2018/19) and below-average rainfall the remaining years, becoming the driest decade since the 1978/79-1986/87 period (Cifuentes Sánchez, 2021). The 2004/2005 drought was especially severe, with a total rainfall of 169.8 mm (30% of the historical mean precipitation). In addition, such drought coincided with a particularly cold winter with several days below 0 °C (Figure 1, Díaz-Delgado, 2006). Therefore, elevated die-off was reported across shrubland species in spring (Díaz-Delgado, 2006) which has recovered irregularly (Paniw *et al.* 2021).

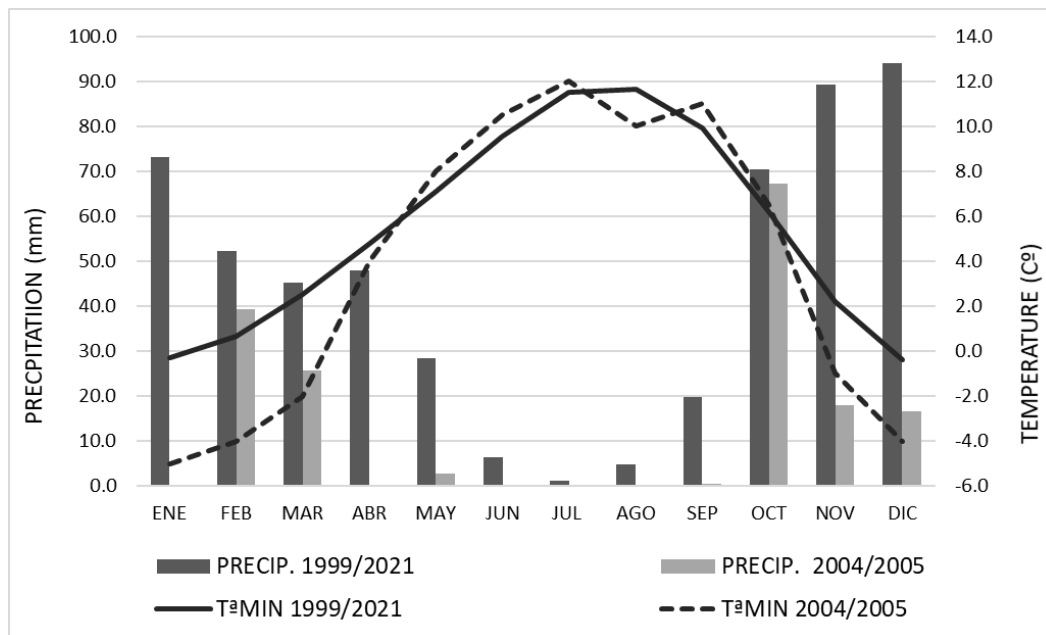


Figure 1. Monthly mean precipitation and monthly minimum absolute temperature of the historical record and the drought episode (Source: Estación Biológica de Doñana, 2021).

The study was focused on shrublands, particularly in “monte-blanco”, a heliophilic and xerophilic vegetation mostly composed of chamaephytes and nanochamaephytes with high capacity for water uptake and storage in dry environments. These shrublands correspond to *Halimio halimifolii-Stauracanthetum genistoidis* (Rivas-Martínez *et al.*, 1980), composed predominantly of shrubs such as *Cistus libanotis* L., *Cistus salvifolius* L., *Cytisus grandiflorus* (Brot.) DC., *Erica scoparia* L., *Halimium commutatum* Pau, *Halimium halimifolium* (L.) Willk., *Helicrhysum picardii* Boiss. & Reut., *Lavandula stoechas* L., *Rhamnus lycioides* L., *Salvia rosmarinus* Schleid., *Stauracanthus genistoides* (Brot) Samp., *Thymus mastichina* L., and *Ulex australis* Clemente (García Murillo & Sousa Martín, 1999; Rivas-Martínez *et al.*, 1980).

