

Plant canopies promote climatic disequilibrium in Mediterranean recruit communities

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Abstract

Current rates of climate change are exceeding the capacity of many plant species to track climate, thus leading communities to be in disequilibrium with climatic conditions. Plant canopies can contribute to this disequilibrium by buffering macroclimatic conditions and sheltering poorly adapted species to the oncoming climate, particularly in their recruitment stages. Here we analyse differences in climatic disequilibrium between understorey and open ground woody plant recruits in 28 localities, covering more than 100,000 m², across an elevation range embedding temperature and aridity gradients in the southern Iberian Peninsula. This study demonstrates higher climatic disequilibrium under canopies compared with open ground, supporting that plant canopies would affect future community climatic lags by allowing the recruitment of less arid-adapted species in warm and dry conditions, but also it endorse that canopies could favour warm-adapted species in extremely cold environments as mountain tops, thus pre-adapting communities living in these habitats to climate change.

KEYWORDS

climate change, climatic bonus, climatic debt, climatic disequilibrium, climatic lag, establishment, facilitation, plant community assembly, recruit–canopy interactions, recruitment

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INTRODUCTION

Plant species tend to spread across sites suitable for their establishment and persistence in concordance with the climatic conditions of their fundamental niche (Hutchinson, 1957; Pulliam, 2000; Soberón, 2007). However, multiple biotic and abiotic factors may hinder a perfect match between fundamental climatic niches and species' distributions (Pausas & Bond, 2018; Pulliam, 2000), so that species are often excluded from suitable sites or temporally persist under suboptimal conditions. Hence, plant communities and their constituent species are, to a greater or lesser extent, in climatic disequilibrium with the concurrent climatic conditions of the sites where they occur (Blonder et al., 2015; Davis, 1984; Svenning & Sandel, 2013). The climatic disequilibrium (CD, also referred to as climatic lag or climatic debt) of a given community represents the amount of mismatch between the observed macro-climate of the site where the community occurs and the optimal climatic requirements of the community's constituent species (Bertrand et al., 2011, 2016; Dullinger et al., 2012; Svenning & Sandel, 2013).

Historical contingency, species traits, soil characteristics and biotic interactions are first-rank drivers of climatic disequilibrium in plant communities. Historical contingency through priority effects (Fukami, 2015) may cause climatic disequilibrium by preventing the establishment of immigrants that are better adapted to the local macro-climate. Similarly, functional traits contribute to explain the variation in the magnitude of disequilibrium among different species by limiting the dispersal of species that are well adapted to the prevailing macro-climate (Stahl et al., 2014; Svenning & Sandel, 2013) or allowing the persistence of long-lived individuals under suboptimal conditions (Eriksson, 1996; Holt, 2009; Jackson & Sax, 2010), which ultimately results in increased climatic disequilibrium. Environmental filtering imposed by non-climatic factors, such as soil characteristics or plant–animal interactions (e.g. herbivory) may also impede the establishment of climatically adapted species (Kaarlejärvi et al., 2013; Lenoir et al., 2010; Svenning et al., 2014). Interestingly, plant–plant interactions can also induce climatic disequilibrium through competition or facilitation. On the one hand, competition can lead to the exclusion of climatically suitable species that are weak competitors (Svenning et al., 2014) but, on the other hand, established plants can modify the climatic conditions under their canopies, which may in turn facilitate the recruitment of species that are poorly adapted to the predominant macro-climate (de Frenne et al., 2013, 2019; Lenoir et al., 2013) (Figure 1).

Plant canopies can effectively ameliorate macro-climatic conditions by buffering extreme temperatures, reducing high irradiance, mitigating evapotranspiration and increasing nutrient and water availability (Brooker et al., 2008; Pritchard & Comeau, 2004), thus favouring the establishment of species that are in disequilibrium with the concurrent macro-climate. de Frenne et al. (2013,

2019) showed that forest canopies reduce high temperatures, enhancing the performance of heat-intolerant understorey individuals, and other authors have proved that such differences between micro and macro-climatic conditions allowed heat-intolerant species to endure past and ongoing climatic changes (Anthelme et al., 2014; Valiente-Banuet & Verdú, 2007). Furthermore, plant canopies can also buffer extremely low temperatures (as in high mountain areas) by absorbing part of the long-wave radiation emitted by the surface and re-radiating it back to the ground (Grimmond et al., 2000), thus creating warm refugia for cold-intolerant species (Odorico et al., 2013). Therefore, canopy amelioration may result in increased disequilibrium towards a net gain in either heat- or cold-intolerant species in the understorey relative to open ground (Figure 1). Under the current context of climate change, the persistence of cold-adapted species under plant canopies in warm sites can be understood as climatic debt—species lagging behind warming trends—, while the persistence of warm-adapted species under plant canopies in current cold sites can be understood as climatic bonus—pre-adaptation to newly emerging conditions (Duchenne et al., 2021). This duality is especially relevant for understanding the impacts on plant biodiversity of increasing warming and aridification in the Mediterranean region (Berdugo et al., 2022).

The effect of plant–plant interactions on climatic disequilibrium may vary along environmental stress gradients. Under low stress conditions, such as those characterized by mild temperatures and absence of water limitation, microclimatic amelioration would be less relevant, and thus understorey and open ground communities will show similar climatic disequilibrium values. Conversely, as environmental harshness increases towards more arid and/or hotter/colder temperatures, the buffering effect of canopies may turn critical for the recruitment of species that are less tolerant to these macro-climatic conditions (Maestre et al., 2009), thus broadening the differences in climatic disequilibrium between understorey and open ground communities. However, the positive effects of plants on recruitment can be limited at the edge of the harshness gradient if facilitation turns into competition (Maestre & Cortina, 2004; Michalet et al., 2006).

