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RESEARCH ARTICLE

Climatic disequilibrium modulates canopy service across abiotic stress gradients

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Abstract

1. Canopy service (CS) is defined as the extent to which established (canopy) plants affect the recruitment of new individuals in the community. This service, when positive, is known as facilitation and is mainly driven by the modification of the microenvironment that plants induce under their canopies, often by buffering the macroclimate.
2. The importance of canopy service in maintaining diversity may increase in the context of climate change. Climate change may also push species away from their niche optima, increasing their so-called climatic disequilibrium (CD). This process can provoke poorer performance, defoliation and decay of the canopy species, jeopardizing the canopy service they provide. Therefore, canopy CD is expected to modulate canopy service under current climate conditions.
3. In this study, we test (1) whether canopy species experiencing greater CD will exhibit diminished canopy services and (2) whether the negative impact of CD on canopy service will be more pronounced under increasing abiotic stress conditions (i.e. aridity and continentality). To address these questions, we used a database of 54 communities, mainly distributed across the Mediterranean basin, which includes a total of 316 canopy species involved in 35,941 recruiting interactions.
4. The CD of the species in a given community resulted in contrasted effects on their canopy service depending on the level of climatic stress. The maximum canopy service occurs at intermediate aridity levels, following a humped-shaped pattern when considering this single climatic stressor. However, when continentality is also considered, a greater intensity of both stressors together increases a positive canopy service linearly, following the Stress Gradient Hypothesis.
5. *Synthesis*. Our results indicate that abiotic stressors, combined with CD, modulate the canopy service. Consequently, under future climate change scenarios that may increase stress and CD, canopy service will become crucial for the maintenance of the recruiting community.

KEYWORDS

biogeography and macroecology, climatic disequilibrium, climatic niche, community dynamics, ecosystem function and services, plant population, plant–climate interactions, plant–plant interactions

1 | INTRODUCTION

Climate change is shifting plant distributions, with some species expanding in newly favourable areas and others declining in increasingly hostile habitats (Kelly & Goulden, 2008). This rapid change has a great scientific and societal relevance and has prompted researchers to devote a great effort to predict the consequences of climate change through species distribution models (Elith & Leathwick, 2009). Early influential studies of species distributions made predictions mainly based on abiotic factors—typically temperature—but it soon became evident that there was a need to include concurrent biotic interactions to increase predictions' accuracy (Austin & Van Niel, 2011; Wisz et al., 2013).

A relevant ecological process that needs to be addressed to correctly predict plant community assembly and dynamics under a changing environment is that occurring between the already established plants (referred as *canopy species* in this context) and the plants recruiting in their neighbourhood defined as *recruit species*, which will eventually replace that canopy species (Alcántara et al., 2018; Valiente-Banuet & Verdú, 2013). The extent to which canopy species positively or negatively enhance the *recruit species* abundance can be named as *canopy service* (Alcántara et al., 2024; Perea et al., 2021). In some cases, *canopy service* is positive (i.e. there is a positive interaction); in such cases, we refer to *facilitation*, where the canopy plants act as *nurse species* to other recruit species in the communities enhancing their survival beneath them. One mechanism explaining this positive interaction is that canopy species typically buffer the stressful macroclimatic conditions beneath them, enabling the recruit species to remain in the community even beyond their optimal climatic conditions (O'Brien et al., 2019; Perea et al., 2021). This climatic buffering provided to recruiting plants has been shown to be ambivalent, cooling the understory during hot ambient temperatures and warming it when ambient temperatures are cold (De Frenne et al., 2021). However, in other cases, *canopy service* can be negative in relative terms, as the conditions beneath the canopy may depress recruitment compared to open ground areas (i.e. negative interaction). Factors such as species traits, competition, herbivory and other biotic and abiotic agents play a role in how *canopy service* varies across communities and species.

In general, canopy plants tend to shift from depressing to enhancing the recruitment of other species as environmental stress levels increase (He et al., 2013; Stress Gradient Hypothesis, SGH; Bertness & Callaway, 1994) That is, canopy service would tend to become more positive as environmental stress intensifies. Indeed, several studies have shown that facilitation is more prevalent in stressed environments, like arid and alpine habitat systems (Armas et al., 2011; Callaway et al., 2002; Cavieres et al., 2006). However, in extreme situations, facilitation can collapse because canopy species are unable to sufficiently improve microclimatic conditions, resulting in a non-linear (i.e. humped-back shape) relationship between stress and facilitation (Michalet et al., 2006). This pattern may also reflect the competition—facilitation trade-off across stress gradients as well (Michalet et al., 2014); however, the overall pattern of facilitation across contrasting environmental stresses has not yet been clearly elucidated.

The improvement of microhabitat conditions offered by canopy plants has been a crucial factor in mitigating the impacts of climatic aridification in the past, helping to prevent the extinction of stress-sensitive species (Valiente-Banuet & Verdú, 2013). This mechanism is likely in operation in plant communities, so it must be considered when predicting the future occurrence of species in the face of current climate change (Bulleri et al., 2016). In fact, current species distribution models predict that threatened species may persist in future stressful climates thanks to the microclimatic buffering effect of dominant plant canopies (Stark & Fridley, 2022). However, the extent to which canopy plants can mitigate the impacts of climate change may depend on their own tolerance to new conditions, which is quantified as the difference between their niche's climatic optimum and the actual local conditions (the so-called *climatic disequilibrium* [CD]; Blonder et al., 2015; Svenning & Sandel, 2013). In recent years, there has been an accumulation of evidence that plants experiencing greater CD require more facilitation from canopy plants (Díaz-Borrego et al., 2024; Perez-Navarro et al., 2024). However, the other side of this relationship, that is, how the CD of canopy species determines their interactions with recruiting plants, remains largely unexplored.