We tested the effect of the canopy to buffer temperature (°C) and relative air humidity (%) during spring (March) and summer (August) under a set of plant canopies of two representative species (*Salvia rosmarinus* and *Halimium commutatum*) with different defoliation degree and in gaps (see Appendix S1 for details). In spring, significantly higher humidity in the 22:00 – 8:00 timeslot and lower temperature in the 11:00 – 18:00 timeslot were recorded under the canopy. In summer, higher humidity and lower temperature in the 10:00 – 17:00 timeslot were recorded under the canopy. Altogether these measures supported the ability of shrub canopy to modify the microclimate.

2.2. Recruitment data

Data was collected during March 2021. We sampled 45 plots of 4 × 20 m separated at least 150 m from each other. In each plot, all recruits of woody species and their location (in an open gap or under canopy) were recorded. We considered a recruit each woody plant (i.e., with some signs of lignification) older than one year (i.e., without recent cotyledon scars), but without visible signs of attaining the first reproductive stage (absence of buds, flowers, or fruits. If recruits were found under canopy, its defoliation degree was visually estimated.

To standardize the number of species interactions (recruit-canopy adult) by canopy cover (Alcántara *et al.*, 2019), two 20 m transects were established in each plot, one in the middle of the plot, and the other in one plot side (selected trying to maximize the representativeness of the plot cover). In each transect, the length of gaps and of each individual canopy segment were measured.

Defoliation degree was visually estimated as the proportion of remaining green canopy, ranging between 0% (totally defoliated, dead plant) to 100%, (full green canopy, healthy plant) (Lloret & García, 2016). Visual estimations of defoliation have demonstrated to be a robust approach to determine plant defoliation compared with methods based on dry-matter weight of alive plants (Sapes *et al.*, 2017) or length measures of dead or defoliated parts of stems (Pérez-Navarro *et al.*, 2019).

The kind of interaction - facilitation, neutral or inhibition - was determined by using a linear mixed effects model (LME) (lmerTest R package, ver. 3.0-1; Kuznetsova *et al.*, 2017). The response variable was the difference between the observed recruits of a given species registered under canopies and the expected number of recruits (R_E ; see next paragraph) of the same species growing under canopies if they showed a neutral interaction with them and, therefore, its distribution in the plot were random (Alcántara *et al.*, 2018), divided by R_E to standardize such difference. The species identity of recruits was included as explanatory variable and the plot as random factor. The contribution of each plot to the model was weighted by the total number of observed recruits in each plot.

The R_E of a given species per plot is proportional to the total number of recruits (R_T) and the total canopy cover in the plot (regardless canopy species identity, which is not considered in our study). It was calculated as the product of R_T by the total percentage of canopy cover in the plot (%Canopy):

$$R_E = (R_T \times \%Canopy) / 100$$

Next, we performed post-hoc analyses, considering a slope intercept of 0. When, for a given species, the difference between the observed value of recruits under canopy and the expected one was significantly smaller than 0 (p -value < 0.1), the species was considered as inhibited. If the difference was significantly higher than 0, the species was considered as facilitated. Finally, it was considered a neutral relationship if the difference was not significantly different from 0. This procedure is similar to the chi-square test, however the use of LMEs allows weighing the influence of each sample (plot) in the analysis, and obtaining a measure of significant.

Two datasets of recruiting subcommunities were established within each plot attending to two different criteria. One set was established according to canopy cover criteria: growing under dead individuals (with less than 10% of green canopy), under affected individuals (green canopy ranging from 10% to 70%), under alive individuals (with more than 70% of green canopy) and growing in open gaps. The other set of subcommunities only included individuals sited under canopies and was classified according to the recruit-canopy interactions criteria: facilitated, or inhibited.

2.3. Community climate characterization

2.3.1. Species occurrences

The geographical distributions of the observed 22 species were compiled from the Global Biodiversity Information Facility (GBIF) database (GBIF 2021, <http://www.gbif.org>; see Table S1 Appendix S2). The corresponding occurrences were filtered to avoid geographic and taxonomic inconsistencies (f.e., inaccurate synonyms). Finally, possible sampling bias and spatial autocorrelation were prevented by reducing occurrences density to 1 per km² (equivalent to the grid resolution of the climate dataset; Franklin, 2010). As result, we obtained an occurrences dataset ranging from 42,500 to 140 observations per species.

