

RESEARCH ARTICLE

Shrub canopies preserve climatic niche disparity among recruit species in Mediterranean drylands

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Funding information

Generalitat Valenciana, Grant/Award Number: CIPROM/2021/63 and CIPROM/2026/046; Ministerio de Ciencia, Innovación y Universidades, Grant/Award Number: PID2020-113157GB-I00, PID2020-115264RB-I00 and PID2023-146535NB-I00

Handling Editor: Bérangère Leys

Abstract

1. Plant performance has a climatic optimum, especially during early establishment, and declines when conditions deviate from this optimum. However, shrubs can buffer unfavourable climatic conditions by creating more suitable microclimates beneath their canopies, facilitating the establishment of species with disparate climatic niches.
2. Across 10 Mediterranean shrubland sites, we compared climatic niche disparity and phylogenetic structure of plant recruits under shrub canopies versus open ground, integrating environmental, niche and phylogenetic data to reveal underlying abiotic and evolutionary drivers.
3. We show in 10 Mediterranean shrublands that the climatic niche disparity of recruits established under shrub canopies is significantly greater than that of those in open ground. This pattern was only weakly associated with shrub-driven microenvironmental heterogeneity, estimated using variability in photosynthetically active radiation as a coarse proxy, suggesting that additional abiotic factors may also contribute to recruit niche disparity. In addition, recruit assemblages beneath shrubs were composed, on average, of more distantly related species. Combined with phylogenetic conservatism in the aridity-response axis of their climatic niche, this pattern results in the co-occurrence of recruits with higher disparity in key climatic niche axes beneath canopies.
4. *Synthesis.* Plant canopies host recruit species that exhibit a wide diversity of climatic niches, which may play a role in maintaining biodiversity under ongoing and future climate change.

KEYWORDS

canopy plants, climatic disequilibrium, niche conservatism, phylogenetic signal, recruit plants

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1 | INTRODUCTION

Species performance tends to reach a maximum under specific climatic conditions, referred to as the climatic optimum, particularly during the early stages of establishment (Grubb, 1977; Sánchez-Gómez et al., 2006). As environmental conditions deviate from this optimum, plant performance declines due to increasing physiological and ecological constraints (Pérez-Navarro, Lloret, Ogaya, et al., 2024). In ecological theory, this decline is often interpreted through the distinction between stress and strain: *stress* refers to the intensity of external abiotic pressures acting on plants, whereas *strain* describes the physiological response of individuals, expressed as their deviation from the optimal functioning imposed by those pressures (Chapin III & Shaver, 1985; Liancourt et al., 2005, 2017). Building on this perspective, Gross et al. (2010) proposed that facilitation arises from the interplay between stress and the resulting strain, with species becoming more dependent on neighbouring plants when changes from the local climate from their optimum reduce performance. Under such suboptimal conditions, facilitation tends to prevail because neighbours buffer harsh climatic conditions, thereby reducing species strain by creating more favourable microhabitats (Díaz-Borrego et al., 2024; Margalef-Marrasé et al., 2025; Michalet et al., 2006), enhancing recruitment and promoting more diverse communities (Brooker et al., 2008), even though these communities may exhibit greater climatic disequilibrium (CD) (Pérez-Navarro, Lloret, Molina-Venegas, et al., 2024). Competition may also be operating under suboptimal conditions, depending on the

interacting species, community composition, resource availability, and the specific type and intensity of stress (Maestre et al., 2009). In such cases, limited resources or asymmetric competitive abilities may outweigh the potential buffering effects of neighbours, leading to competitive dominance even in stressful environments.

The CD of a local community is represented as the difference between the actual climate in the locality and the average optimum climate of its species (Davis, 1986; Mäkinen et al., 2025; Svenning & Sandel, 2013), and it can be applied to communities of recruits (Pérez-Navarro et al., 2022). This calculation focuses on the community's average climatic position, thereby overlooking the disparity among species in their individual climatic optima. This means that two communities may exhibit equivalent levels of disequilibrium, regardless their species' optima are either highly similar (i.e. exhibiting low niche disparity) or markedly different (i.e. exhibiting high niche disparity, Figure 1). A high disparity of climatic niches within the community reflects the presence of species that require contrasting climatic conditions. For example, greater disparity of climatic niches beneath plant canopies suggests the co-occurrence of species adapted to warmer conditions alongside those preferring cooler environments, as well as species from humid habitats occurring together with those from drier environments.

To better predict ecological changes in plant communities under ongoing climate warming, it is crucial to understand the range of climatic conditions in which their individual species can persist (Chapin III & Shaver, 1985). However, the responses of plant species to climate can be modulated by ecological interactions (Suttle