At present, we have evidence that populations and communities under high climatic disequilibrium are physiologically limited, show poorer plant performance and higher canopy defoliation rates, especially under extreme climatic events (Perez-Navarro et al., 2022; Sapes et al., 2017). In Mediterranean ecosystems, populations in warmer and drier environments tend to have higher disequilibrium (Perez-Navarro et al., 2024). Under these conditions, climatic disequilibrium, combined with susceptibility to aridity, likely contributes to poor plant performance. In contrast, canopy plants in populations close to the species' optimal conditions may achieve greater biomass production or growth (Margalef-Marrase et al., 2023), as well as more aerial biomass and leaf area (Treurnicht et al., 2020). Therefore, it is expected that plants in climatic equilibrium will be more vigorous and more prone to develop complex canopies that would enhance climatic buffering (De Frenne et al., 2021), ultimately increasing the *canopy* *service* to the recruitment communities. However, some studies have found that populations with CD located in less arid environments (closer to the wetter edge of the niche) may also develop greater aerial biomass than populations with less CD (Stanik et al., 2020). This suggests that the direction of disequilibrium across the climatic gradient (i.e. wetter vs. drier edge) may also influence the extent of canopy services provided by canopy plants. Overall, this rationale indicates that the relationship between canopy service and CD may be non-linear. This is partly due to the effect of the population's relative position within its species' niche (i.e. along cold-warm and arid-humid gradients) on plant competition, multitrophic interactions and fitness (O'Brien et al., 2017). As previously mentioned, canopy plants with less CD can promote the development of more complex canopies and enhance canopy service, but it may also amplify competition among species (Christiansen et al., 2024). This dual effect suggests a trade-off, where the expected improvement in canopy service due to low CD is counterbalanced by increased competition.

In light of these observations, we hypothesize that canopy species experiencing greater CD will exhibit diminished canopy services, leading to lower recruitment beneath their canopies. We also hypothesize that this relationship is non-linear. Furthermore, we propose that canopy species experiencing drier and hotter conditions than their optimum will provide reduced canopy services compared to both species close to their climatic equilibrium and those near the wetter, low thermal stress edge of their niche.

We anticipate that the reduction in the canopy service will be more pronounced under increasing stress conditions, where facilitation is expected to be more crucial for the recruits persistence. We test these hypotheses along a broad biogeographical and climatic gradient characterized by varying levels of aridity and continentality (latitudinally from North Africa to Central Europe and longitudinally from the Iberian Peninsula to Anatolia) after assessing the CD of more than 300 canopy species and the service they provide to recruiting species.

2 | MATERIALS AND METHODS

2.1 | Study area/region

We used the RecruitNet database (Verdú et al., 2023) that contains the recruitment networks of 143 communities world-wide, describing >110.000 canopy-plant recruitment interactions among >3000 plant species world-wide and, in most cases, the cover of canopy plants. To encompass a broad geographic and climatic gradient, we selected all communities from North Africa to Central Europe that included information on the cover of canopy species. We excluded tropical and South American communities because they tend to have many species with low occurrences in the Global Biodiversity Information Facility (GBIF) database (GBIF.org, 2024, http://www.gbif.org) making it practically impossible to build their climatic niches. Using this information, we finally built a database of 54 communities, mainly distributed in the Mediterranean basin area (Figure 1), which included a total of 316 canopy species involved in 35,941 canopy-recruit interactions. The information of the final dataset was collected from 2010 to 2021 (Verdú et al., 2023).

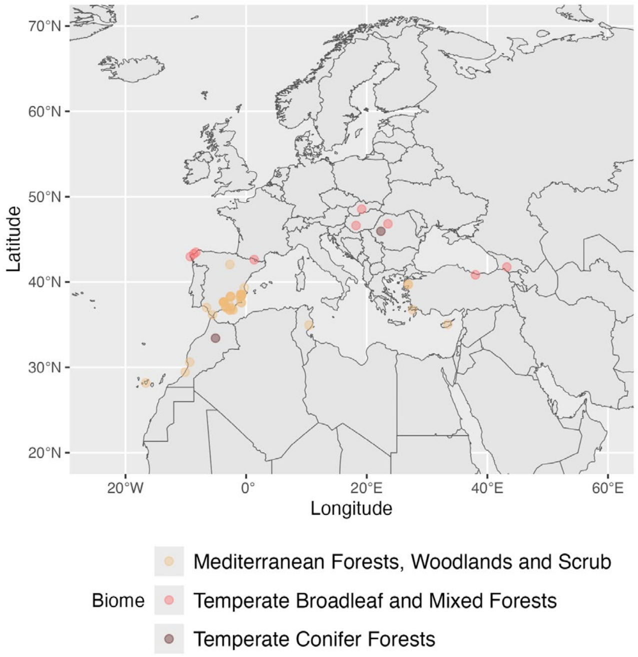

FIGURE 1 Location of the 54 communities where canopy-recruit interactions are studied. All of them were obtained from the RecruitNet database (Verdú et al., 2023). The colour of the dots indicates the biome of the community.