The impact of plant canopies on understorey communities can be more readily studied by focusing on recruits than on adult individuals (Serra-Diaz et al., 2016). Adult individuals, and especially those of long-lived species, may have established and grown under past conditions that differ from current climate (Zhu et al., 2014). In contrast, seedlings have been established more recently, and are frequently more climatically sensitive than adults (Lloret et al., 2009), and thus they can more precisely portray current microclimatic conditions under plant canopies. In addition, the seedling stage, despite its short duration, is where natural selection exerts its greatest influence, determining the demographic fate of the species

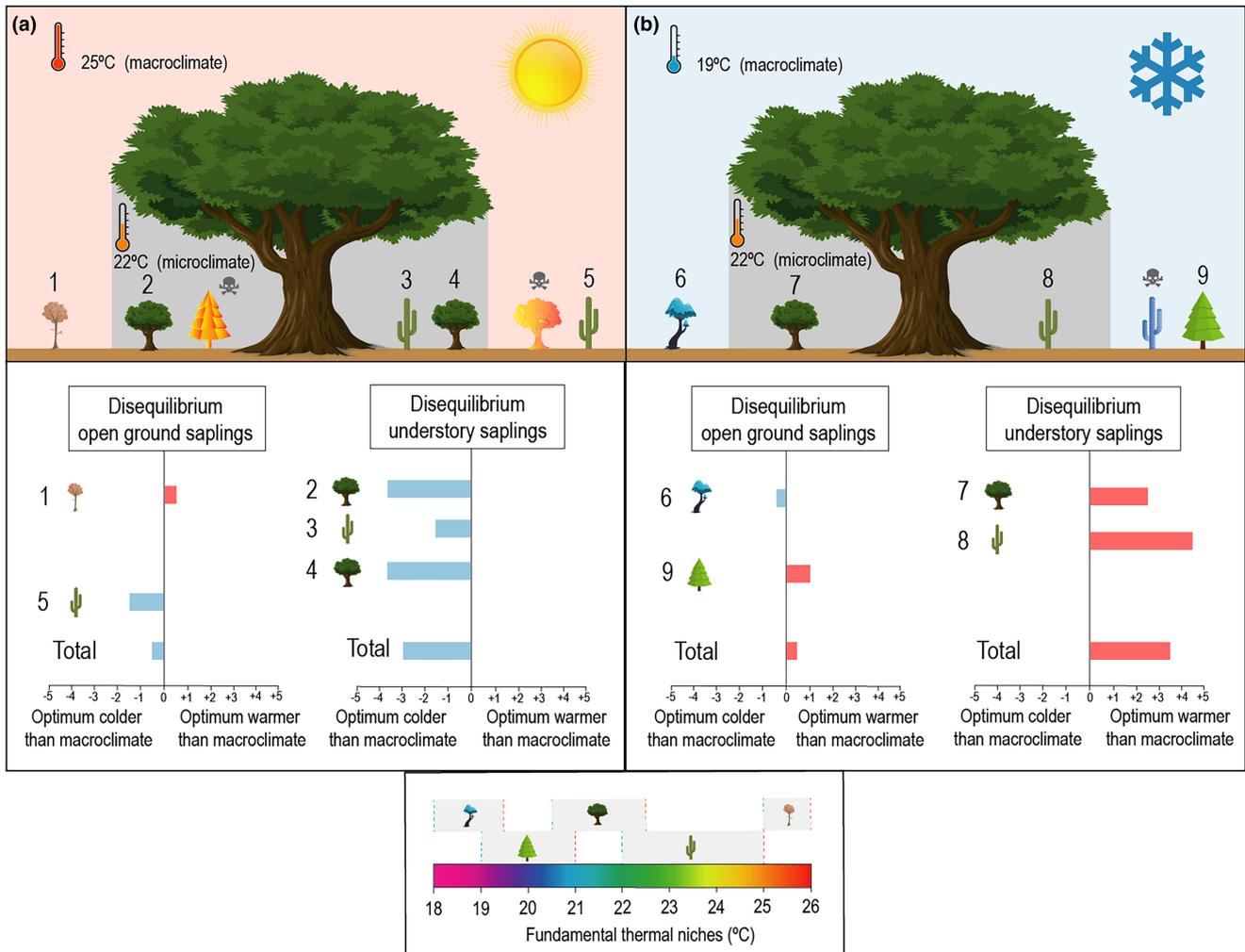


FIGURE 1 Conceptual framework representing differences in climatic disequilibrium between understory and open ground saplings under warm (a) and cold (b) macro-climatic conditions (temperature in this example). Total disequilibrium is estimated as the difference between the local temperature (macro-climate) and the temperature inferred from community composition. To infer the latter temperature, it is necessary to know the thermal niche of each species (left inset). For example, the thermal niche of the cactus-type species ranges between 22 and 25°C with an optimum of 23.5°C. Therefore, its optimum is 1.5°C colder than the macro-climate in the warm site (25°C) and 4.5°C warmer than that of the cold site (19°C). Finally, we obtain the total community climatic disequilibrium as the difference between the abundance-weighted mean of the climatic optima of all the species present in the community and the observed local macro-climate. Canopy-induced microclimates allow heat- and cold-intolerant species to recruit under warm and cold macro-climatic conditions, respectively, with greater disequilibrium in understory recruits relative to open ground. Note that the numbers refer to individuals that may or may not be of the same species.

and ultimately community assembly (Poorter, 2007). Therefore, considering recruits rather than adults allows to envisage the future composition of plant communities, although their predictive capacity in the medium to long term should be taken with caution (Batllori et al., 2020).

