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Research article

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

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Positive plant–plant interactions (facilitation) may enhance the recruitment and establishment of species less adapted to local macroclimatic conditions. A major cause of this effect is climatic buffering, which implies an increased 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 niche 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 the community growing in the gaps. The facilitated recruiting community growing under dead and living canopy showed the highest disequilibrium, followed by the community 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 indicate that the climatic disequilibrium of the recruiting community is determined by the facilitation–competition balance. Living 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: climatic debt, climatic disequilibrium, drought-induced die-off, facilitation, global change ecology, plant population and community dynamics, plant recruitment, plant–plant interactions, species climatic niche

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Introduction

Extreme climatic events (ECEs) – drought, heatwaves, cold snaps, windstorms, flooding – are expected to increase in the near future because of climate change, profoundly altering the abiotic and biotic conditions of ecosystems (IPCC 2023). Among them, the impacts of severe droughts are expected to increase in magnitude, frequency and length in many regions (Smith 2011, Ploughe et al. 2019). In fact, die-offs and mortality due to extreme drought episodes have already been reported in forests (Breshears et al. 2005, Allen et al. 2010) and shrublands (Sapes et al. 2017, Jacobsen and Brandon 2018, Pérez-Navarro et al. 2021) around the world. This new scenario of increasing aridity will produce strong impacts on biodiversity and ecosystem functioning in different ways, even leading to vegetation shifts (Anderegg et al. 2012, Martínez-Vilalta and 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 and Shaw 2001, Geng et al. 2019, Batllori et al. 2020). Indeed, vegetation shifts are not as common as may be expected. This may be because, at a demographic level, a mismatch between recruitment and mortality in the medium term is required (Lloret et al. 2012, Martínez-Vilalta and Lloret 2016). Therefore, processes that balance this recruitment–mortality ratio after ECEs can be considered to be stabilizing mechanisms (Bertrand et al. 2011, Lloret et al. 2012). 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).

Therefore, positive plant–plant interactions may play a vital role in ecological stability. Specifically, interactions between recruiting plants and canopy (recruit–canopy, hereafter) modulate community demography by enhancing recruitment and establishment (Brooker 2006, Callaway 2007, Michalet and Pugnaire 2016). This phenomenon is promoted by several mechanisms such as herbivory exclusion, perch effect, allelochemical exudation or climatic buffering, which increase the actual niches used by plant species (Callaway 2007). In the context of a changing climate, this last mechanism is particularly important as it will promote the persistence of species that would otherwise find the macroclimatic conditions challenging (O'Brien et al. 2019). On the other hand, plant–plant interactions can also lead to a negative effect on species recruitment, due to competitive exclusion (Liancourt et al. 2005, Callaway 2007).

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 interactions would prevail under low-stress conditions (Choler et al. 2001, Michalet and Pugnaire 2016, Ploughe et al. 2019). Consequently, during extreme drought episodes or gradual increments of dry periods, the

stabilizing effect produced by facilitation on microclimate conditions would appear to be enhanced. This mechanism likely increases the system's resistance and resilience by promoting the survival and recruitment of plants during and after ECEs (Callaway 2007, Lloret et al. 2012, Lloret and Granzow-de la Cerda 2013, Reyer et al. 2015). Nonetheless, how likely a species is to be facilitated also depends on some traits, such as those involved in the ability to be highly competitive (Liancourt et al. 2005) or exhibit low stress tolerance (Liancourt et al. 2005, 2017, Berdugo et al. 2019). In addition, structural attributes, such as coverage continuity, affect facilitation by providing community-scale positive effects (Liancourt and Dolezal 2021).

In a climate change context, stabilizing mechanisms may hinder the migration and colonization of species that are predisposed to live under new conditions emerging from climate-driven disturbances (Bertrand et al. 2011, Urban et al. 2012, Svenning and Sandel 2013). So, stabilizing mechanisms would be translated into an increasing mismatch between the macroclimatic conditions and the climatic requirements of the existing community. This mismatch is known as climatic disequilibrium (CD, Svenning and Sandel 2013, Blonder et al. 2015, Duchenne et al. 2021), which will be higher in resilient communities as a consequence of the maintenance of the composition of the established community. In contrast, local extinctions or abundance changes triggered by climatic disturbances may lead to a reduction in CD due to increasing selective pressure on 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 in non-facilitated interactions. In contrast, if competitive interactions are dominant, we can expect reduced values in the 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 CD values in plant communities growing under canopies, suggesting that canopies buffer macroclimatic temperatures (Zellweger et al. 2020), while 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 regarding how canopy die-off may affect facilitation and recruitment capacities, thus modifying the CD of understory communities.