2.2 | Plant canopy service

We define plant canopy service as the effect of the plant's canopy for the overall establishment of recruits, both of the same species and of others, under its canopy. This effect can be measured on the basis of the abundance of recruiting plants in the community and the area occupied by each canopy species versus open ground (Alcántara et al., 2024). Mathematically, it can be calculated with the relative interaction intensity (RII) index for each canopy plant species *i* (Armas et al., 2004) as follows:

$$\mathrm{RIIi} = \frac{ri - ro}{ri + ro}$$

where r_i and r_o are the density of the recruits from all the species under a given canopy species *i* and in the open, respectively. This index ranges from −1 to 1, with positive values indicating that the canopy species enhances recruitment of the overall set of recruiting species compared to open environments, and negative values indicating that it depresses recruitment compared to open environments.

2.3 | Climatic disequilibrium (CD)

To calculate the CD of each canopy species, we first characterized their realized niches based on presence and climatic data using a principal component analysis (PCA) following Broennimann et al. (2012). Then, we compared their climatic optimums against the local climatic conditions in each location. Below, we explain in detail all the steps.

2.3.1 | Climatic and species distribution data

We used climatic data from the native range area of the 316 canopy plant species to construct their climatic niches. The occurrences of the studied species were extracted from the GBIF database (GBIF.org, 2024, http://www.gbif.org; Supporting Information S2). Raw occurrences were filtered to avoid taxonomic errors. We also excluded occurrences from collections to avoid potential errors of coordinates. We only used records from 1970 onwards. We filtered out occurrences with an error greater than 1 km and an uncertainty greater than 707 meters to match coordinate precision with climatic resolution. Nevertheless, we retained occurrences with missing information on coordinate accuracy to prevent information loss, as a significant proportion of the data lacked this information. Further, a maximum density of 1 occurrence per km^2 was imposed to avoid climatically duplicated records (Franklin, 2010) as the resolution of the climatic data was 1 km^2 (Karger et al., 2017).

The CHELSA 2.1 database (CHELSA Version 2.1, Karger et al., 2017, https://chelsa-climate.org) was used to characterize the climatic space of the distribution of the 316 canopy plant species. Composed bioclimatic variables, that is, variables that are a combination of precipitation and temperature (e.g. mean temperature of the wettest quarter) were not included to avoid possible orthogonal correlation effects in the climatic space generated by a PCA (Díaz-Borrego et al., 2024). Therefore, the 13 bioclimatic variables used to build a common climatic space were: annual mean temperature (bio 1), temperature seasonality (bio 4), maximum temperature of the warmest month (bio 5), minimum temperature of the coldest month (bio 6), annual range of temperature (bio 7), mean temperature of the warmest quarter (bio 10) and mean temperature of the coldest quarter (bio 11) relative to temperature. Additionally, we selected other variables related to precipitation: annual precipitation (bio 12), precipitation of the wettest month (bio 13), precipitation of the driest month (bio 14), precipitation seasonality (bio 15), precipitation of the wettest quarter (bio 16) and precipitation of the driest quarter (bio 17). Thus, we extracted the target 13 biovariables from the 1980 to 2010 period from all the occurrences of all studied species. Possible sampling bias and spatial autocorrelation (Legendre & Fortin, 1989) were prevented by reducing occurrence density to a non-significant autocorrelation distance based on our bioclimatic data using the *ecodist* R package (Goslee & Urban, 2007) Thus, we obtained 316 occurrence clean datasets ranging from 25 to 27,159 observations per species (median: 1816 observations; Supporting Information S2).

2.3.2 | Climatic niche characterization and climatic disequilibrium (CD) analysis

The common climatic space of the 13 bioclimatic variables extracted from all the filtered occurrences was characterized through a correlation-based PCA using *dudi.pca* function of the *ade4* R package (Dray & Dufour, 2007). To reduce the dimensionality of our variables, we used the two main axes of the PCA. Then, the climatic niches of all the studied species were built following Broennimann et al. (2012): each species' geographic occurrences were translated into the common climatic space by using *suprow* function of the *ade4* R package (Dray & Dufour, 2007). From this calculation, we extracted all the scores of the two first axes of all species occurrences. Then, two-dimensional kernel density function was applied to smooth the density of its occurrence scores along the two main axes of the PCA. We applied a Gaussian kernel function, which allowed us to determine the expected value of occurrence density in each cell of the climatic space (PCA). The optimal bandwidth matrix for each density function was selected by cross-validation (Duong & Hazelton, 2005). After, the climatic optimum of each species' niche was obtained by calculating the center of gravity (centroid) of the 2-D kernel distribution by using *COGravity* function of the SDMTools R package (VanDerWal et al., 2014).

Simultaneously, the mean 1980–2010 observed climate (OC) for the locations of each studied community was extracted again from the aforementioned CHELSA climate database (Karger et al., 2017). The OC scores of the two main axes of the PCA were extracted with the subrow function of the *ade4* R package (Dray & Dufour, 2007). Finally, the CD in each PCA axis was calculated for every canopy plant species and location. This CD measure was the distance between the species' niche centroid and OC along the PC1 and PC2 dimensions (noted as CD1 and CD2 respectively hereafter). The Euclidean distance (two-dimensional CD) would provide information about climatic suitability (Perez-Navarro et al., 2022) but it would not indicate on which side of the optimum the studied population resides, as it is an absolute value. In contrast, a disequilibrium decomposed into PCA components allows us to assess the directionality of the disequilibrium (Perez-Navarro et al., 2024; i.e. whether it occurs in environments that are, for instance, more humid or more arid than expected for the species' niche optimum). As a result, the calculation allows for both positive and negative univariate disequilibrium. Each distance was weighted by the size of the niche (i.e. niche diameter) to account for the fact that species with narrow niches are more susceptible to being pushed out of their optimum by smaller climatic differences compared to species with broader niches (Perez-Navarro et al., 2022). Diameter of the niche was calculated from the environmental area that represents the 99th percentile of the expected density values in the climatic space of the PCA.