Here, we aim to assess differences in climatic disequilibrium between understory and open ground plant recruits across an elevation range embedding temperature, radiation and aridity gradients in the southern Iberian Peninsula (western Mediterranean region). We use a community climate framework, based on species climatic niche optimum and recruit abundances to measure the magnitude of climatic disequilibrium and test the following hypotheses: (1) the understory recruit communities show higher climatic disequilibrium than those growing in open ground

due to canopy-induced microclimatic buffering; (2) differences in climatic disequilibrium between recruiting communities growing under canopies and in open ground will vary along the climatic gradient, with canopy-induced disequilibrium being higher under more extreme conditions (coldest, warmest and most arid edges of the climatic gradient).

MATERIALS AND METHODS

Study region

The study comprised 28 localities distributed along the southern Iberian Peninsula (Figure S1; Table S1), and across an altitudinal gradient ranging between 20 m a.s.l.

and 2100 m a.s.l. The sampled area captures a wide range of environmental conditions both in terms of temperature and precipitation, including three major climate types (Bernabé Chazarra et al., 2018): mediterranean climate, mostly towards the centre and west areas; semi-arid climate, covering mostly the eastern part of the study region; and the alpine-mediterranean climate at mountain tops. Annual average minimum temperatures range between -5°C and 13°C and average maximum temperatures range between 12°C and 25°C from the coldest top of the mountains to the warmest southeast plains respectively. Annual rainfall concentrates during autumn and spring, and it ranges between 1000 mm in humid mountainous sites and 200 mm in the most arid areas towards the eastern—reference period 1981–2010, (Bernabé Chazarra et al., 2018).

The dominant vegetation varied from mediterranean dwarf shrublands in high-elevation localities, towards *Pinus* and *Quercus* mixed forests in mid altitudes and summer deciduous shrublands dominated by *Cistaceae* and *Lamiaceae* species in the most arid localities (see Table S1, for a full list of vegetation types).

Community recruitment data

Sampling protocols were adapted in each locality to the type of vegetation (see Table S1 for details), following the recommendations in Alcántara et al. (2019) (see Appendix S1 for further details). We considered a recruit as every woody plant older than 1 year, smaller than 25% the typical adult size and without visible signs of having reached reproductive stage. We recorded whether the recruits were growing in open ground or under the canopy of other individuals. A total of 26,252 recruit individuals of 141 species were recorded across all sites (Table S2). Finally, we also estimated the percentage of open ground surface as the accumulated longitude of the midline of the transect or quadrat without plant intersection $\times 100$, and canopy surface corresponds to 100 minus open ground surface.

Estimation of community climatic disequilibrium

Species occurrences

We downloaded all geographic occurrences for the 141 sampled species from the Global Biodiversity Information Facility (GBIF, 2020, www.gbif.org) removing records with geographic and taxonomic inconsistencies or referring to non-living organisms. We also randomly thinned species occurrences to avoid spatial autocorrelation (Appendix S2). The final number of occurrences per species dataset after data cleaning varied between 50 and 27,639, totalling 669,392 records across all species (Table S2).

Climatic data

We collected 13 bioclimatic variables from CHELSA database version 1.2 (Karger et al., 2017) for the average reference period 1979–2013. We used 13 bioclimatic variables: annual mean temperature, temperature seasonality—standard deviation $\times 100$ —, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality - coefficient of variation-, precipitation of wettest quarter and precipitation of driest quarter; all of them with 30 arcsec resolution ($\sim 1 \text{ km}^2$). We excluded bioclimatic variables containing interactions between temperature and precipitation (e.g. precipitation of the warmest quarter) to avoid problems in PCA orthogonality (Perez-Navarro et al., 2021).

Community climatic niche calculations

We built a common climatic space using principal component analysis (PCA) with scaled climatic data of all the 1 km^2 grid-cells with at least one species occurrence (PCA-occ sensu Broennimann et al., 2012). This approach reduced the climatic dimensionality from 13 bioclimatic variables to a two-dimensional space without considerable reductions in the total explained variance (the first two PCA axes retained 74.9% of the total variance, Figure S2). Further, this approach facilitated the visualization of the community climatic niche and also allowed to obtain an overall climatic disequilibrium value per recruiting community by integrating multiple climatic variables at the same time. The first PCA axis positively correlated with temperature variables and negatively with precipitation ones, thus representing an aridity gradient; and the second PCA axis positively correlated with temperature seasonality and negatively with both temperature and precipitation variables. We then characterized the climatic niche surface and optimum of each species in the multivariate climatic space by translating species occurrences into the two-dimensional climatic space (Broennimann et al., 2012). To do so, we followed the procedure described in Perez-Navarro et al. (2022) and in Appendix S3. Accordingly, species' climatic niche corresponded to the 2d occurrence density surface, and niche optimum to the centre of mass of this surface. We also built the climatic space using data from the 1979–2003 period to assess the possible effect of fast climatic shifts during the last decade in our niche models, but we did not observe significant differences (Appendix S3).