2.3.2. Environmental data

We selected 12 bioclimatic variables from CHELSA database (ver 1.2, Karger et al., 2017) related to temperature and precipitation (1 km² resolution). They were calculated with average macroclimate data (mean temperature and maximum and minimum precipitation) from the period 1979 to 2013.

Relative to temperature, we used annual mean temperature, temperature seasonality, maximum temperature of the warmest month, mean temperature of the warmest quarter, minimum temperature of the coldest month and mean temperature of the coldest quarter (bio 1, bio 4, bio 5, bio 10, bio 6, bio 11, respectively). In relation to precipitation, we selected annual precipitation, precipitation seasonality, precipitation of the wettest month, precipitation of the wettest quarter, precipitation of the driest month, and precipitation of the driest quarter (bio 12, bio 15, bio 13, bio 16, bio 14, bio 17, respectively). Variables related to the interaction between temperature and precipitation (e.g., mean temperature of the wettest month) were discarded to avoid possible undesired orthogonal correlation effects.

2.3.3. Niche and climate disequilibrium modeling

At first, we built a common environmental space for all the target species by reducing the dimensionality of the selected 12 bioclimatic variables into two multivariate axes, using principal components analysis (PCA-occ *sensu* Broennimann *et al.* 2012). For such purpose, the scaled climate data corresponding to all species occurrences previously filtered were used. The first two axes explained 73.77% of the total climatic variability. The first axis (44.62% of the variability) overall correlated positively with temperature-related variables, while the second one (29.15% of the variability) overall correlated negatively with humidity-related variables (see Table S2 and Figure S1 Appendix S2).

Then, the species' realized niches were inferred by translating species' geographical occurrences into the common PCA and applying kernel density functions to smooth the density of occurrences. This procedure allowed each species to obtain an occurrence density for each cell of the climatic space. The smoothed functions also allowed reducing the effect of sample bias, which might not represent the real distribution of the species (Broennimann *et al.*, 2012). We used Gaussian kernel functions, selected the bandwidth matrix by cross-validation (Duong and Hazelton, 2005), and discarded density values under 0.05 density percentile to avoid outliers (Broennimann *et al.*, 2012).

The centroid of each species was estimated as the center of gravity of the species' niche. Then, the community inferred climate (CIC) of each subcommunity was calculated as the center of gravity of the centroids of all the species present in each subcommunity of each plot, weighted by their relative species abundance. The observed climate (OC) of each plot was obtained from CHELSA and was also translated to the common environmental space. Finally, the CD was

calculated for each recruiting subcommunity as the two dimensional Euclidean distance between these two values -CIC and OC- (Blonder *et al.*, 2015).

2.4. Statistical analyses

We analyzed the differences in the CD between different categories of subcommunities, using linear mixed effect models -LMEs- (lmerTest R package, ver. 3.0-1; Kuznetsova *et al.*, 2017). We run two different LMEs: i) with CD as response variable and canopy cover category (alive, affected, dead, gap) as explanatory variable; and ii) with CD as response variable and the recruit-canopy interaction category (facilitation, inhibition, neutral), the defoliation category (alive, affected, or dead) and the cross-product between them as explanatory variables. These two LMEs were needed because gap category could not be included in the second model addressing the effect of defoliation degree. In all cases, plot was included as a random factor and the total number of observations (recruits) of each subcommunity was included as a weighting factor. We also run post-hoc models (Tuckey test) for each model (emmeans package, ver 1.8.1-1).