2.4 | Statistical analyses

The relationship between plant canopy service (measured as RII) and CDs of the canopy plant was tested through general linear models (GLM) with a normal distribution of errors using the *glm* function of the *stats* R Package (R core team, 2019). RII was the response variable while the predictor variables were CD and the decomposed OC of each community (that is, the scores of each canopy species in the PC1 and PC2 of the climatic space for each community). To test for the existence of a non-linear relationship between canopy service and climate (Michalet et al., 2006), we added a quadratic term to the explanatory variables PC1, PC2 and CD. The interaction between the two components of the OC (PC1 and PC2) was also included in the model, as well as the interaction between the components of the OC and CD. Two models were built, one with the decomposed CD in the first dimension of the PCA (CD1) as a predictor and another with the decomposed CD in the second dimension of the PCA (CD2). This approach allows us to assess whether the position of the niche along the climatic gradients is relevant. CD1 and CD2 were converted to positive values before building the model to ensure the correct application of the quadratic term. Finally, both bivariate interactions, CD1 and PC1 and CD2 and PC2, were excluded from the models due to their high correlation (0.46 and 0.66, respectively; see Figure S3).

To meet the normality and heteroscedasticity assumptions of the GLM, we used the Box-Cox transformation by exponentiating the response variable (RII, ranging from −1 to 1) to a power after adding a constant to ensure all values were positive before the transformation. The power of the transformation ($\lambda = 0.6$) was determined following Box and Cox (1964) using *EnvStats* R package (Millard, 2013). Although several canopy plants belonged to the same study community (site), we did not include community as a random factor, as it would be redundant with the OC of the community, which was already included in the model. The model fitting was performed using weights derived from the abundance of species' recruits to account for the greater stochastic variation in the distribution of communities with low abundance of recruits, both beneath the canopy and in gaps. In other words, the canopy service (RII) calculated using a greater number of recruits will carry more weight in our analysis. All the statistical analyses were carried out with R version 4.3.3 (R Core Team, 2024).

3 | RESULTS

3.1 | Climatic space characterization

The PCA reduced the 13 bioclimatic variables in two principal components explaining 47% and 29% of the variance, respectively (Figure S1). Overall, the first axis (PC1) correlated positively with temperature-related variables (such as mean annual temperature or mean temperature of the warmest quarter) and negatively with precipitation-related variables (such as mean annual precipitation and precipitation of the driest month; Table S1). Thus, PC1 can be interpreted as a gradient of aridity, as corroborated by the significant correlation with the Aridity Index (UNEP, 1997; $r = -0.88$, $p < 0.0001$; Figure S2; Note that the negative correlation emerges because the Aridity Index, as originally formulated, decreases with aridity). Then, higher values of PC1 indicate higher aridity. The second axis (PC2) correlated positively with variables associated with the variability in temperature values (annual range of temperature and temperature seasonality; Table S1), indicating a gradient of continentality, also supported by the significant correlation with the simplified continentality index (Ic, Currey, 1974; $r = 0.86$, $p < 0.0001$; Figure S2). Thus, higher values of PC2 indicate higher continentality. Accordingly, a positive disequilibrium along the PC1 axis (aridity) indicates that the population experiences drier conditions than its optimum, whereas a negative disequilibrium suggests that the population is in a wetter site than its optimum. A similar pattern applies to the PC2 axis disequilibrium. A positive disequilibrium along the PC2 axis suggests that the population inhabits more continental sites than the species' optimum, whereas a negative disequilibrium indicates that the population inhabits less continental conditions.

The current OC of the study communities (circles in the Figure 2) range from humid to arid and from low to high continentality. Most of the studied canopy species have their climatic optima (squares in Figure 2) in dry sub-humid and semiarid climates with moderate levels of continentality (axis PC1 and PC2 respectively in Figure 2). In general, a large overlap exists between the climatic optima of the canopy species (squares in Figure 2) and the climate experienced (circles) but in many cases this overlap does not occur, indicating climatic disequilibria of varying magnitude across species (species' CD1 ranges from −0.97 to 0.84 and CD2 ranges from −1.38 to 0.96).

3.2 | Canopy service and CD along the aridity and continentality gradients

In both models, where the CD of the canopy plants was calculated along the aridity axis (PC1-based CD or CD1) and along the

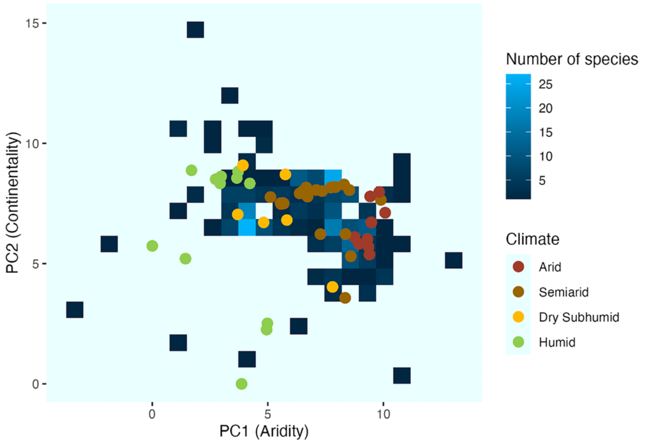

FIGURE 2 Visual representation of the PCA summarizing the climatic space and the climatic distribution of the niche centroids (i.e. climatic optima) of the 319 studied canopy species. Dots represent the climatic conditions of the 54 study communities, coloured according to its Aridity index. The colour of the squares indicates the number of canopy species whose niche centroids are located in the climatic space delimited by the quadrat.