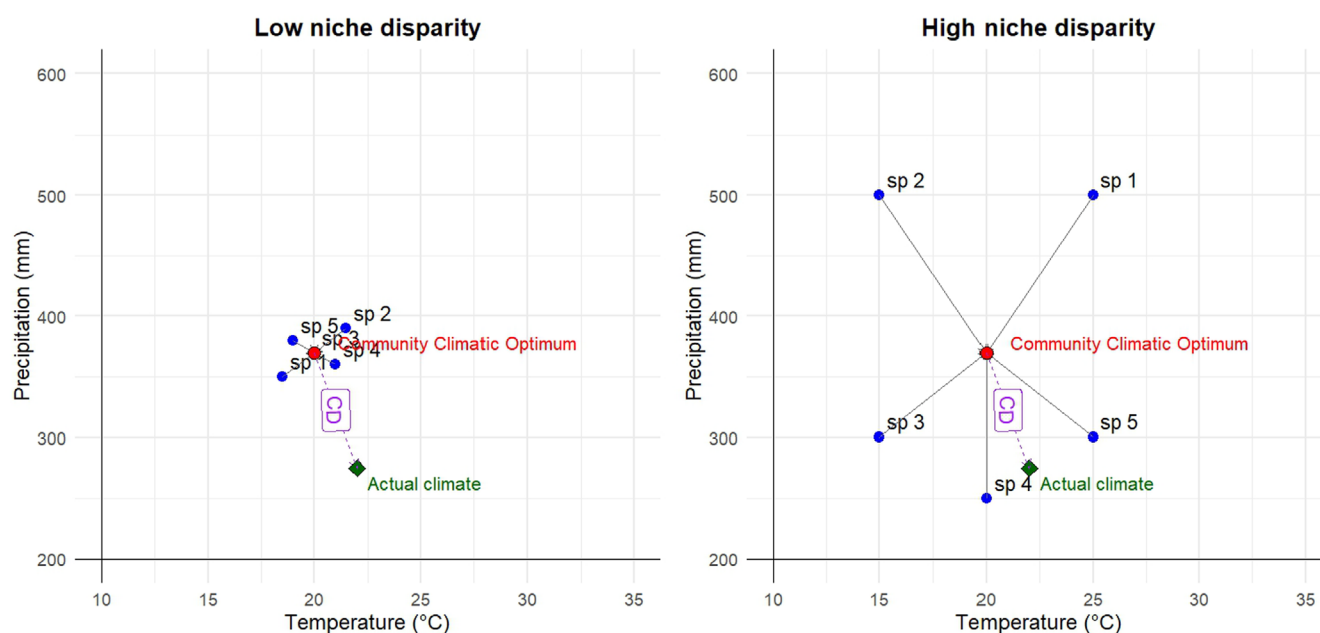


FIGURE 1 Representation of two communities that share the same climatic optimum—and therefore the same climatic disequilibrium at a given local climatic condition—but differ in the disparity of their species' climatic optima. Each of the five species (sp1 to sp5) has a climatic optimum in terms of temperature and precipitation. The climatic optimum of the community is represented as the centroid of the five species (red circle). The difference between this optimum and the current climate (green diamond) is the community climatic disequilibrium (CD), represented as a purple dashed line. In the right-hand community, species' climatic optima are widely dispersed around the centroid, indicating that species have different climatic optima. In contrast, in the left-hand scenario, all species in the community share a similar climatic optimum.

et al., 2007; Valiente-Banuet et al., 2006), which eventually determine community assembly. Recruitment represents a critical stage in plant community assembly, as the climatic niche for germination and seedling survival is typically more restrictive than that of adults (Young et al., 2005). However, plant canopies can buffer the niche of recruits against climatic extremes by modulating local microhabitat conditions, both biotic and abiotic. Consequently, the combined effects of biotic and abiotic microhabitat conditions are expected to influence the disparity of climatic niches within recruit communities beneath plant canopies (Callaway, 2007).

Plant canopy may ameliorate abiotic constraints such as temperature extremes, soil moisture deficits and solar radiation stress, but this effect is unlikely to be uniform across its entire coverage (Sánchez Martín et al., 2024). High microenvironmental heterogeneity beneath canopy plants can enhance recruitment by broadening the range of conditions that are favourable for multiple species (López-Pintor et al., 2006; Sánchez Martín et al., 2024). This heterogeneity can produce a mosaic of microsites with differing levels of light, moisture and/or temperature, increasing the likelihood that many recruit species meet their specific ecological requirements to establish. Under harsher environmental conditions, however, successful recruitment may rely less on the diversity of microsites and more on the canopy's capacity to buffer extreme abiotic stress (Sánchez Martín et al., 2024). Thus, by reducing variability in factors like temperature and moisture, some canopy plants create more stable microhabitats that act as refuges for recruits (Anthelme et al., 2014).

Among the biotic processes contributing to increased climatic niche disparity under plant canopies, the presence of functionally and/or phylogenetically distant species provides insight into underlying competitive interactions. Species that establish beneath the canopy of other plants tend to compete with one another (Schöb et al., 2013), resulting in recruit communities that are functionally and phylogenetically diverse (Castillo et al., 2010). Competitive exclusion tends to eliminate functionally similar species; thus, assuming evolutionary conservatism of functional traits, closely related species are also more likely to be excluded (Pausas & Verdú, 2010). Since climatic niches are generally phylogenetically conserved (Harris et al., 2022), the resulting disparity in climatic niches among recruits is expected to reflect the phylogenetic distances between species—that is, the phylogenetic diversity of the recruit community.

In this study, we calculate the disparity of climatic niches of 170 recruit species across 10 Mediterranean shrubland communities. These species were sampled both beneath the canopy of 150 shrubs belonging to 30 species and in adjacent open areas along a climatic gradient across the Iberian Peninsula. This gradient encompassed a wide range of temperature and aridity conditions, allowing us to capture a substantial variation in climatic disequilibria and providing an ideal framework to assess microsite effects on niche disparity. We hypothesize that shrub canopies support recruit communities characterized by greater climatic niche disparity relative to adjacent open microsites. This disparity is expected to arise from the heterogeneous abiotic conditions beneath the canopy, which enable the

establishment of sets of species representative of a broad range of climatic optima. Additionally, we propose that this increased niche disparity is associated with the recruitment of functionally and phylogenetically distinct species, potentially reflecting the imprint of competitive exclusion on community assembly processes.

2 | METHODS

2.1 | Study sites

The study was conducted in 10 shrubland communities distributed across a climatic gradient in the Iberian Peninsula, with annual precipitation ranging from 280 to 760 mm and mean annual temperature from 11.8 to 17.3°C (Figure S1). The region has a Mediterranean-type climate, characterized by high inter- and intra-annual variability in temperature and precipitation, with pronounced drought periods mainly occurring in summer (Coll et al., 2017). Due to these climatic and ecological constraints, plant communities exhibit sparse vegetation cover (Aguar & Sala, 1999), composed of patches of chamaephytes and shrubs, usually surrounded by open areas of nearly bare soil (Figure S2; see species composition of patches and open areas in the data available at <https://zenodo.org/records/20457090>; Verdú (2026)). In our study communities, plant cover ranged from 25.2% to 87.2% (Figure S1). The woody vegetation patches typically facilitate the recruitment of other plant species beneath their canopy, primarily by ameliorating the microhabitat conditions (e.g. through the accumulation of organic matter and nutrients, and buffering of climatic extremes), particularly in the driest sites (Brooker et al., 2008). Soil physicochemical properties varied among sites (Table S1), with pH ranging from moderately acidic to alkaline conditions and textures spanning from sandy to clay-rich soils.

Across the 10 studied communities, we established 150 paired sampling units to assess plant recruitment under shrubs and in adjacent open ground. Each community included five shrub species, with three replicate individuals per species. For each shrub, we sampled two matched areas: one located beneath the shrub canopy and another in nearby open ground, resulting in 15 paired sampling units per community (5 shrubs $\times$ 3 replicates $\times$ 2 paired microsites). The open-ground area was matched in size and shape to the corresponding shrub canopy projection, which had a mean area of 2.00 m² (SD = 2.63; range 0.12–16.85 m²). The paired sampling units were randomly distributed within each study site, which covered approximately 3 ha, to capture local spatial heterogeneity. Open-ground areas were placed at a distance sufficient to minimize the influence of their paired shrub while remaining close enough to reduce broader spatial variability. Consequently, larger shrubs required longer distances, whereas smaller shrubs had shorter distances to their paired open plots. In high-density communities, open plots were sometimes located farther from the canopy patch. In our study, the median distance between paired plots was 4.5 m (range: 0.8–28 m), with 75% of pairs separated by less than 8 m. Distance between paired samples was not significantly related to differences in

soil variable ($r = -0.045$, d.f. = 148, $p = 0.583$), indicating that spatial separation does not influence observed patch-gap soil differences (Figure S3).