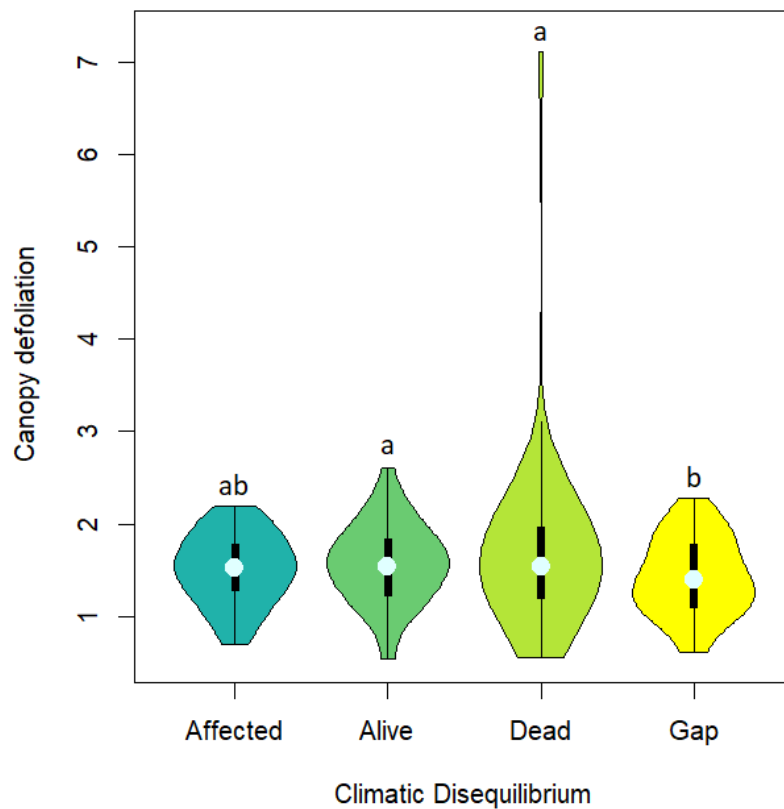
As some species were poorly recorded (less than ten individuals in total, see Table S1 Appendix S2) and each species can only be in one category of recruit-canopy interaction, thus affecting the category dispersion, the second model was run with and without these rare species, to analyze their contribution to the model results. Indeed, no differences between these two models including or excluding rare species were found (see Table S1 and S2 Appendix S3), and here we only show the results of the model including all the species. All statistical analyses were carried out with R version 4.0.3 (R core Team, 2020).

3. Results

A total of 5,181 recruits from 22 species were recorded in the 45 sampled plots (see Table S3 Appendix S3). The facilitated subcommunity was composed by recruits of seven species: *Cistus salviifolius* L., *Halimium commutatum* Pau, *Juniperus phoenicea* subsp. *turbinata* (Guss.) Nyman, *Pistacia lentiscus* L., *Salvia rosmarinus* Schleid., *Thymus mastichina* L. and *Stauracanthus genistoides* (Brot.) Samp. The inhibited subcommunity was composed by recruits of two species: *Halimium halimifolium* (L.) Willk and *Lavandula latifolia* Medik. Finally, the neutral subcommunity was composed by recruits of eleven species: *Asparagus horridus* L., *Cistus libanotis* L., *Cytisus grandiflorus* (Brot.) DC., *Erica scoparia* L., *Helianthemum hirtum* (L.) Mill.,

274 *Helichrysum picardii* Boiss. & Reut., *Lavandula stoechas* L., *Osyris lanceolata* Hochst. & Steud.,
 275 *Phillyrea angustifolia* L., *Pinus pinea* L., and *Ulex australis* Clemente (see S4 Appendix S3).

276 Community CD showed significant differences (p -value < 0.05) between canopy categories. As
 277 expected, the model predicted the lowest CD for the recruiting subcommunity in gaps ($1.38 \pm$
 278 0.06 , mean \pm SE hereafter), and recruits growing under dead plants had the highest CD ($1.50 \pm$
 279 0.07). Accordingly, post-hoc analyses (Tukey test) found significant differences between the CD
 280 of recruiting subcommunity in gaps respective to the ones established under dead and alive
 281 canopy (p -value < 0.05 ; Figure 2).



282
 283 Figure 2. CD of the recruiting subcommunities found under the different canopy categories (dead, affected and alive)
 284 and in gaps. Significant differences between categories are indicated with different letters on the bars (p -value < 0.05 ,
 285 Tukey test). The dot represents the CD means value.

286 The community CD of recruits also showed significant differences between recruit-canopy
 287 interactions categories, being the facilitated subcommunity the one with the highest CD ($1.91 \pm$
 288 0.11). Post-hoc analyses (Tukey test) showed significant differences between the CD in the
 289 facilitated recruiting subcommunity respective to the neutral and inhibited ones (Figure 3).