TABLE 1 Generalized linear models (GLMs) explaining the plant canopy service (RII) as a function of their climatic disequilibrium (CD) along the aridity (PC1) and continentality (PC2) gradients.

	PC1-based CD (CD1)		PC2-based CD (CD2)	
Predictors	**Estimate**	***p***	**Estimate**	***p***
(Intercept)	1.64	<0.001	1.54	<0.001
Aridity (PC1)	−0.03	0.425	−0.06	0.12
Aridity^2 (PC1)	−0.01	<0.001	−0.01	<0.001
Continentality (PC2)	−0.08	0.049	−0.10	0.06
Continentality^2 (PC2)	−0.01	<0.001	−0.005	0.27
CD	0.13	0.607	0.35	0.27
CD^2	−0.29	0.008	−0.21	0.04
Aridity × Continentality	0.03	<0.001	0.03	<0.001
Aridity × CD	–	–	0.02	0.380
Continentality × CD	0.06	0.040	–	–

Note: The table presents the model estimates and *p*-values. Two models are shown: (i) the PC1 CD-based model (CD1), which uses the decomposed CD in the first axis of the PCA, that is, considering CD along the aridity gradient (PC1-based CD) and (ii) the PC2 CD-based model (CD2), which uses the decomposed CD along the second axis of the PCA, that is, considering the continentality gradient (PC2-based CD).

continentality axis (PC2-based CD or CD2), canopy service (RII) followed a negative quadratic humped relationship with the aridity of the local community (Table 1). The inflection point of this relationship depended on continentality conditions, as indicated by the significant interaction between aridity and continentality (Table 1, Figure 3). This interaction suggests that aridity exerts a stronger influence on RII under high continentality, resulting in an almost linear relationship between climatic stress (coupled effect of aridity and continentality) and RII (Figure 3). Additionally, both CDs (CD1 and CD2) had a negative quadratic effect on RII (Table 1; Figure 4a,b). Continentality also modulated the response of RII to the aridity-based climatic disequilibrium of canopy plants, as evidenced by the significant positive interaction between continentality and CD1 (Table 1, Figure 4a). Thus, in highly continental sites, canopy plants with high climatic disequilibrium in PC1 (i.e. those experiencing drier conditions than their optimum) exhibited greater canopy service, whereas in low continentality sites, the effect of climatic disequilibrium was reversed.

Considering the CD2-based model, the relationship between plant canopy service (RII) and aridity followed the same negative quadratic trend (Table 1). However, in this case, aridity (PC1) did not significantly modulate the effect of CD2 on RII response.

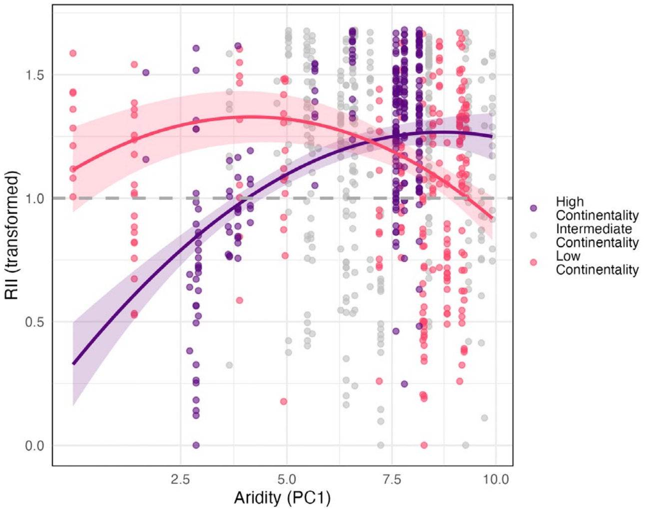

FIGURE 3 Effect of the interaction between aridity (PC1) and Continentality (PC2) on the canopy service (Box-Cox transformed value of RII; see Section 2) of the studied communities. The pink line represents the effect of aridity on canopy service (RII) in communities with low continentality (1 SD below the mean of PC2), while the purple line represents the effect of aridity on RII in communities with high continentality (1 SD above the mean of PC2).

4 | DISCUSSION

4.1 | Climatic stressors and facilitation

Our results show a non-linear, unimodal relationship between aridity and canopy service across the studied geographic gradient. We observed that canopy service tends to be higher in environments with intermediate levels of aridity, that is in semiarid to sub-humid climates, compared to those with either arid or humid conditions. Our findings align with Holmgren and Scheffer (2010) who described more positive interactions in mildly stressed environments, and with Maestre and Cortina (2004) who observed more competitive interactions at the extremes of the stress gradient.