In this study, we explore the effect of drought-induced defoliation on shrubland canopy on recruit–canopy interactions, analyzing changes in the 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 that suffers recurring droughts, taking into account open gaps and canopies with different degrees of defoliation (die-off). This quantification will likely allow the detection of subsets of recruiting species

(subcommunities) experiencing positive (i.e. facilitation), negative (i.e. inhibition) or neutral effects.

Specifically, we aim 1) to test the existence of a positive effect of the shrubland canopy on the overall recruitment of woody species; 2) to compare the CD in the facilitated, neutral and inhibited recruit subsets of species, provided they exist; 3) to test the effect of the degree of canopy defoliation on the CD of the overall recruiting community; and 4) to test the effect of the degree of canopy defoliation on the CD in the facilitated, neutral and inhibited recruiting subcommunities. We hypothesized that 1) the canopy will have an overall positive effect on recruitment; 2) the facilitated subcommunity will present the highest CD due to the canopy effect on microclimate, while the inhibited subcommunity will present the lowest CD; 3) defoliation will generally diminish the canopy buffering, so the CD will diminish with the degree of defoliation; and 4) in particular, the CD of the facilitated subcommunity will decrease as defoliation increases, while the CD of the inhibited subcommunity will increase, since the effects of drought are expected to diminish the competitive capabilities of adult shrubs.

Material and methods

Description of the study area

The study area was the Doñana National Park, located 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 month (January). Additionally, 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. Specifically, in the 2010 decade, the site suffered four drought

periods (2011/2012, 2013/2014, 2014/2015 and 2018/2019) and below-average rainfall in the remaining years, making it the driest decade since the 1978/1979–1986/1987 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, that drought also coincided with a particularly cold winter, with several days below 0°C (Fig. 1, Díaz-Delgado 2006). Consequently, an elevated die-off was reported across shrubland species in the spring (Díaz-Delgado 2006), and since then recovery has been irregular (Paniw et al. 2021).

The study focused on shrublands, particularly the '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 communities correspond to *Halimio halimifolii–Stauracanthetum genistoidis* (Rivas-Martínez et al. 1980), composed predominantly of shrubs such as *Cistus libanotis*, *C. salviifolius*, *Cytisus grandiflorus*, *Erica scoparia*, *Halimium commutatum*, *H. halimifolium*, *Helichrysum picardii*, *Lavandula stoechas*, *Rhamnus lycioides*, *Salvia rosmarinus*, *Stauracanthus genistoides*, *Thymus mastichina* and *Ulex australis* (Rivas-Martínez et al. 1980, García Murillo and Sousa Martín 1999).

We tested the effect of the canopy to buffer air temperature (°C) and relative air humidity (%) during spring (March) and summer (August) under a set of plant canopies of two representative species (*S. rosmarinus* and *H. commutatum*) with different degrees of defoliation and gaps. We obtained measurements every 30 min (48 measurements each day) using dataloggers (Supporting information). We ran two different LMEs for each season, where temperature and humidity were set as response variables, time and nurse species (*S. rosmarinus*, *H. commutatum* or gap) were set as explanatory variables, and recording day was considered as random. We also ran post hoc analyses (Tukey test) to test differences between plant canopies and gap at the same time (every 30 min). We found
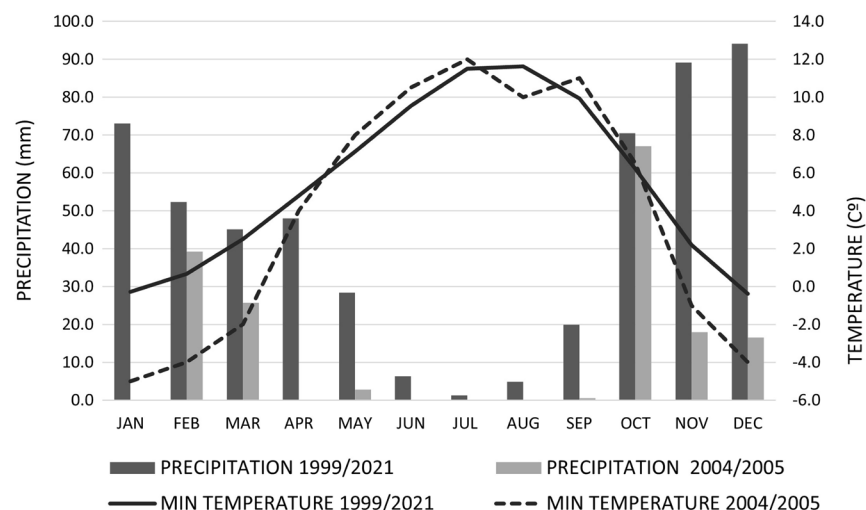