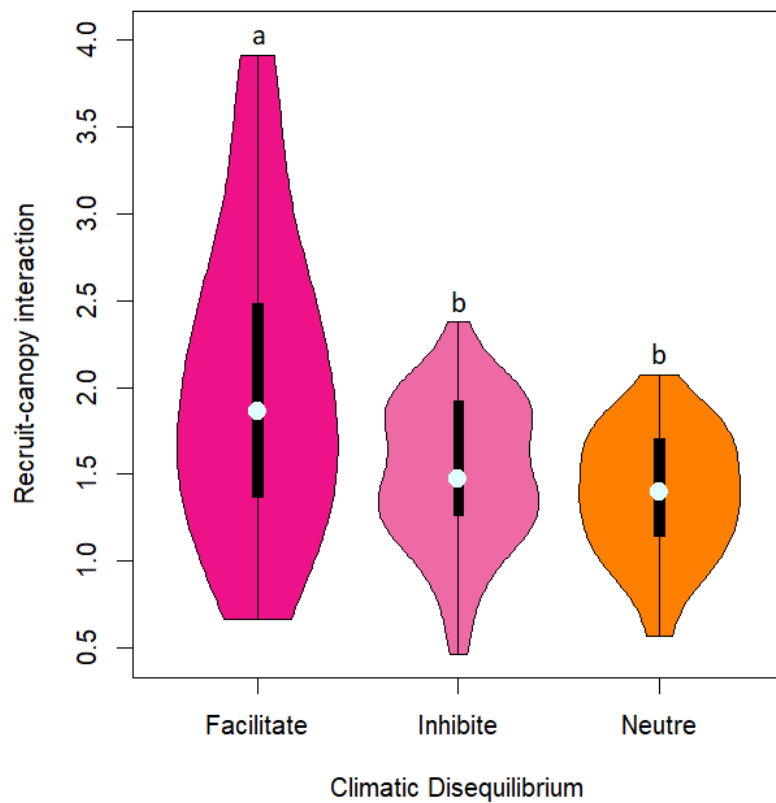


Figure 3. CD of recruiting subcommunities corresponding to the different recruits-canopy interaction categories (facilitated, inhibited, neutral). Significant differences between categories are indicated with different letters on the bars (p-value < 0.05, Tukey test). The dot represents the CD means value.

The overall cross-product of the recruit-canopy interaction and the canopy category did not show a significant effect (F-value = 1.63, p-value = 0.167) on the CD of recruiting communities (See Table S2 Appendix S3). However, post-hoc analyses (Tukey test) revealed significant differences in CD within the facilitated subcommunity: the CD of the facilitated recruiting subcommunity growing under dead canopy was significantly higher (2.39 ± 0.13 SE) than the one of the facilitated recruiting subcommunity under affected canopy (2.01 ± 0.09). Differences in CD between the recruiting inhibited and neutral subcommunities under different canopy categories were not statistically significant (Figure 4).