The mechanisms behind these patterns stem from the fact that, in very arid environments, potential recruit species end up competing with canopy plants for water resources (Díaz-Borrego et al., 2024; Maestre et al., 2009). Hence, the amelioration of microclimatic conditions beneath the canopy would not compensate for the reduced water availability for recruits (O'Brien et al., 2017), especially during drought periods (Wright et al., 2015). Further, in

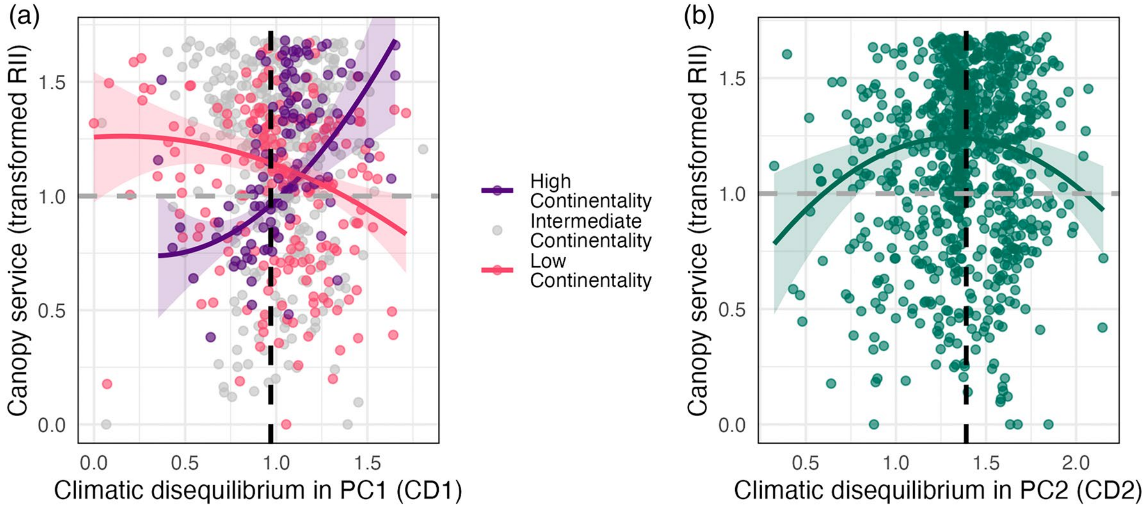

FIGURE 4 (a) Effect of the interaction between continentality (PC2) and CD1 (Climatic disequilibrium along the PC1 dimension) on the canopy service (RII) of the studied communities. The pink line represents the effect of CD1 on canopy service (RII) in communities with low continentality (1 SD below the mean of PC2), while the purple line represents the effect of CD1 in communities with high continentality (1 SD above the mean of PC2). (b) Effect of CD2 (Climatic disequilibrium along the PC2 dimension) on canopy service (RII). In both plots, values of CD to the right of the black dotted line indicate positive disequilibrium (canopy plants experiencing drier conditions (a) or higher continentality (b) than their niche optimum), while values to the left indicate negative disequilibrium (canopy plants experiencing wetter conditions (a) or less continentality (b) than their optimum). In both plots, RII values above the dashed horizontal line indicate that canopy plants facilitate the recruitment of other species, while values below indicate that they hinder it. Each dot represents a canopy plant species in a given community.

benign environments, the climatic buffering effect of the canopy plant would not offer a significant advantage to the potentially beneficiary recruit species. That is, the benefit of facilitation would be minimal (Holmgren et al., 1997). Thus, in the absence of (macro) climatic stress, it would be more beneficial for recruiting species to establish outside the canopy plant's influence to avoid competition for nutrients, light and other resources (Craine & Dybzinski, 2013). In fact, the SGH also supports the idea that in communities growing in low-stress environments, such as those without hydric stress, negative interactions prevail over facilitation (Armas et al., 2011; Bertness & Callaway, 1994).

However, our results also show that both climatic stressors (aridity and continentality) interact, and this interaction alters the non-linear relationship between aridity-induced stress and canopy service (Figure 3). As a result, the peak where maximum canopy service is observed shifts towards more arid environments—almost in the extreme end of the aridity gradient (Figure 3)—under high continentality. When we focus on communities that experienced higher continentality, this relationship does not follow the expected humped shape function between stress and facilitation (Holmgren & Scheffer, 2010; Michalet et al., 2006). Therefore the SGH may serve as a theoretical model to explain canopy service and plant–plant interaction patterns when multiple abiotic stressors are considered within a broad geographic context (Adams et al., 2022). In contrast, the non-linear relationship between stress and facilitation proposed by Holmgren and Scheffer (2010) falls short of explaining the cumulative effect of multiple stressors on plant–plant interactions. It is clear from our results that, as noted by Liancourt et al. (2017), the length of the examined gradients significantly influences the study's conclusions, as reducing the gradient length could impede our ability to detect unimodal trends.

In areas that have a continental climate, without the climatic buffering effect of the oceans, a high range of temperature is expected, with cold winters and warm summers (Stonevicius et al., 2018). This wide temperature fluctuation associated with continentality emerges as another stressor, impacting the survival of plant recruits. Extreme temperatures, both cold and hot, can threaten recruit survival (Germino et al., 2002; Ordoñez-Salanueva et al., 2021), as they are sensitive to harsh climates and their variability (Xu et al., 2022). Therefore, the benefits of growing under the canopy are more pronounced when the temperature range is extreme, as the probability of survival outside the canopy may be lower. Although competition for water between nurse and recruit plants may occur in dry environments, survival under the canopy remains higher (Cruz-Alonso et al., 2020), even under elevated thermal stress conditions, thus confirming the SGH when these two abiotic stresses are considered together. Importantly, although recruit delayed mortality or long-term declines might still occur, these processes would also likely affect the recruits in open areas. It is important to note that, in our study system, canopy service implicitly compares recruits growing under and outside the canopy. Thus, even if delayed mortality is present, the comparative outcome still indicates that conditions under the canopy are more favourable and that recruit survival is higher beneath canopies.