Figure 1. Monthly mean precipitation and monthly minimum absolute temperature of the historical record and the drought episode (source: Estación Biológica de Doñana 2021).

that both explanatory variables and the interaction between them had a significant effect on temperature and air humidity ($p\text{-value} < 0.001$, Supporting information). Post hoc analyses showed significant differences between nurse categories for the majority of times (Supporting information). Overall, these measurements supported the ability of shrub canopy to modify microclimate.

Recruitment data

Data were collected during March 2021. We sampled 45 plots of 4×20 m, separated by 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 to be a 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 a canopy, the degree of defoliation 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 on one side of the plot (trying to maximize the representativeness of the plot cover). Within each transect, the length of gaps and of each individual canopy segment were measured.

The degree of defoliation 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 and García 2016). Visual estimations of defoliation have been demonstrated to be a robust approach to determine plant defoliation compared to methods based on the dry-matter weight of living plants (Sapes et al. 2017) or length measurements of dead or defoliated stem parts (Pérez-Navarro et al. 2019).

The kind of interaction present – facilitation, neutral or inhibition – was determined by using an 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 recorded under canopies and the expected number of recruits (R_E; see next paragraph) of the same species growing under canopies, 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 was calculated considering a neutral interaction between recruits and canopy, so its distribution in the plot was random (Alcántara et al. 2018). It was calculated as the product of the species total number of recruits (R_T) by the total percentage of canopy cover in the plot (%Canopy) regardless canopy species identity, which was not considered in our study:

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

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 value was significantly smaller than 0 ($p\text{-value} < 0.05$), the species was considered as inhibited. If the difference was significantly higher than 0, the species was considered as facilitated. Finally, the relationship was considered neutral if the difference was not significantly different from 0. This procedure is similar to a χ^2 test; however, the use of LMEs allows weight the influence of each sample (plot) in the analysis, and obtaining a measure of significance.

Two different datasets of recruiting subcommunities were established within each plot. One set related 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 living 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.

Community climate characterization

Species occurrences

The geographical distributions of the observed 22 species were compiled from the Global Biodiversity Information Facility (GBIF) database (http://www.gbif.org; Supporting information). The corresponding occurrences were filtered to avoid geographic and taxonomic inconsistencies (e.g. inaccurate synonyms). Finally, possible sampling bias and spatial autocorrelation were prevented by reducing occurrences density to 1 per km^2 (equivalent to the grid resolution of the climate dataset; Franklin 2010). As a result, we obtained an occurrences dataset ranging from 42 500 to 140 observations per species.

Environmental data

We selected 12 bioclimatic variables from the CHELSA database (ver. 1.2, Karger et al. 2017) related to temperature and precipitation (1 km^2 resolution). They were calculated with average macroclimate data (mean temperature, and maximum and minimum precipitation) from the period 1979–2013.

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 and 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 and 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.

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 this 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. Overall, the first axis (44.62% of the variability) correlated positively with temperature-related variables, while the second axis (29.15% of the variability) overall correlated negatively with humidity-related variables (Supporting information).

The species' realized niches were then 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 the effect of sample bias to be reduced, as this 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 below a 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. The community inferred climate (CIC) of each subcommunity was then 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).