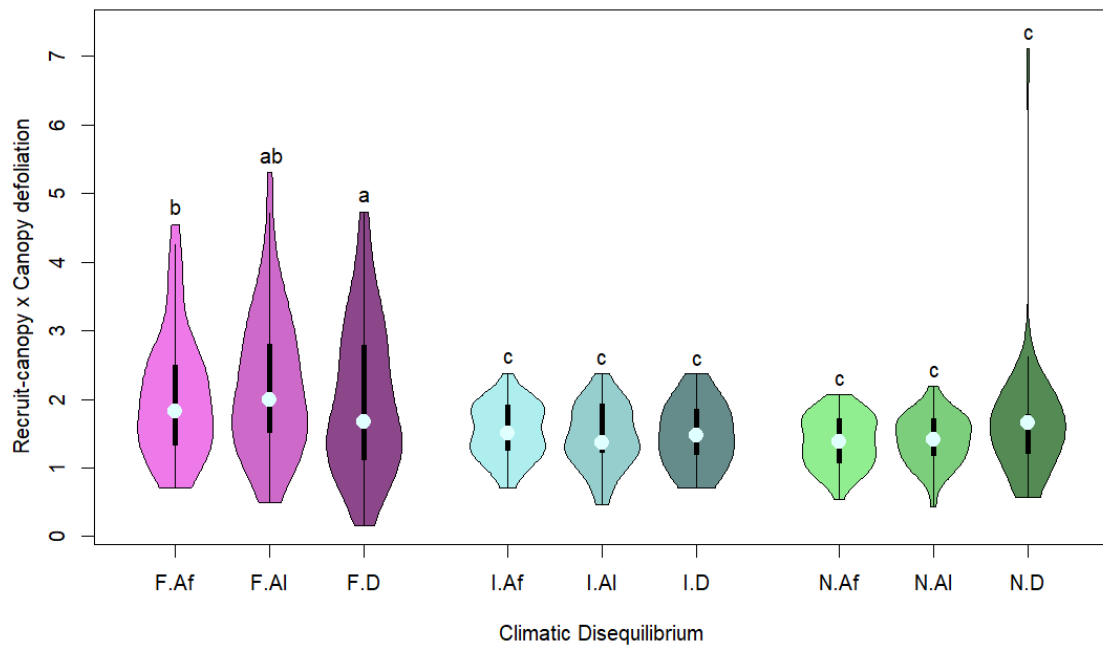


Figure 4. CD of the recruiting communities corresponding to different recruits-canopy interaction categories (facilitated, inhibited, neutral) under the different canopy categories (dead, affected and alive). Significant differences between categories are indicated with different letters (p-value < 0.05, Tukey test). The dot represents the CD means value.

4. Discussion

This study reveals the contribution of facilitation in determining the CD of the recruiting community. These results are consistent with tree canopy effects on CD of forest understory (Zellweger *et al.*, 2020), expanding the pattern to shrublands and communities experiencing climate change-induced ECEs. As hypothesized, recruits growing under canopy exhibited a higher CD than those growing on gaps. Accordingly, the subset of facilitated recruits showed higher CD than those that were inhibited by canopy or those that showed a neutral relationship. The effect of defoliation degree on the CD revealed more complex, likely due to the concurrence of different degrees of facilitation and competition (Resco de Dios *et al.*, 2014), according to the proportion of canopy defoliation.

4.1. Recruit-canopy interaction

Although the most common plant-canopy interaction was the neutral one (53% of cases), we found that the percentage of positive relationships, was clearly higher (37%) than the

percentage of negative - inhibition - ones (10%). This result agrees with our hypothesis and the SGH, considering that our semiarid study system suffers recurring drought and would be closer to the stress edge in the climatic gradient. These results are similar to those found in previous studies in which it was concluded that facilitating and inhibiting interactions equaled the number of neutral interactions in the Mediterranean forest (Alcántara *et al.*, 2018). However, the low representation of some study species might have influenced the observed proportions of recruits in the different interaction categories, resulting in an overestimation of neutral relationships.

Considering facilitation as any relationship in which one of the participants benefits while none is harmed (Stachowicz, 2001), several mechanisms could lead to that kind of interaction in the recruit-canopy relationship: perch effect, in which the plants (usually trees) standing out above the vegetation layer favor the deposition by animals of seeds from fleshy fruits (Bustamante *et al.*, 2012; Pausas *et al.*, 2006); herbivory exclusion, commonly mediated by spiny shrubs (Lloret & Granzow-de la Cerda, 2012; Saixiyala *et al.*, 2017); climatic buffering (Lozano *et al.*, 2020; Lozano *et al.*, 2017); chemical exudates which increase the availability of soil nutrients and water (Wang *et al.*, 2020) or inhibit depressing allelochemicals (Xia *et al.*, 2016); symbiosis with soil microorganisms or mycorrhizal networks (van der Heijden & Horton, 2009); or improvement of soil structure (Svenning and Sandel 2013). Except for the climatic buffering, these mechanisms are not directly related to a preferential increase in the performance of the species far from their climatic optimum. However, they indirectly may diminish the relative role of climate constraints on demographic processes. In addition, some studies advocate that the propensity to maintain positive relationships will be more likely in species less tolerant to stress and in those with the highest competitive response (Liancourt, 2005).