Vegetation sampling was conducted between February and July 2023. Within each sampling unit, plant recruitment was quantified using a line-intercept method along equidistant parallel transects scaled to the patch size. This approach was chosen to standardize the sampling effort across varying shrub dimensions, ensuring that larger units received proportionally more sampling lines to maintain representative data. The number of transects per sampling unit was determined by the shrub's maximum dimension: units with a maximum length shorter than 1.2 m were sampled with five transects, whereas units with a maximum length longer than 1.2 m were sampled with seven transects. Transects traversed the full extent of the canopy or open sampling areas, recording all recruited plants intersecting the transect lines. We identified all woody species (phanerophytes and chamaephytes) and perennial herbaceous plants (hemicyptophytes). Annual plants were excluded from this study, as their inclusion would require continuous sampling throughout the growing season to account for the temporal dynamics of their emergence.

Fieldwork was conducted in protected areas, and the authors obtained all necessary permits from the relevant administrations throughout the study period.

2.2 | Community climatic niche metrics

To calculate the climatic niche metrics—CD and niche disparity—for each plot, we first characterized species' climatic niche optima using a principal component analysis (PCA) of climatic variables, following Broennimann et al. (2012). The PCA-defined climatic space was then used to estimate both the community-inferred climate (CIC) and the observed climate (OC), projected into the same reduced space. Using these representations, we calculated the CD and niche disparity of the recruit communities as explained below.

The species climatic niche was constructed using climatic data from the native range of the studied plant species. Species occurrence data were obtained from the GBIF database (GBIF, 2025, <http://www.gbif.org>; Table S2). To ensure data accuracy, raw occurrences were filtered to remove taxonomic and geographic errors. To minimize geographical inconsistencies and exclude potentially extinct localities, only records from 1970 onward were considered. Additionally, a maximum density of one occurrence per km² was applied to prevent climatic data redundancy (Franklin, 2010), given that the resolution of the climatic dataset was 1 km² (Karger et al., 2017). Climatic niche characterization was based on 13 bioclimatic variables developed for the BIOCLIM program (Booth, 2025), which we extracted for each occurrence from the CHELSA 2.1 database (Karger et al., 2017, <https://chelsa-climate.org>) to build the common climatic space of all species distributions (see Table S3 for a description of the biovariables). Of these 13 variables, seven were temperature-related: annual mean

temperature (bio01), temperature seasonality (bio04; measured as the standard deviation of monthly mean temperatures $\times 100$, reflecting the degree of temperature variation over the year), maximum temperature of the warmest month (bio05), minimum temperature of the coldest month (bio06), annual temperature range (bio07; difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month), mean temperature of the warmest quarter (bio10) and mean temperature of the coldest quarter (bio11). The remaining six variables were precipitation-related: annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), precipitation seasonality (bio15; expressed as the coefficient of variation of monthly precipitation, indicating how unevenly rainfall is distributed over the year), precipitation of the wettest quarter (bio16) and precipitation of the driest quarter (bio17). Other variables in the CHELSA database which combine temperature and precipitation (e.g. mean temperature of the wettest quarter), were excluded to avoid potential issues with orthogonal correlations in the climatic space generated through the subsequent PCA (Díaz-Borrego et al., 2024). The selected 13 bioclimatic variables were extracted for the period 1980–2010 for all species occurrences. To reduce the effects of spatial autocorrelation, we used Mantel correlograms implemented in the *ecospat.mantel.correlogram* function from the *ecospat* R package (Broennimann et al., 2012; Di Cola et al., 2017) to identify the minimum distance at which correlations among occurrence records were no longer significant ($p \geq 0.05$), hereafter the no-autocorrelation distance. Occurrence records were then randomly thinned so that only one record was retained within a radius equivalent to this distance). As a result, clean occurrence datasets were obtained for the studied species, ranging from 82 to 24,445 observations per species (Table S2).

The common climatic space derived from the 13 bioclimatic data 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 the 13 variables, we used the two first 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 projection, we extracted all the scores for the first two PCA axes corresponding to each species' occurrences. For each species, a two-dimensional kernel density function was then applied to smooth the density of occurrence scores along the two first PCA axes. A Gaussian kernel function was used to estimate the expected density of occurrences within each cell of the climatic space. The optimal bandwidth matrix for each density function was selected by cross-validation (Duong & Hazelton, 2005). The climatic niche optimum of each species' was defined as the centre of gravity (centroid) of its two-dimensional kernel distribution (Pérez-Navarro et al., 2021). This was calculated using the *COGravity* function of the *SDMTools* R package (VanDerWal

et al., 2014). It is important to note that the climatic niche estimates used in this study represent empirical approximations of the Grinnellian (climatic) niche. As such, they should be interpreted as species-level climatic affinities reconstructed from their realized distributions rather than direct measurements of physiological tolerances or regeneration niches. This framework is widely used in macroecological and ecological niche studies to characterize climatic preferences across broad spatial scales and provides a consistent basis for comparing community-level climatic structure (Broennimann et al., 2012; Díaz-Borrego et al., 2024; Pérez-Navarro et al., 2022; Pérez-Navarro, Lloret, Molina-Venegas, et al., 2024; Pérez-Navarro, Lloret, Ogaya, et al., 2024). We quantified two key metrics of the recruit communities: CD and climatic niche disparity. CD was defined as the Euclidean distance between the community-inferred climate (CIC) and the observed climate (OC), with higher values indicating a greater mismatch between the community's climatic composition and the local macroclimate. The CIC was estimated for each plot as the abundance-weighted centroid of the climatic optima of the species present in the community. The OC was derived by projecting the mean observed climate for each locality during the reference period (1980–2010) into the same PCA space, using the same 13 bioclimatic variables employed to characterize species' climatic niches. Similarly, for each plot, climatic niche disparity was calculated as the abundance-weighted mean of the Euclidean distances between each species' climatic niche optimum and the centroid of the community. Species' cover within the plot was used as the weighting factor to calculate the disparity. Higher disparity values within a plot indicate that the community includes species adapted to a broader range of climatic conditions. Although various measures can capture niche diversity, they are often correlated with each other. For instance, the metric used here (niche disparity) is strongly correlated with the standard deviation of climatic distances between species' niche optima and the community centroid (Pearson's $r = 0.61$, $p < 0.00001$).