We estimated the community inferred climate (CIC) of the recruiting communities of each locality and microhabitat, that is, individuals growing beneath plant

canopies and in open ground respectively (totalling 56 recruiting communities, 28 localities \times 2 microhabitats). Specifically, CIC values were calculated as the gravity centre of the niche optima of all the species present in the community, that is, the mean niche optimum in the multivariate 2d-space weighted by species abundance. In addition, the average observed climate (OC) of each locality during the reference period 1979–2013 was translated into the common multivariate climatic space. Finally, the climatic disequilibrium (CD) was estimated as the Euclidean distance between CIC and OC (Figure 2; Figures S4 and S5). CD equal to 0 indicates a perfect climatic equilibrium between the recruiting community and the macro-climate of the locality, and CD values higher than 0 indicate disequilibrium in any of the directions of the 2d climatic space (hereafter ‘multivariate 2d CD’). In addition, to facilitate the interpretation of the results, we also calculated one-dimension CD for each PCA axis separately, and for mean annual temperature, minimum temperature of coldest month and annual precipitation. In this case, CD was estimated as the difference between CIC and OC (CIC-OC).

While multivariate CD in the two-dimensional space only shows the absolute distance between OC and CIC, the CD estimated for each separate climatic variable (each separate PCA axis and the 3 climatic variables) can be calculated either as absolute or directional CD,

that is, including signs. Directional CD in one dimension can take positive values (when recruiting communities have warmer or wetter optima than the observed macro-climate) and negative values (when recruiting communities have colder or drier optima than observed macro-climate), hence informing about the direction of the disequilibrium (hereafter ‘directional CD’). However, absolute values portray CD magnitude independently of its direction (hereafter ‘absolute CD’). It is worth noting that CIC, OC and CD are macro-climatic estimates, since they refer to climate conditions measured at relatively high spatial resolutions (1 km²).

Statistical analyses

Prevalence of recruit–canopy interactions

We applied a chi-squared test to disentangle whether species recruited more under plant canopies than in open ground. Specifically, we compared the observed and expected number of individuals recruiting under canopies given the proportion of surface occupied by plant canopies in the community. Thus, significant positive or negative differences between the number of observed and expected recruits under canopies indicate that saplings recruit under canopies more or less often than expected by chance respectively.

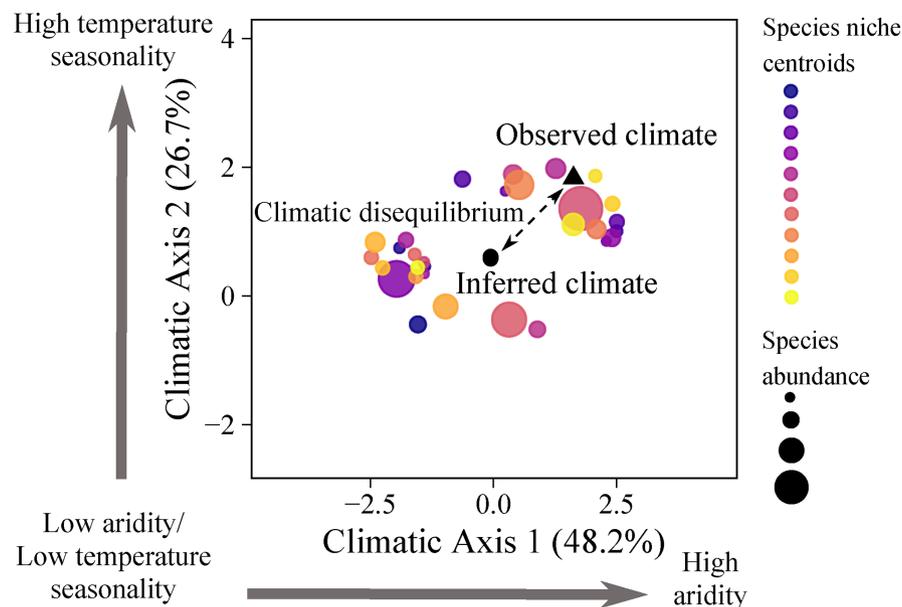


FIGURE 2 Example of a community climate diagram. The panel shows a two-dimensional climatic space obtained from the PCA analysis with the 13 selected climatic variables (Figure S2). The first PCA axis positively correlated with temperature variables and negatively with precipitation ones, thus representing an aridity gradient; and the second PCA axis positively correlated with temperature seasonality and negatively with both temperature and precipitation variables. Axis are unitless as they come from a PCA combination of precipitation and temperature variables. Each colour dot represents the niche optima of each species present in the community, and dot size represents its abundance in the community. Black dot shows the community-inferred climate (CIC), obtained by averaging niche optima of all the species weighted by their relative abundance, and the black triangle represents the observed climate (OC) of the locality. The dashed arrow represents the 2d multivariate climatic disequilibrium (CD) between observed and inferred climate. Species and abundance data for that figure comes from real data of recruiting community growing in open spaces for QUIBJ site (Table S1).

Differences in climatic disequilibrium between recruiting communities growing in open ground and under canopies

We first conducted a chi-square test to assess the number of localities in which understory recruiting communities showed greater 2d-multivariate CD than recruiting communities in open ground. Next, we analysed differences in climatic disequilibrium between recruiting communities growing under plant canopies and in open ground using mixed effect models with CD in the multivariate 2d-space as response variable, microhabitat (under canopy or open ground) as explanatory variable and locality as random intercept (lme4 R package, Bates et al., 2015).

We also analysed differences in CD for mean annual temperature, minimum temperature of coldest month and annual precipitation (i.e. univariate analyses) and the two first PCA climatic axes separately. In these cases, we tested for significant differences in both directional and absolute CD. Specifically, we run (1) five mixed effect models—one model per each of the three univariate climatic variables and two PCA climatic axes—including directional CD as response variable and microhabitat (canopy vs. open ground) as explanatory variable with locality as random intercept; (2) five mixed effect models with the same model structure but including absolute CD as response variable (Table S3).