Our results evidence the effects of recruit-canopy interaction in the CD of the recruits, as the lowest CD was found in recruits growing in gaps and the facilitated subcommunity shows a significantly higher CD than the neutral and the inhibited ones, according to the study's hypothesis. Therefore, this result suggests that species growing far from their climatic optimum are prone to experience facilitative relations with canopy, which will allow recruitment under stressful conditions (Choler, 2001; Liancourt, 2005). These results also support the conclusion of previous studies, in which positive interactions are considered to expand the species' realized niche (Bruno *et al.*, 2003). This relationship between climatic requirements and population success is often mediated by functional and demographic traits, as previously observed in the studied system (Paniw *et al.*, 2021). The results also agree with the measured microclimatic record, which demonstrates the climatic buffering capacity of shrubland canopies. Although

previous studies have demonstrated the impact of the canopies' buffering capacity on the understory of temperate forests (Zellweger *et al.*, 2020), this study highlights the buffering capacity of even medium to small sized shrubs, which constitute key refuges for survival in arid environments.

Otherwise, the fact that the CD of the inhibited recruiting subcommunity was not significantly lower than the CD of the neutral subcommunity, does not support that competition is excluding those species that are climatically less suitable. This may be due to the existence of competitive mechanisms that are not directly related to climatic suitability, like those related to shade intolerance (Nieto-Lugilde *et al.*, 2014), soils preference and nutrient uptake (Yan *et al.*, 2016), or the synthesis of allelopathic compounds (Pierik *et al.*, 2013). Nevertheless, this absence of significant differences should be taken with caution, since the inhibited subcommunity was composed by a low number of species and also of individuals.

4.2. Canopy defoliation

When assessing the role of canopies with different degrees of defoliation, significant differences between the CD of the recruit subcommunities growing under alive, affected, or dead canopy were not found, contrasting with previous studies where highest CD was associated with areas of decreasing canopy (Zellweger *et al.*, 2020). The small differences found between these canopy categories may be due to the variability associated with the different species in the canopy, which likely exhibit distinct structural features. This variability between canopy species may have masked the effect on the recruiting community of the broad defoliation categories which indistinctly included different canopy species. This indicates the importance of considering not only the species identity of recruits, but also the identity of canopy species in future studies. Also, the assessment of the role of species' functional traits could be useful to find out what factors make a species a good facilitator (Perea *et al.*, 2021). This would increase our ability to predict community dynamics in the face of drought events or changing macroclimatic conditions (Paniw *et al.*, 2021).

4.3. CD of facilitated, neutral and inhibited subcommunities and defoliation degree

According to the study hypothesis, post hoc analyses showed significant differences in CD within facilitated subcommunity when considering different canopy defoliation categories, although the cross-product between canopy defoliation and recruits-canopy interaction categories did

not show a significant effect in the general model. In that subcommunity, contrary to our expectations, the recruits growing under dead canopy exhibited similar CD value than the recruits growing under alive canopy, while the recruits established under affected canopy had the lowest CD. That is, there was a non-linear pattern in which CD of recruiting communities did not diminish proportionally when canopy defoliation increase and it may be explained by the different contribution of two main effects of canopy on the recruiting community: climatic buffering and competition.

Although some facilitation mechanisms - such as those involving chemicals exudation or mycorrhizal symbiosis - require the canopy plant to be alive, previous studies indicate that dead canopy could still providing structural positive effects on recruits by increasing soil moisture and reducing soil and surface temperature - thus enhancing microclimatic buffering - (Resco de Dios *et al.*, 2014), and also by providing perch to dispersal, and by excluding herbivory, particularly under spiny canopy. This effect combined with an absence of competition counterpart could allow the establishment of species with a low-stress tolerance which are not prone to recruit under alive canopy due to its low competitive response (Liancurt, 2005). On the other side, alive canopy provides higher facilitative climatic buffering linked to its higher canopy cover but potentially also implies competitive relationships, so potentially excluding those species with low competitive response and explaining similar disequilibrium values in the recruiting communities under alive and dead canopies. Finally, defoliated canopies could produce competitive relationships with the recruits and additionally would have a diminished climate buffering capacity, explaining lower CD of the facilitated subcommunity living under affected canopy. Therefore, these results highlight the importance of studying facilitative relationships considering the canopy defoliation status, since the specific composition of the facilitated community may change depending on the state of the vegetation.