2.3 | Canopy effects on abiotic and biotic parameters

2.3.1 | Abiotic effects: Light microenvironments

Light availability was used as a proxy for the abiotic influence of shrub canopies on recruits, as it integrates key microenvironmental changes, such as shading, temperature buffering and soil moisture retention, associated with canopy presence (Callaway, 1995). The variability in light conditions was calculated as the coefficient of variation (CV) of photosynthetically active radiation (PAR) measurements taken at ground level at five points beneath each shrub canopy and at five paired points in adjacent open ground. Measurements were taken using a 1-cm diameter quantum sensor (Skye Instruments, Llandrindod-Wells, UK). Since PAR levels fluctuate throughout the day, each pair of canopy and open-ground measurements was taken sequentially within a short

time window to ensure temporal matching and avoid confounding effects due to diurnal light variation.

To confirm that CV_PAR accurately reflects broader abiotic variation in these communities, we empirically validated this premise using an extensive monthly dataset collected over a full year across three Mediterranean shrubland communities sharing similar climate, soil and vegetation structure (Sot de Chera, included in the present study, Salinas; 38°32' 24" N, 0°53' 24" W) and La Calderona (39°39' 36" N, 0°29' 24" W). In each community, PAR, soil temperature and soil moisture were measured across 12 points beneath each of 100 shrub canopies and in their adjacent open clearings. This empirical validation confirmed that spatial variation in PAR consistently tracks broader microclimatic spatial heterogeneity, showing significant positive correlations with spatial heterogeneity in both soil moisture ($r = 0.47$ in Sot de Chera, $r = 0.31$ in Salinas, $r = 0.37$ in La Calderona; $p < 2.2 \times 10^{-16}$ in all cases) and soil temperature ($r = 0.20$ in Sot de Chera, $r = 0.62$ in Salinas, $r = 0.49$ in La Calderona; $p < 2.2 \times 10^{-16}$ in all cases).

2.3.2 | Biotic effects: Taxonomic and phylogenetic diversities

The taxonomic diversity of the recruit communities was estimated using the Shannon diversity index, which accounts for both species richness (the number of species) and evenness (the relative abundance of each species) in a community (Shannon, 1948).

The phylogenetic diversity of the recruit communities was estimated as the mean phylogenetic distance between all pairs of species within each community. To calculate phylogenetic distances, we reconstructed the phylogenetic tree representing the evolutionary relationships among all recruit species with the help of the R package *VPhyloMaker2* (Jin & Qian, 2022). This tool generates dated phylogenies from a species list by leveraging a comprehensive megaphylogeny (GBOTB.extended.TPL.tre; Jin & Qian, 2022; Smith & Brown, 2018) as a backbone. We employed the *phylo.maker* function with the insertion option set to 'S3' to incorporate species not present in the backbone tree (Jin & Qian, 2019; Qian & Jin, 2021), resulting in a complete phylogeny for all species recorded at our study sites.

2.4 | Statistical analysis

Paired *t*-tests were used to assess differences between microhabitats (shrub canopy and their adjacent open areas) for all studied variables, including community CD, niche disparity, light variability and both taxonomic and phylogenetic diversity.

The phylogenetic signal of the climatic optima of the recruit species was estimated by calculating Blomberg's *K* using the *phylosig* function from the *phytools* package in R (Revell, 2024). This function quantifies the degree to which trait similarity among species reflects their phylogenetic relatedness by comparing the observed variance of trait values across the phylogeny with the variance expected under a Brownian

motion model of evolution. The analysis was conducted using the species-level values of climatic optima as the trait data and the corresponding phylogenetic tree of the recruit species as the evolutionary framework. Significance was assessed through randomization tests that compare the observed K to a null distribution generated by permuting trait values across the tips of the phylogeny.

The relationship between climatic niche disparity and heterogeneity in light availability was tested through a general linear mixed model (GLMM) with a normal distribution of errors using the *lmer* function of the *lme4* R package (Bates, 2010). Climatic niche disparity was the response variable, and the CV of the light (PAR) incident on the plots was the explanatory variable. We first fitted a model with community and shrub species as random effects. However, only community accounted for a significant portion of the variance, so we retained community as the sole random factor in the final model. The same model structure was used to test the effects of shrub canopy, phylogenetic diversity and CD of the recruit communities in its climatic niche disparity. Variance explained (R^2) was calculated by the *r.squaredGLMM* function of the *MuMIn* R package (Bartoń, 2018). Significance of the estimates was obtained by the *lmer*test package (Kuznetsova et al., 2017).

We used abundance-weighted metrics as the primary approach following standard practice in community-level diversity and disequilibrium metrics. In any case, weighted and unweighted niche disparity metrics were highly correlated ($r=0.91$; $p<0.001$), and all analyses repeated using unweighted metrics yielded qualitatively identical results, with no change in the main ecological conclusions (data not shown).

The statistical analyses were carried out with R version 4.3.3 (R Core Team, 2024). All data and scripts to reproduce the analyses and figures can be found at <https://zenodo.org/records/20457090>; Verdú (2026)).

3 | RESULTS

3.1 | Climatic space

The PCA reduced the 13 climatic biovariables to two principal components explaining 48% and 28% of the variance, respectively (Figure S4). 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 S3). Thus, PC1 can be interpreted as a gradient of aridity, with higher values corresponding to increased aridity. The second axis (PC2) is positively correlated with variables related to temperature variability (e.g. annual temperature range and temperature seasonality; Table S3), thus representing a gradient of continentality. Consequently, species whose optima are located in the upper right quadrant of the multivariate space defined by the PCA are adapted to more stressful climatic conditions, whereas species situated in the opposite quadrant are less adapted to such stressors.

3.2 | Climatic disequilibrium of recruit communities

The recruit communities established beneath the shrub canopies and in the open ground had similar levels of CD (Figure 2a; Estimate $\pm$ SE = 0.027 ± 0.062 ; $t_{147.4} = 0.43$, $p = 0.67$; linear mixed model). However, the disparity of the climatic niches under shrub canopies was significantly larger than that in the open (Figure 2b; 0.168 ± 0.054 ; $t_{148.9} = 3.09$, $p = 0.002$).