4.2 | Canopy climatic disequilibrium and facilitation

Overall, we have found that both CD (CD1 and CD2) of canopy plants drive canopy-recruit interactions by modifying the *canopy service* they provide. Additionally, the impact of climatic disequilibrium depends on the dimension of the climatic space considered—specifically, the disequilibrium along the aridity or the continentality gradient (i.e. CD1 vs. CD2).

In this sense, canopy plants experiencing drier conditions than their niche optima exhibited reduced canopy service, but only under environments with low continentality. Populations close to the dry edge of the niche may experience more defoliation and build less dense canopies (Pérez Navarro et al., 2019; Sapes et al., 2017), which would fail to create beneficial microclimates for recruits. In contrast, in areas that have continental climates, canopy plants inhabiting the drier edge of their niche tend to provide more canopy service. The macroclimatic conditions outside the canopy's influence may force facilitation to prevail over competition, as suggested by the SGH, especially when cumulative stressors appear (Liancourt et al., 2017). That is, even when canopy performance is low (as expected in the drier edge of the niche; Sapes et al., 2017), its buffering effect can still be sufficient to promote facilitation in thermal stressed environments. In fact, in some highly stressed sites, facilitation may be greater under defoliated, decayed or even dead canopies, suggesting that even a small degree of buffering is enough to enhance facilitation while reducing the competitive ability of the respective canopy species (Díaz-Borrego et al., 2024). To summarize, the directionality of CD (in which edge—dry vs. wet—of the niche a given community is placed) may influence canopy service, though the patterns are not entirely consistent. In addition, higher facilitation is expected to be greater when the canopy is in higher climatic equilibrium, but this ultimately depends on external macroclimatic conditions of the system. Once again, this suggests that the accumulation of stressors promotes facilitation, even in the face of reduced climatic suitability for the canopy species.

According to these observations, we demonstrate that the CD of canopy species is also important in explaining the assembly of community interactions across a broad climatic and geographic gradient. Therefore, canopy CD emerges as a target for future studies on how plant–plant interactions contribute to plant community assembly, as has already been demonstrated in the case of recruit CD (Perez-Navarro et al., 2024). This reinforces the idea of how crucial canopy plants are, by modulating the microclimate beneath them. So, they will influence future community composition and diversity (Kemppinen et al., 2024) by potentially enabling the recruitment of species that are poorly adapted (i.e. that live outside their niche optimum) to the current and expected future climate (De Frenne et al., 2013; Perez-Navarro et al., 2024).

4.3 | Facilitation under global change scenario

Facilitation helps to maintain species that are less adapted to the current changing climate at the cost of exacerbating the so-called climatic debt (Richard et al., 2021). Over the next few decades, increases in temperature and aridity in temperate ecosystems (Essa et al., 2023; Zittis et al., 2022) are expected to aggravate this climate debt for understory communities (Richard et al., 2021). Under this scenario, the canopy service becomes increasingly important for the recruits' survival and the maintenance of the diversity of the plant community (Rey et al., 2016). Furthermore, rising temperatures and aridity could lead to a loss of climatic suitability for the canopy species itself, potentially causing defoliation, plant decay or even its local extinction if the new conditions push the population outside its climatic niche (Pérez Navarro et al., 2019). This loss of canopy—related to CD- can lead to a loss of canopy service (Sánchez-Martín et al., 2024) as observed in some communities. Consequently, facilitative relationships might break down even before the actual death of the canopy plant occurs, as pointed out in other studies (Verdú et al., 2024; Verwijmeren et al., 2013). However, in some communities, particularly those experiencing highly contrasting thermal conditions (i.e. high continentality), facilitation may persist even if the performance of canopy species is poor, as the benefits of growing under defoliated or decayed canopy plants can surpass the costs of growing outside, as suggested by our results. Ultimately, in such cases, canopy species may continue to provide facilitation, which could be prolonged over time if the remaining structures—even decayed plants—generate a sufficient buffering effect to support part of the recruit community (Díaz-Borrego et al., 2024). Furthermore, climate change is expected to increase plant thermal stress (Breshears et al., 2021) and temperature variability (Perkins-Kirkpatrick & Gibson, 2017), so canopy plants will be necessary to buffer climate change induced temperature-related meteorological events (such as heat waves or late frost). As observed in our results, climates with greater temperature range tend to provoke more facilitation across plant communities. This strengthens the idea that, in the future and under predicted climate change scenarios, facilitation will become even more crucial than it already is at present.

As suggested by the quadratic relationship between CD and canopy service, facilitation may disappear if canopy plants are pushed further from their climatic niche optima, particularly in areas with mild climates. Under climate change, facilitation will be crucial for the maintenance of recruit species within the community. However, we expect that the effectiveness of canopy service on the community may have certain limits. A rapid increase of CD in canopy plants could lead to the disappearance of community recruit species in the mid-term, even before the eventual extinction of canopy plants themselves. However, recruiting plant diversity and abundance could persist in such situations if other ecological mechanisms come into play, such as interaction rewiring (Sánchez-Martín et al., 2024). Communities are dynamic systems, and the colonization of species better adapted to future warmer and drier climates is anticipated (Anderson & Wadgymar, 2020). Therefore, we can hypothesize that future persistence of species requiring facilitation will depend on their ability to recruit under the canopies of newly established species, which are expected to be more climatically equilibrated, or under pre-existing species whose CD will decrease with the new climatic conditions. In other words, the persistence of species within the community will depend on the recruits' ability to rewire their facilitative interactions, which are expected to be phylogenetically conserved and driven by canopy traits (Sánchez-Martín et al., 2023; Valiente-Banuet & Verdú, 2013).