In contrast, the absence of differences in the CD of neutral and inhibited recruiting subcommunities growing under different canopy state might imply that the composition or species abundances of these subcommunities are independent of canopy defoliation, which actually was expected in the case of the neutral subcommunity. Therefore, we can infer that, as only a subset of the species community is influenced by the canopy state, the canopy effect on the recruitment is species-specific. The specificity of the facilitating relationships has been previously reported (Alcántara *et al.*, 2018; van der Heijden & Horton, 2009) and reveals the importance of this kind of interaction in species distribution or community dynamic models (Brooker *et al.*, 2008).

According to these results and assuming that climatic buffering is a widespread phenomenon under canopies, some species may remain in the community despite being far from their climatic optimum when facing an extreme event, thanks to the facilitation relationship they maintain with the canopy plants. The canopy die-off due to drought would reduce the facilitation effect of plant canopies, regarding the lower CD of the facilitated subcommunity observed under affected canopy. However, dead canopy could enhance the recruitment of climatically disadvantaged species with low competitive capacity, as its macroclimate buffering capacity is not counterbalanced by competition. This phenomenon could act as a stabilizing process which reinforces the system resilience: the event causes a great mortality, especially endangering species far from their climatic optimum (Pérez-Navarro *et al.*, 2019), but dead individuals in turn may promote their recruitment. Nevertheless, depending on the drought magnitude, the microclimatic conditions under the canopy may become restrictive enough to impede the recruitment of some of these species (Davis *et al.* 2019). Finally, species belonging to the neutral and inhibited subcommunities are not so vulnerable to disappear as their CD is already low, suggesting previous and higher climatic filtering. Although these interpretations should account for the limited statistical soundness of the overall model, this study reveals the value of considering plant-plant interactions in relation to the drought impact, when assessing species susceptibility to remain or disappear in face of extreme climatic events.

5. Concluding remarks

Although not all species show positive plant-plant interactions, these allow to maintain the abundance of less climatically adapted species in the studied Mediterranean shrubland community. This is supported by the finding of higher CD in the recruiting subcommunity growing under canopy - where facilitation is likely to be occurring. The results also suggest that facilitating relationships are variable, as CD of facilitated subcommunity was not independent of the degree of canopy defoliation.

The high effect on CD observed on subcommunities growing under dead canopies illustrates the combination of the positive structural effect of adults even after death, likely including the maintenance of soil structure and humidity, temperature buffering, provision of perch to dispersal and herbivory exclusion, and the absence of competition from alive plants.

Our results support previous studies that affirm that species far from their climatic optimum are prone to have facilitative relationships (Choler, 2001; Liancourt, 2005). This highlights the

importance of including biotic interactions when assessing species' climatic niche and ultimately when building species distribution models. This would particularly enrich the capacity of predicting future species range in the context of global change (Bruno *et al.*, 2003; Wisz *et al.*, 2013). Further, studies addressing species-specific recruit-canopy interactions would provide more detailed information of species persistence and replacement dynamics (Alcántara *et al.*, 2018).

When considering extreme droughts, our results suggest that most of the species that constitute the studied community would likely remain in the system. In a first step, the increase of heavily affected individuals could endanger the persistence of recruits of species that are far away from their climatic optimum. But interestingly, the increase of dead individuals following drought could enhance the recruitment of those species. This phenomenon could play an important role in ecosystem resilience by acting as a stabilizing mechanism and deserves further investigation, particularly for assessing the coupling between different life-history stages of the populations.

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675

676 **SUPPORTING INFORMATION**

677 **Appendix S1.** Datalogger microclimate tests.

678 **Appendix S2.** Community climate characterization.

679 **Appendix S3.** Statical analyses results.