3.3 | Effect of shrub canopy on abiotic and biotic variables

Shrub canopies generated a higher variability of light microenvironments than the open ground (Figure 3; 58.63 ± 3.25 ; $t_{298} = 18.05$, $p < 0.0001$). The variability of light environments significantly explained the disparity of the climatic niches of the recruit plants (0.001 ± 0.0006 ; $t_{294} = 2.18$; $p = 0.02$), but with a very low R^2 ($R^2 = 0.015$).

The taxonomic diversity of the recruit communities was higher beneath the shrub canopies than in the open ground (Figure 4a; 0.19 ± 0.05 ; $t_{149} = 3.72$, $p\text{-value} = 0.0003$). Similarly, shrub canopies harboured communities of recruits that were phylogenetically more diverse than those established in the open ground (Figure 4b; 14.68 ± 5.45 ; $t_{149} = 2.69$, $p\text{-value} = 0.008$).

The phylogenetic signal of the climatic optimum of the recruit species, estimated from the species scores on the climatic PCA, was significant for the first PCA axis (PC1; related to aridity; Blomberg's $K = 0.09$, $p = 0.005$) but not for the second axis (PC2; related to continentality; Blomberg's $K = 0.04$, $p = 0.706$; Figure S5). These results indicate that closely related species tend to resemble each other's aridity optima more than expected by chance. As expected from this climatic niche conservatism in the first axis, niche disparity is positively associated with phylogenetic diversity (phylogenetic diversity term in Table 1), and this association was not dependent on the microhabitat (open ground, beneath canopies) (Phylogenetic diversity $\times$ Microhabitat term in Table 1).

This trend indicates that more phylogenetically diverse communities of recruit plants contain higher disparity of climatic niches (Figure 5a). Furthermore, niche disparity is dependent on the interaction between microhabitat and climatic disequilibrium (Microhabitat $\times$ Climatic disequilibrium term in Table 1). This interaction arises because niche disparity in the recruit communities beneath shrubs canopy increases more strongly with CD than it does in the open ground (Figure 5b).

4 | DISCUSSION

Plant canopies attenuate environmental filters enabling the recruitment of species that would otherwise not be able to establish in open areas (Callaway, 2007). Consequently, species recruiting beneath other plants do not experience the actual macroclimate, as it is modified by the plant canopy. In this sense, it has been found

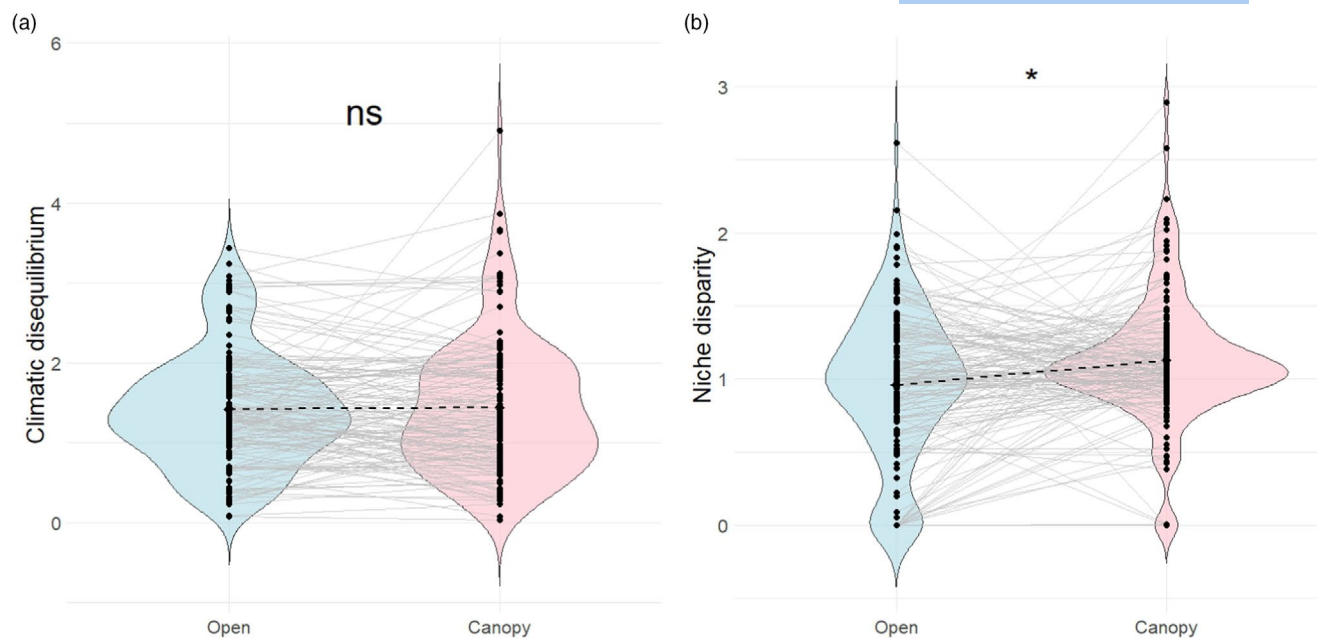


FIGURE 2 Violin plots showing (a) the climatic disequilibrium and (b) the disparity of niches of the recruit communities established on the open ground and beneath shrub canopies. Significant differences between these microhabitats are shown with an asterisk while ns indicates non-significant differences. Lines connecting the two violins represent paired canopy and open plot measurements taken in the field.

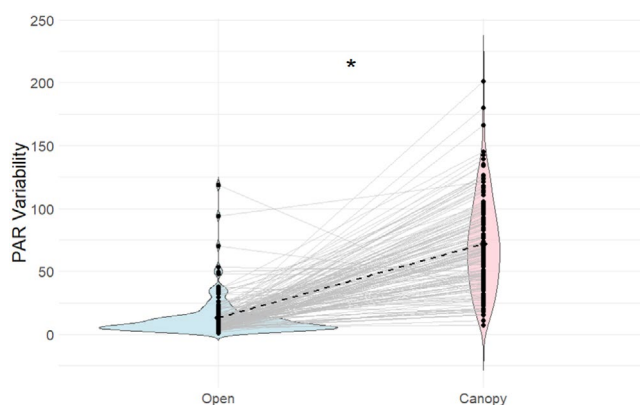


FIGURE 3 Violin plots showing the variability (i.e. coefficient of variation) in photosynthetically active radiation (PAR) on the open ground and beneath shrub canopies. Significant differences between microhabitats are shown with an asterisk. Lines connecting the two violins represent paired canopy and open plot measurements taken in the field.

that recruit communities under canopy plants exhibit higher CD than those living in close gaps (Pérez-Navarro, Lloret, Molina-Venegas, et al., 2024). However, an important and overlooked implication of this process is that the same average community disequilibrium can be the result of either a small or a large disparity in the climatic optima of the recruit species. While a low disparity of optima under shrubs would suggest that plant canopies host species with similar climatic niches, a high disparity would indicate that the canopies preserve a broad diversity of niches, potentially serving as a reservoir of plants preadapted to variable climatic conditions. These recruit communities represent a necessary but not sufficient condition to

determine the future of plant communities, as other biotic interactions, such as herbivory or predation, are likely to play pivotal roles in determining the long-term composition and dynamics of vegetation under emerging climatic conditions (Hamann et al., 2021; Zvereva & Kozlov, 2006).