We performed the validation of the climatic niche models using area under ROC (Receiver Operating Characteristic) curve (AUC) test analyses (Lobo et al. 2008), with the *evaluate* function from the 'dismo' package (ver. 1.3–14; Hijmans et al. 2023). Specifically, we calibrated niche models with 90% of species occurrences, and reserved 10% of species occurrences as an evaluation subset. In addition, we simulated the same number of random points distributed throughout the common climatic space as pseudo-absences or background (Barbet-Massin et al. 2012). An AUC test was performed using suitability values, which were calculated as the ratio between the density predicted by the model in the coordinates of each point and the maximum density predicted by the model. We repeated this process ten times (10-fold) for each species, using a different subset of species occurrences and random points. The AUC values of our models were between 0.875 ± 0.01 and 0.958 ± 0.0003 (mean $\pm$ SE; Supporting information), and supported the validity of the performance of our climatic niche models (Krzanowski and Hand 2009). We also measured the suitability of the historical climate predicted by our climatic niche models at the study sites. We calculated these values as the ratio between the density predicted by the model for the historical climate of our 45 plots, and the maximum density predicted by the model. The values ranged between 0 and 0.475 ± 0.024 (mean $\pm$ SE; Supporting information).

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 ran two different LMEs: 1) with CD as response variable and canopy cover category (living, affected, dead, gap) as explanatory variable; and 2) with CD as response variable and the recruit–canopy interaction category (facilitation, inhibition, neutral) as explanatory variable. To understand how defoliation affects CD within each interaction category, we also ran three models with community CD as response variable and defoliation as explanatory variable for each interaction category, separately. 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 ran post hoc models (Tukey test) for each model ('emmeans' R package, ver. 1.8.1-1; Lenth et al. 2022).

Some species were poorly recorded (fewer than ten individuals in total, see Supporting information) and each species could only be in one category of recruit–canopy interaction, thus affecting the category dispersion. For this reason the models in which CD is predicted by defoliation within each interaction category were run with and without these rare species, to analyze their contribution to the model results. Indeed, differences between these two models including or excluding rare species were negligible (Supporting information). Here we show the model with all the species since our methodology weighted CD values by the abundance of the species. All statistical analyses were carried out with R ver. 4.0.3 (www.r-project.org).

Results

A total of 5181 recruits from 22 species were recorded in the 45 sampled plots (Supporting information). The facilitated subcommunity was composed of recruits of seven species: *C. salviifolius*, *H. commutatum*, *Juniperus phoenicea* subsp. *turbinata*, *Pistacia lentiscus*, *S. rosmarinus*, *T. mastichina* and *S. genistoides*. The inhibited subcommunity was composed of recruits of two species: *H. halimifolium* and *Lavandula latifolia*. Finally, the neutral subcommunity was composed of recruits of eleven species: *Asparagus horridus*, *C. libanotis*, *C. grandiflorus*, *E. scoparia*, *Helianthemum hirtum*, *Helichrysum picardii*, *L. stoechas*, *Osyris lanceolata*, *Phillyrea angustifolia*, *Pinus pinea* and *U. australis* (Supporting information).

Community CD showed significant differences (F-value = 3.38; p-value < 0.05) between canopy categories. As expected, the model predicted the lowest CD for the recruiting subcommunity in the gaps (1.38 ± 0.06, mean $\pm$

SE hereafter), and recruits growing under dead plants had the highest CD (1.50 ± 0.07). Accordingly, post hoc analyses (Tukey test) found significant differences between the CD of the recruiting subcommunity in gaps compared to the subcommunity established under dead and living canopy (p-value < 0.05; Fig. 2).

The community CD of recruits also showed significant differences between recruit–canopy interactions categories (F-value = 28.96, p-value < 0.001). The facilitated subcommunity had the highest CD (1.91 ± 0.11). Post hoc analyses (Tukey test) showed significant differences between the CD in the facilitated recruiting subcommunity and the CD in the neutral and inhibited subcommunities (Fig. 3).

For the neutral and inhibited communities, the analyses did not predict a significant effect of defoliation on community CD (F-value = 0.97, p-value = 0.380; and F-value < 0.001, p-value > 0.999, respectively). However, defoliation showed a significant effect on the CD of the facilitated community (F-value = 3.26, p-value < 0.05). Post hoc analysis (Tukey test) found marginally significant differences (p-value = 0.07) between a facilitated community CD growing under affected and under dead canopy (Fig. 4).