4.4 | Study limitations and future research

The database used in this study has a geographic bias towards the Iberian communities. However, despite this geographic limitation, the database compiles a large diversity of climates and vegetation types, a typical characteristic of Mediterranean regions like the Iberian Peninsula (Andrade & Contente, 2020). Indeed, such variability has allowed us to detect patterns in the canopy service associated with environmental stress gradients. Admittedly, our models leave a significant portion of the canopy service variance across the studied communities unexplained, indicating that other factors beyond the climate are operating. Here, we characterize the climatic niche and, consequently, climatic disequilibrium by assuming that species distribution matches its climatic requirements. In several studies, the realized niche is referred to as the climatic niche, as it is based on actual species presence data rather than its climatic requirements (Batllori et al., 2020; Elvira et al., 2021; Serra-Diaz et al., 2013). It is known that species distributions may be constrained by negative interactions (such as competition) as well as limitations in dispersal. Still, this approach to characterizing the climatic niche and climatic disequilibrium provides a useful framework for identifying patterns and explaining processes across contrasting environments or populations (Jaime et al., 2022; Margalef-Marrase et al., 2020; Perez-Navarro et al., 2024); as it allows for the identification of general patterns across different communities across regions.

Other factors coupled with climate will affect facilitation trends at a local scale. For example, herbivory coupled with drought stress has been shown to alter the outcome of canopy-recruit interactions (Michalet et al., 2014; Smit et al., 2009; Verwijmeren et al., 2019). Similarly, management practices, past legacies and soil characteristics may also emerge as factors to be considered to predict the effect of canopy on recruits, especially in local predictions and in the context of climate change (Losapio & Schöb, 2017; Perring et al., 2018; Van de Voorde et al., 2011).

It should also be noted that the climatic niche of recruits (CD) may influence their need to grow under canopies, thereby increasing or decreasing the overall canopy service observed in a canopy community. We hypothesize that higher canopy service would be expected in recruit communities with high CD, as species with greater climatic disequilibrium are likely to require more climatic buffering from the canopy to tolerate macroclimatic conditions (Díaz-Borrego et al., 2024; Perez-Navarro et al., 2024). In the light of better understanding how both climatic disequilibrium modulates the bivariate (canopy-recruit) interaction, future research should add the triple interaction with OC and both CD (from canopy species and recruit species).

5 | CONCLUDING REMARKS

Our results highlight the potential consequences of displacing canopy plants from their optimal climatic range due to increasing aridity or continentality, as this could significantly alter the crucial canopy effect on the regeneration of plant communities. We also found that SGH and Humped-Back Shape remain useful good frameworks to explain canopy service (and facilitation) depending on the multiplicity of considered stressors, as suggested by previous studies (Adams et al., 2022; Kawai & Tokeshi, 2007). Additionally, the loss of canopy service concurrent with CD will be particularly critical in environments with cumulative climatic stressors (higher aridity and continentality). This suggests a possible future loss of diversity if recruit species are unable to rewire their positive interactions with better-adapted canopy species, especially in areas with more stressful environments. We also emphasize the importance of considering the climatic optima of canopy species to predict plant–plant interactions, suggesting that both canopy and recruit CD shape community assemblage. Future studies should incorporate other abiotic and biotic stressors to better capture the variability of canopy effect on recruits across distinct climatic gradients.

AUTHOR CONTRIBUTIONS

Miguel Verdú, Francisco Lloret and Jordi Margalef-Marrase conceived the ideas and designed the methodology. All the authors collected the data. Jordi Margalef-Marrase analysed the data, with inputs from Alicia Montesinos-Navarro and Miguel Verdú. Miguel Verdú and Jordi Margalef-Marrase led the writing of the manuscript. All authors contributed to writing the manuscript and providing feedback on drafts.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Climatic time series are openly available in CHELSA at http://chelsa-climate.org/download. Species occurrences data were extracted from the GBIF raw occurrence datasets that are openly available at http://www.gbif.org and see Table S1 in the SM for further details of all the species' datasets. Canopy–recruit interactions data was extracted from the Recruitnet global database at: https://doi.org/10.5281/zenodo.6567608 (Verdú et al., 2023). Recruitnet selected data to build up the analyses, and R.script is available via the Zenodo repository https://doi.org/10.5281/zenodo.15450396 (Margalef-Marrase et al., 2025).

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SUPPORTING INFORMATION

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

Table S1. Summary of the PCA constructed to characterize the common climatic space of the distributions of the 317 studied species, in which their respective niches have been modeled.

Figure S1. Visual representation of the PCA obtained from the thirteen climatic variables selected (see methods section in the main text), considering the distribution of the 319 studied species.

Figure S2. Interpretation and summary of the two main Principal Components of the PCA based on 13 bioclimatic variables.

Figure S3. Correlation between the components of climatic disequilibrium (CD) and their respective components of OC (PC1 and PC2).

Supporting Information S2. Supplementary information about the number of occurrences of the studied canopy species.

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