Here, we found that while the mean CD of recruits was similar beneath plant canopies and open ground (in contrast to Díaz-Borrego et al. (2024) and Pérez-Navarro, Lloret, Molina-Venegas, et al. (2024)), the disparity of niches was larger beneath shrub canopies. These results illustrate that the same CD value can represent species with either similar optima close to the current climate or species with varying optima distant from it. This distinction highlights that CD alone does not fully capture the complexity of niche diversity within recruit communities. Two potential mechanisms may explain the greater disparity of climatic niches observed in recruits under plant canopies: an abiotic one, stemming from the microclimatic buffering provided by the canopy, and a biotic one, related to the interplay between facilitation and competition during species establishment.

From the abiotic perspective, shrub canopies can generate greater diversity of microhabitats, thus facilitating the recruitment of species with different climatic niches (De Frenne et al., 2013, 2021). Indeed, our results indicate that niche disparity increases with the CD of the recruit community, particularly beneath shrub canopies. This pattern aligns with the concept of climatic buffering provided by canopies, which create a more benign microclimate that facilitates the coexistence of species with climatic requirements that diverge from the prevailing regional climate, thereby contributing to broader niche disparity (Pérez-Navarro, Lloret, Molina-Venegas, et al., 2024).

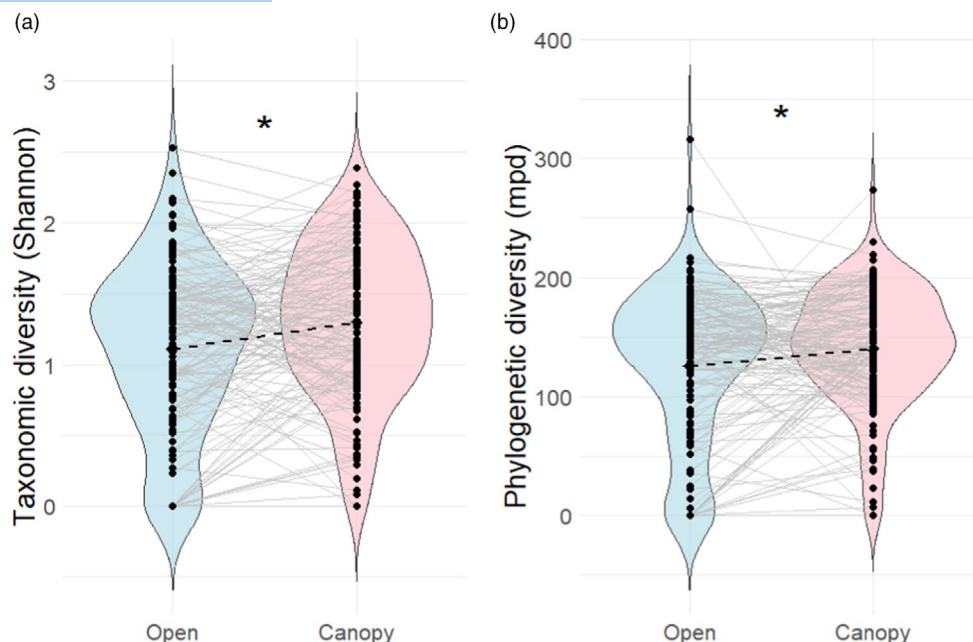


FIGURE 4 Violin plots showing the (a) taxonomic (i.e. Shannon index) and (b) phylogenetic (i.e. mean phylogenetic distance, in million years) diversity of the recruit communities established on the open ground and beneath shrub canopies. Significant differences between microhabitats are shown with an asterisk. Lines connecting the two violins represent paired canopy and open plot measurements taken in the field.

	Estimate $\pm$ SE	df	t	p-value
(Intercept)	0.209 $\pm$ 0.121	70.8	1.73	0.087
Phylogenetic diversity	0.005 $\pm$ 0.0005	290	9.40	2.00E-16
Microhabitat (Shrub)	-0.041 $\pm$ 0.147	282	-0.28	0.778
Climatic disequilibrium	0.103 $\pm$ 0.0509	264	2.02	0.044
Phylogenetic diversity $\times$ Microhabitat (Shrub)	-0.001 $\pm$ 0.0008	283	-1.42	0.154
Microhabitat (Shrub) $\times$ Climatic disequilibrium	0.194 $\pm$ 0.0551	282	3.51	0.0005

TABLE 1 Generalized linear model showing the effects of climatic disequilibrium and phylogenetic diversity of recruit communities growing in two different microhabitats (open ground (reference factor) and beneath shrubs canopies) on the niche disparity of these communities.

Note: Marginal $R^2=0.35$; Conditional $R^2=0.46$.

Using a coarse proxy for microclimatic spatial heterogeneity (CV of PAR radiation measured over a short temporal window), we found that shrubs generated a more heterogeneous microhabitat than the open ground. This pattern is expected because shrubs create varying levels of shade depending on factors such as canopy density, leaf structure or defoliation. Such spatial heterogeneity in the light levels is necessarily correlated with spatial heterogeneity in other abiotic factors such as soil and air humidity or temperature (Callaway, 1995; De Frenne et al., 2021) providing opportunities for species with different climatic requirements to establish themselves, leading to increased niche disparity. In line with this expectation, we found that microhabitats with greater microclimatic spatial heterogeneity supported recruits with more disparate climatic niches. However, the explanatory power of this relationship was low, indicating that PAR variability alone captures only a limited fraction of the abiotic processes underlying niche disparity. Future studies incorporating longer term and seasonal measurements of microclimatic conditions

could provide a more comprehensive understanding of how temporal fluctuations in environmental heterogeneity influence recruit establishment and niche disparity. Additional factors are therefore likely to contribute to the observed patterns. For instance, soil heterogeneity, shaped by litter decomposition and root inputs, which depend on regional climate and species traits, can generate fine-scale fertility patterns beneath the same canopy (Austin & Vivanco, 2006; Navarro-Cano et al., 2019). Also, rather than microhabitat heterogeneity, the reduction of average stress levels was identified as the main driver enhancing facilitation in a Mexican desert community (Sánchez Martín et al., 2024). Altogether, this contrasting evidence suggests that a complex balance between stress reduction and microenvironmental heterogeneity governs the disparity of climatic niches favoured under plant canopies, and that this balance may vary across climatic contexts.