Discussion

This study reveals the contribution of facilitation, and its interaction with canopy defoliation, in determining the CD of the recruiting community. This facilitation appears irrespective of the nurse species, which supports the role of continuous cover by community-scale facilitative effects (Liancourt and

Figure 3. Predicted climatic disequilibrium (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 dots represent CD means values, the black bars delimitate interquartile ranges and the shapes represent the amount of data in the y-axis.
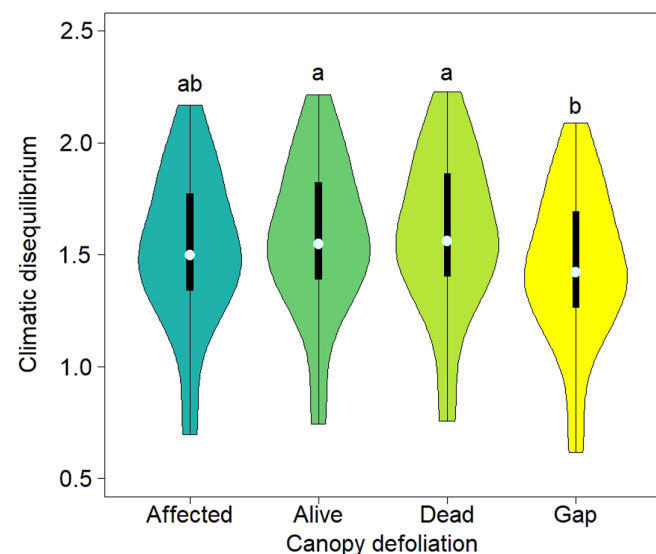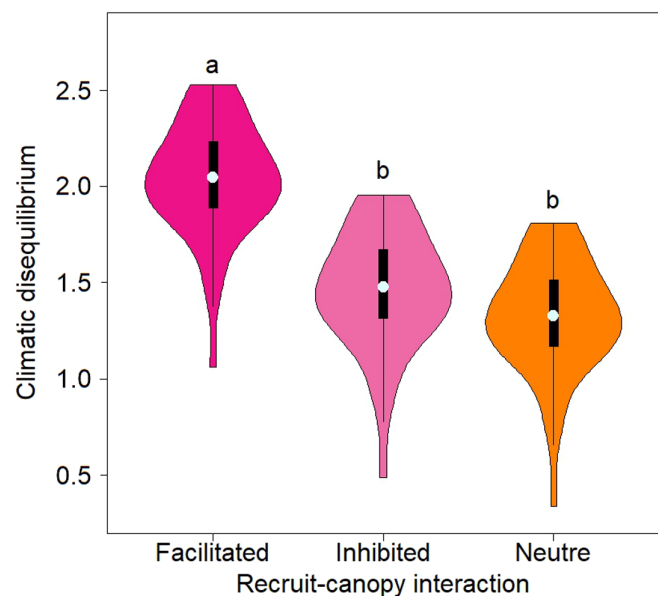
Figure 2. Predicted climatic disequilibrium (CD) of the recruiting subcommunities found under the different canopy categories (dead, affected and living) and in gaps. Significant differences between categories are indicated with different letters on the bars (p-value < 0.05, Tukey test). The dots represent CD means values, the black bars delimitate interquartile ranges and the shapes represent the amount of data in the y-axis.
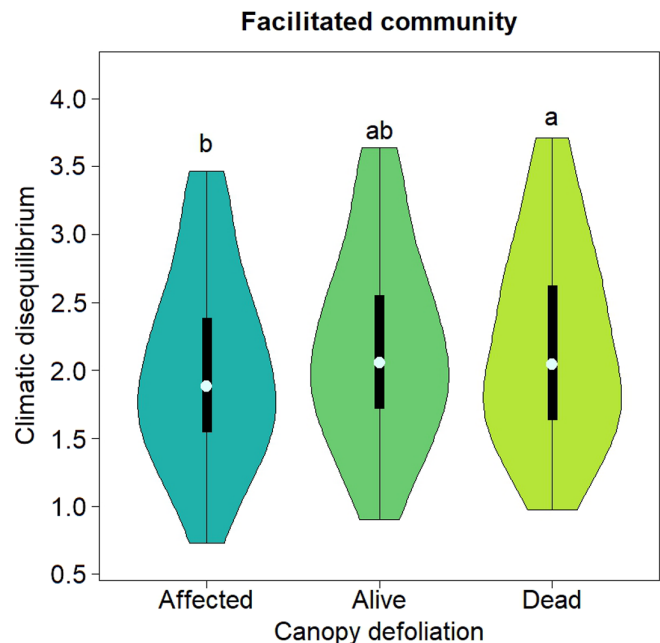
Figure 4. Predicted climatic disequilibrium (CD) of the facilitated recruiting communities under the different canopy categories (dead, affected and alive). Marginal significant differences between categories are indicated with different letters (p-value = 0.07, Tukey test). The dots represents CD means values, the black bars delimitate interquartile ranges and the shapes represent the amount of in the y-axis.