Climate disequilibrium along environmental gradients

We applied mixed effect models to explore if differences in CD between understory and open ground recruiting communities varied along different environmental gradients. Particularly, we included multivariate 2d CD as response variable and aridity index (measured as PET/P), annual radiation, mean annual temperature, and percentage of plant canopy cover in plots interacting with microhabitat (under canopies vs. open ground) as explanatory variables, with locality as random intercept. Aridity index, mean temperature, and radiation for the reference period 1979–2013 were obtained from CHELSA database v.1.2 (Karger et al., 2017). Percentage of canopy cover in each locality was included to control the potential influence of this variable determining differences in CD between microhabitats. All explanatory variables were normalized for the analysis. Additionally, we run gls models (nlme package, Pinheiro et al., 2009) to account for possible spatial autocorrelation in the results (Appendix S4), since several localities belong to the same mountain range (Sierra Nevada) (Figure S1).

Finally, we also tested the relationship between directional CD for the selected univariate climatic variables with their respective climatic gradients. Specifically, we

applied three mixed effect models with (1) directional CD of mean annual temperature as response variable and observed mean annual temperature as explanatory variable, (2) directional CD of minimum temperature of coldest month as response and observed minimum temperature of coldest month as explanatory variable, and (3) directional CD of annual precipitation as response variable and aridity index as explanatory variable. In all cases, microhabitat (under canopies or open ground) was included interacting with explanatory variables, and locality was included as random intercept (Table S3). We also tested if the observed slopes were significantly different from zero (i.e. null scenario of maximum community tracking capacity) and the null expectation that the community composition keeps constant across sites (i.e. null scenario of minimum climatic tracking capacity of communities) using emmeans package (Lenth, 2021; Appendix S5). All analyses were performed using R v. 4.2.1 (R Core Team, 2023).

RESULTS

Prevalence of recruits–canopy interactions

From the total of 26,252 recruited individuals belonging to 141 species and 28 communities, 49.5% occurred on open ground and 50.5% under plant canopies. Regarding the 429 species \times locality records, 40.3% of species showed lower recruitment under canopies, 37.3% showed enhanced recruitment under canopies, and 22.4% showed no differences between the number of individuals observed under canopies and the number of individuals expected by chance given the proportion of plant canopy in the locality.

Differences in climatic disequilibrium between recruiting communities growing in open ground and under canopies

In 20 out of the 28 study communities, the recruit plant communities growing under canopies had a larger 2d multivariate CD than those growing in open ground ($\chi^2_1=5.14$; $p=0.02$; Table S4). The average 2d multivariate CD was 13.3% higher in recruit communities growing under canopies (0.917 ± 0.41) than in open ground (0.767 ± 0.383) (Figure 3), and this difference was statistically significant ($p=0.003$, Table S6).

Differences in absolute 2d multivariate disequilibrium agree with the significant differences in absolute CD in both PCA axes separately and temperature, but not precipitation variables (Figure 4; Table S4). As such, recruits under canopies showed higher absolute values of univariate and multivariate CD indicating that canopies generated climatic disequilibrium by buffering aridity (PCA1), seasonality (PCA2) and temperatures

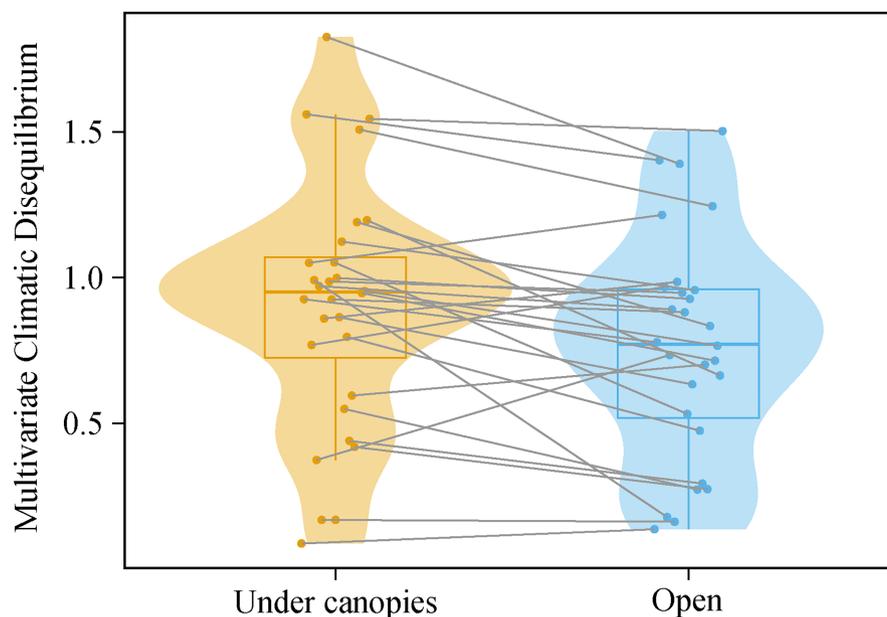


FIGURE 3 Violin plots showing 2d multivariate climatic disequilibrium of recruit communities growing under plant canopies (orange colour) and in open ground (blue colour). Grey lines join pairs of recruiting communities sited in the same locality.

for both the upper colder and hotter limit (Table S3). These results are consistent with the observed significant differences in directional CD for temperature of coldest quarter and PCA2 (Figure S7). In contrast, annual precipitation was marginally significant only for directional CD but no absolute CD. Recruiting communities growing under canopies showed a mean of -0.08 units lower than open ground communities for PCA2, corresponding to niche optima less adapted to temperature seasonality (Figure S2). Minimum temperature of coldest month and annual precipitation showed marginally significant differences, with understory communities showing average optima 0.2°C hotter and 5.88L wetter than open ground communities (Figure S7; Table S4).