From the biotic perspective, it has been shown that plant canopies facilitate the recruitment of a broader range of species, both

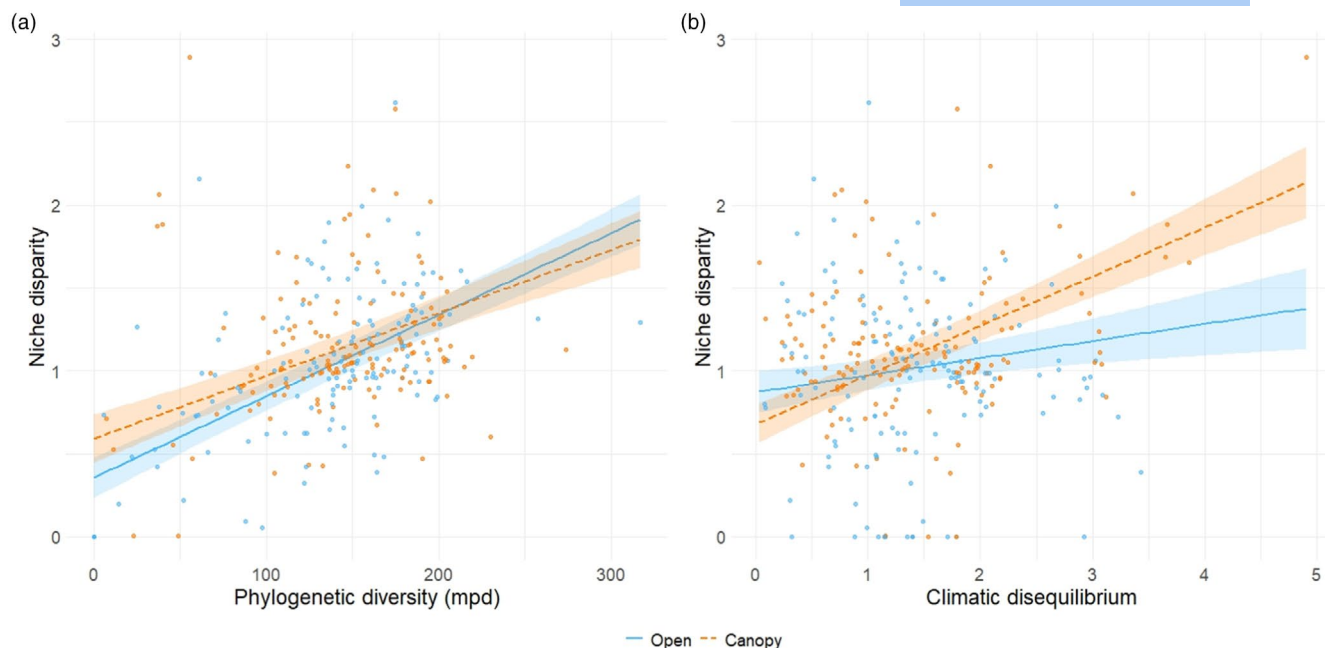


FIGURE 5 Relationship between niche disparity and (a) phylogenetic diversity (i.e. mean phylogenetic distance, in million years) and (b) climatic disequilibrium of recruit communities established in open ground and beneath shrubs canopies.

taxonomically and phylogenetically (Bashirzadeh et al., 2022; Gleiser et al., 2026; Valiente-Banuet & Verdú, 2013). Our results clearly support that taxonomic diversity beneath shrub canopies is higher than that in adjacent open areas. Additionally, this higher species diversity is not randomly distributed from a phylogenetic perspective but instead represents distant lineages, forming a phylogenetically diverse neighbourhood, as shown in other communities (Castillo et al., 2010; Vega-Álvarez et al., 2019). Beyond this contextual comparison, the key point is that shrub canopies facilitate species from lineages more distantly related than those coexisting in the open ground. Therefore, plant canopies are custodians of a deep evolutionary history, gathering diverse adaptive strategies, including responses to climate, as we have found here (Valiente-Banuet et al., 2006).

Several mechanisms may produce high phylogenetic diversity beneath shrubs, including abiotic processes such as microhabitat heterogeneity or relaxed environmental constraints discussed above, as well as biotic processes such as seed dispersal and competition (Vamosi et al., 2009; Webb et al., 2002). Regardless of the mechanisms underlying increased phylogenetic diversity, a direct consequence in the recruit community is a greater disparity in phylogenetically conserved traits (Webb et al., 2002). Similar to various biological attributes, the climatic niche of species has been shown to exhibit phylogenetic conservatism (Harris et al., 2022). We have found phylogenetic conservatism in the climatic niches of our study species, but only along one of the axes defining the niche, specifically, the axis related to aridity response, not the one associated with seasonality. This result could suggest that some Mediterranean species, particularly those that evolved under Tertiary tropical-like climates and lacking strong adaptations to aridity (Valiente-Banuet et al., 2006), may face evolutionary constraints in adapting

to increasingly arid conditions. However, it must be noted that although statistically significant, the phylogenetic signal (Blomberg's $K=0.09$) is relatively low in magnitude. This value is well within the range typically reported for ecologically relevant plant functional traits, particularly those related to water use and physiological performance. For example, Ávila-Lovera et al. (2023) reported similarly low Blomberg's K values across a broad set of structural and physiological water-related traits in plants, despite their strong ecological significance. In this context, the observed signal indicates weak but detectable phylogenetic conservatism, consistent with the generally labile evolution of functional traits in plants. Labile evolution suggests that, although there is some phylogenetic inheritance, it does not strongly constrain the evolution of new adaptations to water availability. This is particularly relevant under the projected intensification of aridification in the Mediterranean, largely driven by rising atmospheric evaporative demand due to significant temperature increases (Vicente-Serrano et al., 2025). In any case, aridification is occurring faster than the time required for perennial plants to adapt to these new climatic conditions, reinforcing the importance of the canopy plants as refugial microhabitats in preserving biodiversity under accelerating climate stress.