Dolezal 2021) and contributes to species persistence under climatic stress, according to previous studies (Choler et al. 2001, Liancourt et al. 2005, 2017, Berdugo et al. 2019, O'Brien et al. 2019). Our results, using a natural defoliation experiment to assess the effects of drought in a Mediterranean shrubland, are consistent with tree canopy effects on CD of forest understory (Zellweger et al. 2020) and expand the pattern to shrublands and communities experiencing climate change-induced ECEs.

As hypothesized, recruits growing under canopy exhibited a higher CD than those growing in gaps. Accordingly, the subset of facilitated recruits showed higher CD than was experienced by those inhibited by canopy or those that showed a neutral relationship. The effect of degree of defoliation on the CD was revealed to be more complex, likely due to the concurrence of different degrees of facilitation and competition (Resco de Dios et al. 2014) relating to the proportion of canopy defoliation.

Recruit–canopy interaction

Although the most common plant–canopy interaction was the neutral one (53% of cases), we found that the percentage of species that tended to have a positive relationship with canopy (i.e. facilitation) was clearly higher (37%) than the percentage of species that tended to have a negative relationship (inhibition) (10%). This result agrees with our hypothesis and the SGH, considering that our semiarid study system suffers recurring drought and will be closer to the stress edge in the climatic gradient. These results are similar to those found in a previous study which 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 can lead to that kind of interaction in the recruit–canopy relationship. These include perch effect, in which the plants (usually trees) standing out above the vegetation layer favor the deposition by animals of seeds from fleshy fruits (Pausas et al. 2006, Bustamante-Sánchez and Armesto 2012); herbivory exclusion, commonly mediated by spiny shrubs (Lloret and Granzow-de la Cerda 2012, Saixiyala et al. 2017); climatic buffering (Lozano et al. 2017, 2020); chemical exudates that increase the availability of soil nutrients and water (Wang et al. 2021) or inhibit depressing allelochemicals (Xia et al. 2016); symbiosis with soil microorganisms or mycorrhizal networks (Van Der Heijden and 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 species that are far from their climatic optimum. However, they may indirectly diminish the relative role of climate constraints on demographic processes. In addition, some studies suggest 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 et al. 2005).

Our results provide evidence of the effects of recruit–canopy interaction in the CD of the recruits: the lowest CD was found in recruits growing in gaps, and the facilitated subcommunity showed a significantly higher CD than the neutral and the inhibited communities, according to the study's hypothesis. Therefore, this result suggests that species growing far from their climatic optimum are predisposed to experience facilitative relations with canopy, which will allow recruitment under stressful conditions (Choler 2001, Liancourt et al. 2005). These results also support the conclusions reached in previous studies, in which positive interactions are considered to expand the species' realized niche (Bruno et al. 2003, O'Brien et al. 2019). This relationship between climatic requirements and population success is often mediated by functional and demographic traits, as previously observed in mediterranean shrublands (Paniw et al. 2021). Our results also agree with our measured microclimatic record (Supporting information), which demonstrates the climatic buffering capacity of shrubland canopies. Although previous studies have demonstrated the impact of a canopy's 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.

The fact that the CD of the inhibited recruiting subcommunity was not significantly lower than the CD of the neutral subcommunity does not indicate 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), soil preference and nutrient uptake (Yan et al. 2016), or the synthesis of allelopathic compounds (Pierik et al. 2013). Nevertheless, close attention should be paid to this absence of significant differences, since the inhibited subcommunity was composed of a low number of species and also of species with few individual member.