Climate disequilibrium along environmental gradients

Despite the geographical aggregation of the study communities (Figure S1), the models relating 2d multivariate CD and environmental gradients did not show a significant effect of spatial autocorrelation (see higher AIC values of models including autocorrelation in Table S6 as well as the lack of slope in the semi-variogram model in Figure S8).

The 2d multivariate CD increased along the aridity gradient in open ground communities but not in those growing under canopies (Figure 5; Tables S7 and S8). Gradients of radiation, mean annual temperature and canopy cover were not significant neither in recruiting communities growing in open ground nor under canopies (Figures S9–S11; Table S7).

Regarding variations of directional CD (including sign) for specific climatic variables, CD in mean annual temperature varied along the annual temperature gradient, with those communities located in colder sites showing positive CD (i.e. warmer niche optima than observed macro-climatic temperature) and those communities located in warmer localities showing negative CD (i.e. colder niche optima than the observed macro-climatic temperature). Interestingly, this trend was significantly stronger for understory communities, which showed higher climatic disequilibrium than open ground communities both in the warmer and colder limit (Figure 6a; Tables S9 and S10). This pattern was similar for the minimum temperature of the coldest month (Figure S11; Tables S9 and S10). CD of annual precipitation increased along the aridity gradient, implying communities with wetter optima than observed climate as aridity increased. In this case, differences in trends of recruiting communities growing under open ground and under canopies were marginally significant with understory communities showing wetter optima than those growing in open ground (Figure 6b; Tables S9 and S10). For all the three variables, the observed slope was significantly different from zero and from the null model of complete correlation between CD and observed climate (Table S9).

DISCUSSION

Our results show a consistent pattern of greater climatic disequilibrium in recruit communities growing under plant canopies (Figure 3). This result is coherent with plant canopies alleviating the macro-climatic conditions

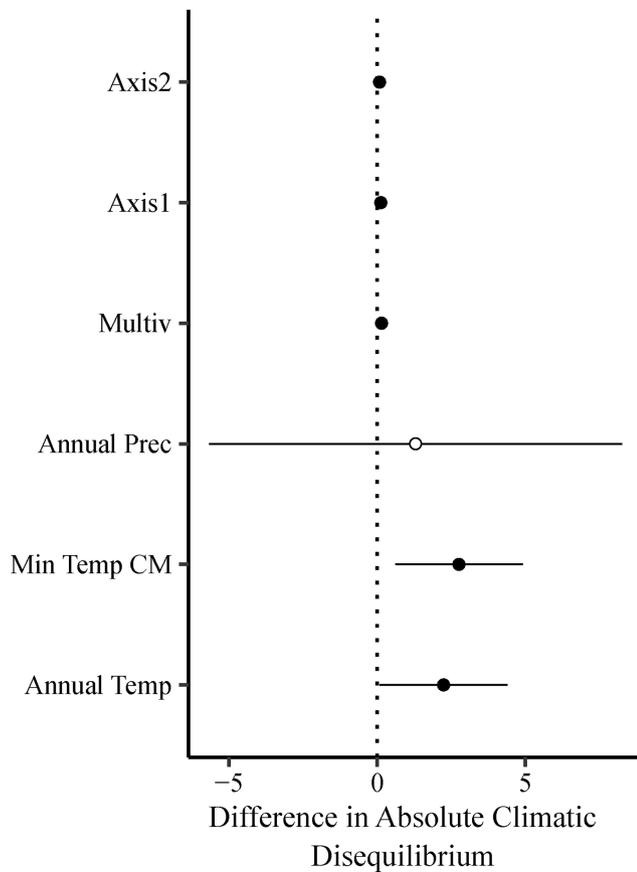


FIGURE 4 Differences in absolute community climatic disequilibrium between recruit communities growing under plant canopies and those growing in open ground ($|\text{CCD}_{\text{under canopies}}| - |\text{CCD}_{\text{open}}|$). Positive differences indicate higher absolute disequilibrium in communities growing under canopies with respect to the open ground ones. Black, grey, and white dots represent significant variables (p value <0.05), marginally significant ($0.1 > p$ value >0.05) and non-significant variables (p value >0.1) respectively. Line-range represents 95% confidence interval for model output. Ranges crossing zero are not statistically significant. Multivariate Axis1 and Axis2 CD are unitless, while precipitation is in L/m^2 and temperature variables are referred in $^{\circ}\text{C} \times 10$.

and improving the recruitment of species that would otherwise be less abundant under concurrent climatic conditions. Particularly, absolute values of climatic disequilibrium were higher for temperature variables (Figure 4), suggesting the role of canopy buffering temperatures. The difference in the climatic disequilibrium between recruiting community growing under canopy and open habitats is not homogeneous across climatic gradients, showing higher differences in disequilibrium in environments characterized by extremely cold or hot temperatures and higher aridity (Figure 6; Table S10).