Previous studies have demonstrated that recruitment under plant canopies is frequency-dependent, benefiting rare species, which promotes species coexistence by lowering local extinctions and holds significant implications for the conservation of globally endangered species (Soliveres et al., 2015). Here, we present another key consequence of plant canopies for species conservation in the face of climate change: by maintaining a higher disparity of niches, they act as an ecological bet-hedging mechanism, increasing the probability that at least some species in the community will be

adapted to future microclimatic conditions. For example, the canopy of shrubs allowed the coexistence of recruit species with a very arid and low-continentiality optimum, such as *Launaea arborescens*, alongside others with less arid and more continental optima, such as *Lavandula latifolia* (see arrows in Figure S3). However, we never detected these two species coexisting in open ground. By accommodating species with contrasting environmental optima, plant canopies help buffer communities against diverse future climatic scenarios, reducing the risk of functional collapse regardless of the specific direction of the climatic change.

A limitation of this study is that annual plants, an important component of Mediterranean ecosystems, were not included in the calculation of niche disparity in recruit communities. Previous work has shown that annual species often rely on canopy-forming plants for recruitment, with interactions ranging from facilitation to competition depending on stress intensity (Holzapfel et al., 2006). As a result, similar patterns to those observed here are likely to apply to annual plants as well. Incorporating this group in future studies would further strengthen and extend these findings. Another limitation is the observational nature of this study. To definitively establish cause-and-effect mechanisms, future research would require experimental manipulations of recruit phylogenetic diversity and niche disparity to test their direct effects on recruit survival and community dynamics under field conditions.

In conclusion, plant canopies may contribute to biodiversity conservation by hosting recruit species with a diverse array of climatic niches. This makes plant canopies important elements in management practices focused on protecting biodiversity and allowing nature to pick the winners, rather than having humans select climate-change winners based on uncertain forecasts (Webster et al., 2017).

AUTHOR CONTRIBUTIONS

Jordi Margalef-Marrase: Conceptualization (lead), methodology (lead), investigation (lead), writing—original draft preparation (supporting), writing—review and editing (equal), Francisco Lloret: Conceptualization (lead), writing—review and editing (equal), Julio M. Alcántara: writing—review and editing (equal), José Antonio Navarro-Cano: Writing—review and editing (equal), Miguel Verdú: Project administration (lead), conceptualization (lead), investigation (lead), writing—original draft preparation (lead), writing—review and editing (equal).

ACKNOWLEDGEMENTS

Financial support was provided by the projects PID2020-113157GB-I00, PID2020-115264RB-I00, PID2023-146535NB-I00 (funded by MCIN/AEI/10.13039/501100011033 and 'ERDF A way of making Europe') and CIPROM/2021/63 and CIPROM/2026/046 (Generalitat Valenciana). We express our sincere gratitude to Alba Navarro and Daniel Rodríguez for their dedicated and invaluable contributions to the fieldwork.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70456>.

DATA AVAILABILITY STATEMENT

All data and scripts to reproduce the analyses and figures can be found at <https://zenodo.org/records/20457090> (Verdú, 2026).

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SUPPORTING INFORMATION

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

Figure S1. Location and characteristics of the studied communities.

Figure S2. Vegetation of the study sites.

Figure S3. Effect of spatial distance between paired canopy and open soil samples on differences in soil physicochemical properties. Colours represent different communities. Soils were collected at 0–10 cm depth from paired patch (beneath shrubs) and gap (open area) locations across all study sites. For each pair, the Euclidean distance between sampling points was related to within-pair differences in soil properties. Samples were homogenized, air-dried and sieved (<2 mm) prior to analysis. Variables measured included pH, electrical conductivity (EC), gravimetric humidity (HG), organic matter (OM), soil texture fractions (clay, fine silt, coarse silt, sand), major elements (Al, Ca, K, Mg, Na, P, S), trace and minor elements (As, Be, Bi, B, Cd, Co, Cr, Cu, Fe, La, Li, Mn, Mo, Ni, Pb, Rb, Sb, Se, Si, Sr, Ti, Tl, V, Zn) and total nitrogen (Ntotal) and total carbon (Ctotal).

Figure S4. Visual representation of the PCA obtained from the 13 climatic variables selected considering the distribution of the 170 studied species. The biovariables are bio01 (annual mean temperature), bio04 (temperature seasonality), bio5 (maximum temperature of the warmest month), bio06 (minimum temperature of the coldest month), bio07 (annual temperature range), bio10 (mean temperature of the warmest quarter), bio11 (mean temperature of the coldest quarter), bio12 (annual precipitation), bio13 (precipitation of the wettest month), bio14 (precipitation of the driest month), bio15 (precipitation seasonality), bio16 (precipitation of the wettest quarter), bio17 (precipitation of the driest quarter). The points represent the projection of the 10 study sites in the climatic space: Calblanque (CB), Doñana (DO), Garraf (GA), Hoces Gabriel (HC), Monegros (MO), Puebla de San Miguel (SM), Sierra Nevada (GR), Sot

de Chera (SC), Tabernas (TA), Tinença de Benifassà (TB).

Figure S5. The evolution of the climatic niche of recruit species, disaggregated into its components of aridity and continentality, as represented in the PCA of Figure S2. Colours indicate the values along the corresponding principal component axes. Orange tones (i.e. positive values in PC axes) correspond to species whose climatic optimum lies in arid and continental extremes, whereas bluish tones (i.e. negative values in the PC axes) indicate species with optima in humid and less continental conditions. The arrows indicate two species with contrasting climatic niches that coexist beneath shrub canopies but not in open ground.

Table S1. Soil physicochemical properties across study sites.

Table S2. List of species, including their GBIF DOI identifiers, along with the final occurrence records retained after applying the filtering criteria described in the Materials and Methods section.

Table S3. Interpretation of the PCA used to describe the shared climatic space across the distributions of the 170 analysed species, for which ecological niches were modelled. Corr.1 refers to the correlation between each bioclimatic variable and the first principal component. Corr.2 refers to the correlation between each bioclimatic variable and the second principal component.

How to cite this article: Margalef-Marrase, J., Lloret, F., Alcántara, J. M., Navarro-Cano, J. A., & Verdú, M. (2026). Shrub canopies preserve climatic niche disparity among recruit species in Mediterranean drylands. *Journal of Ecology*, 114, e70456. <https://doi.org/10.1111/1365-2745.70456>