Canopy defoliation

When assessing the role of canopies with different degrees of defoliation, we found no significant differences between the CD of the recruit subcommunities growing under living, affected or dead canopy, contrasting with a previous study where the 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, as these categories did not clearly indicate the different canopy species included. This emphasises the importance, in

future studies, of considering not only the species identity of recruits, but also the identity of canopy species. Another explanation for this inconsistency is that our methodological approach builds species niches from adult occurrences, and an adult's climatic niche can be different to the species regeneration niche (sensu Grubb 1977). Also, the assessment of the role of species' functional traits may be useful in finding 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).

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

According to the study hypothesis, post hoc analyses showed marginally significant differences in CD within a facilitated subcommunity when considering different canopy defoliation categories. In that subcommunity, contrary to our expectations, the recruits growing under dead canopy exhibited a similar CD value to the recruits growing under living canopy, while the recruits established under affected canopy had the lowest CD. That is, there was a non-linear pattern in which the CD of recruiting communities did not diminish proportionally when canopy defoliation increased. This 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 chemical exudation or mycorrhizal symbiosis – require the canopy plant to be alive, previous studies indicate that dead canopy can still provide structurally positive effects on recruits by increasing soil moisture and by reducing soil and surface temperature. These enhance microclimatic buffering (Resco de Dios et al. 2014); provide perch to promote dispersal; and exclude herbivory, particularly under spiny canopy. These effects, combined with an absence of competition, may allow the establishment of species with a low stress tolerance which are not likely to recruit under living canopy because of its low competitive response (Liancourt et al. 2005). A living canopy, in contrast, 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 living and dead canopies. Finally, defoliated canopies may produce competitive relationships with the recruits and additionally will have a diminished climate-buffering capacity, explaining the lower CD of the facilitated subcommunity living under affected canopy. Therefore, these results highlight the importance of studying facilitative relationships that consider 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 a different canopy state might imply that the composition or

species abundances of these subcommunities are independent of canopy defoliation; this was expected in the case of the neutral subcommunity. We can infer, therefore, 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 previously been reported (Van Der Heijden and Horton 2009, Alcántara et al. 2018) 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 will reduce the facilitation effect of plant canopies with respect to the lower CD of the facilitated subcommunity observed under affected canopy. However, dead canopy may enhance the recruitment of climatically disadvantaged species with low competitive capacity, as its macroclimate-buffering capacity is not counterbalanced by competition. This phenomenon may act as a stabilizing process which reinforces system resilience: the event causes considerable 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 endangered as their CD is already low, suggesting previous and higher levels of 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 the face of ECEs.

Concluding remarks

Although not all species show positive plant–plant interactions, these interactions allow the abundance of less climatically adapted species in the studied Mediterranean shrubland community to be maintained. 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 the CD of a facilitated subcommunity was not independent of the degree of canopy defoliation.

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

Our results support previous studies affirming that species far from their climatic optimum are predisposed to have facilitative relationships (Choler et al. 2001, Liancourt et al. 2005). This highlights the importance of including biotic interactions when assessing species' climatic niches and ultimately when building species distribution models. This will particularly improve our ability to predict future species ranges in the context of global change (Bruno et al. 2003, Wisz et al. 2013). Further, studies addressing species-specific recruit–canopy interactions will provide more detailed information on species persistence and replacement dynamics (Alcántara et al. 2018).

Our results suggest that, in extreme droughts, most of the species that constitute the studied community will likely remain in the system. In a first step, the increase in heavily affected individuals may endanger the persistence of recruits of species that are far from their climatic optimum. The increase in numbers of dead individuals following drought, however, may enhance the recruitment of those species. This phenomenon may play an important role in ecosystem resilience by acting as a stabilizing mechanism, and deserves further investigation, particularly with respect to assessing the coupling between different life history stages of plant populations.

Author contributions

Raquel Díaz-Borrego: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (lead); Software (supporting); Supervision (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **María Ángeles Pérez-Navarro**: Conceptualization (lead); Formal analysis (supporting); Investigation (equal); Methodology (lead); Resources (lead); Software (supporting); Supervision (lead); Writing – review and editing (lead). **Luciana Jaime**: González Investigation (supporting); Writing – review and editing (equal). **Nuria J. Elvira**: Investigation (supporting); Writing – review and editing (equal). **Francisco Lloret**: Conceptualization (lead); Funding acquisition (lead); Investigation (equal); Methodology (lead); Project administration (supporting); Resources (lead); Supervision (lead); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.w3r228102 (Díaz-Borrego et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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