Our results are consistent with the recognized effect of plant canopies on buffering temperatures, both for hot and cold conditions. Along the climatic gradient, both open and understory recruiting communities better adjust to the observed climate than expected by a null scenario where community composition remains

constant (i.e. no community adaptation capacity); however, the scenario of perfect match between community composition and observed climate is even farther to be achieved, highlighting the limited capacity of plant communities to keep up with climate (Appendix S5; Table S9; Figure S13). In any case, open communities always showed lower disequilibrium absolute values (Figures S7 and S13). These results support the findings reported in forest ecosystems, where canopies buffer high temperatures (de Castanho & Prado, 2014; de Frenne et al., 2019), allowing to host plant communities adapted to cooler temperatures than those experienced on the open ground (Richard et al., 2021). Buffering of high temperatures appears to be key in typical Mediterranean climates, particularly in the context of climate change, where extreme temperatures can be lethal for seedlings. As a consequence, understory plant communities accumulate a climatic debt that should be paid if the protective canopies disappear (Lenoir & Svenning, 2015; Richard et al., 2021). Interestingly, our results also showed higher climatic disequilibrium in favour of warm-adapted species under colder temperatures such as those experienced in high mountains, with particularly harsh cold conditions in winter (Figure 6; Figure S7). These results suggest that plant canopy would also act as climatic refugia filtering in favour of warm-adapted species in cold environments, thus likely acting as a source-habitat for species more suitable to the oncoming climate. Given the context of climate warming, the presence of warm-adapted species under canopies in cold sites can be understood as climatic bonus rather than climatic debt, as previously suggested for some plant communities in southern Europe (Duchenne et al., 2021).

The intensity of climate buffering by plant canopies is expected to vary along gradients of environmental stressors (Molina-Venegas et al., 2018). Accordingly, we observed that climatic disequilibrium varied not only along temperature gradients but also along the aridity one. We have detected that the canopy effect on the multivariate climatic disequilibrium remained fairly constant along the aridity gradient (Figure 5), suggesting that canopies were able to buffer the overall macroclimatic conditions in a similar way along the gradient. In contrast, climate disequilibrium increased with aridity in open ground pointing that plant communities did not fit so well under harsher conditions (Perez-Navarro et al., 2023; Serra-Diaz et al., 2014), likely due to the lack of more adapted species in the regional pool (Blonder et al., 2017). However, the univariate climatic disequilibrium for annual precipitation also increased for both open ground and under canopies recruiting communities towards the wet and arid limits (Figure 6b), also suggesting the great influence of observed climate on climatic disequilibrium. Unlike temperature gradients, where plant canopies showed high buffering capacity in both gradient limits, the differences between open ground and understory

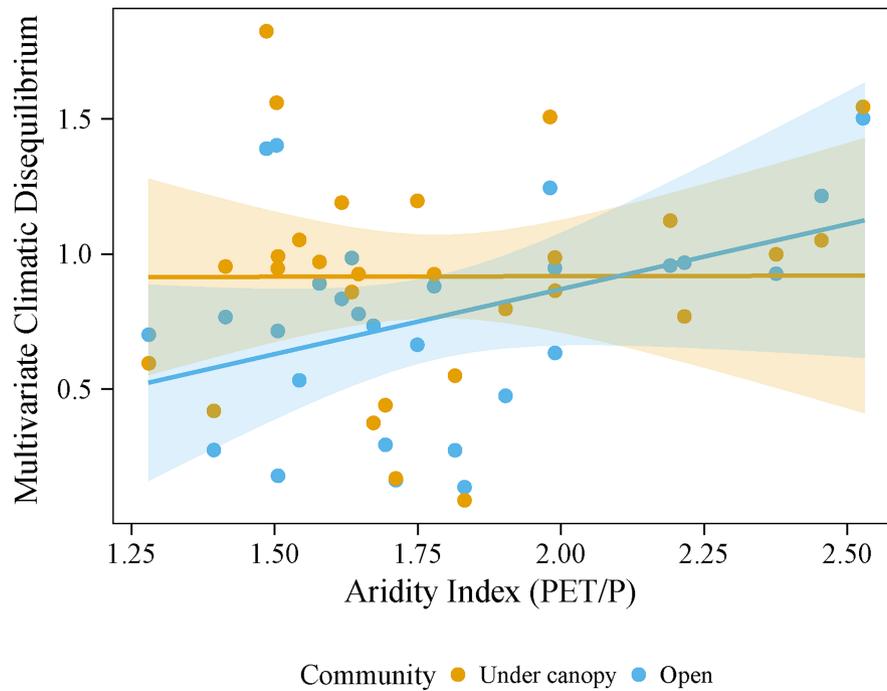


FIGURE 5 Regression plot relating multivariate community climatic disequilibrium and aridity index, measured as the ratio between potential evapotranspiration and precipitation, thus larger values of the x axis correspond to drier habitats. Orange colour represents the recruit communities growing under canopies and blue colour represents the recruit communities growing in open ground. Shadow area of each colour represents the 95% confidence interval.

communities increased only towards the more arid limit, with recruiting communities growing beneath plants always showing wetter climatic optima than open ones (Figure S13). This pattern suggests that the increase in moisture under canopies facilitated the recruitment of species less adapted to dry conditions in arid environments, while the buffer effect of plant canopies was less relevant in environments not so limited by water. This observation is consistent with the prediction of the stress gradient hypothesis, indicating that facilitation prevails over competition in stressful habitats, especially when the stress is driven by water resources (Maestre et al., 2009). However, this result contrasts with experimental studies suggesting that established vegetation can effectively compete for water with recruits under extremely dry conditions (Maestre & Cortina, 2004; Rey et al., 2016). Nonetheless, it cannot be discarded that under environmental conditions even more stressful than those examined in the studied environmental gradient, plant facilitation might turn into competition due to resource limitation.

Despite the increasing evidence on biotic responses lagging behind climate change, empirical information on the role of plant cover leading to future climatic debt or bonus is less frequent, particularly considering recruit communities, which represents a necessary condition determining mid to long-term vegetation dynamics in the absence or further disturbances. These results show that climatic disequilibrium is not only a contemporary consequence of the presence of long-lived species

persisting in sites that have become unfavourable with climate change (Richard et al., 2021), but that new plant generations are also successfully establishing in areas far from their climatic optima due to buffering effect of plant canopies. Other factors such as mycorrhizal fungi (Bennett & Classen, 2020) and phenotypic plasticity (Nicotra et al., 2010) may assist recruitment away from the climatic optimum. Such factors may act in addition to the buffering canopy effect, but their relative contribution to increase the CD remains unknown.

The effect of canopies increasing or reducing temperature and humidity beneath them will likely determine whether understory plant communities are better or worse adapted to future climate conditions. Canopy-driven recruitment may reduce establishment lags by promoting the establishment of species that are adapted to the oncoming climate change conditions. For example, the establishment of non-native species has been shown to be facilitated by native nurses in stressful but not in milder sites (Cavieres, 2021). In contrast, canopy-driven facilitation may increase extinction lags by sheltering resident species from the new adverse climatic conditions (Alexander et al., 2018). In addition, the impact of the canopy on the recruit communities might go beyond the climatic effects and can be produced by ameliorating other abiotic (e.g. increasing soil fertility) or biotic (e.g. decreasing herbivory, promoting mycorrhizal symbiosis) processes (Callaway, 2007; Gómez-Aparicio et al., 2005; Jordano et al., 2003). Any of these processes can reduce climatic

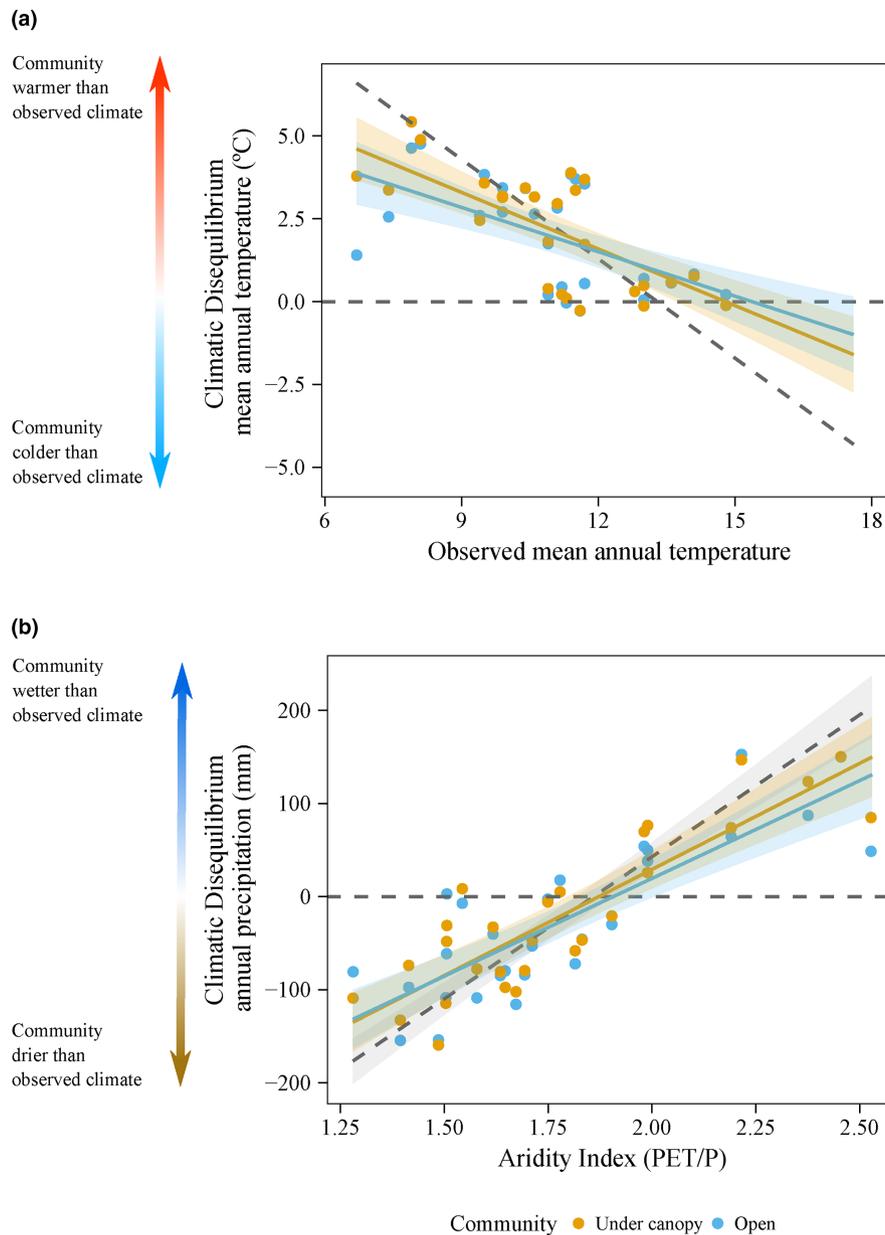


FIGURE 6 Regression plot relating univariate climatic disequilibrium of (a) mean annual temperature with observed macro-climatic mean annual temperature and (b) annual precipitation and annual aridity index (potential evapotranspiration/precipitation). Positive disequilibrium values correspond to recruiting community with disequilibrium values higher than observed macro-climate (wetter or hotter) and negative disequilibrium values correspond to recruiting community with disequilibrium values lower than observed macro-climate (drier or colder). Orange colour represents recruit communities growing under canopies and blue colour represents recruit communities growing in open ground. Shaded area of each colour represents the confidence interval 95%. Grey horizontal dashed line represents 0 climatic disequilibrium in each panel (i.e. null scenario of perfect climatic tracking of recruiting communities), and grey slope dashed line represents perfect correlation between disequilibrium and observed climate (i.e. null scenario of constant community composition across climatic gradient, thus representing that communities have null capacity to adapt to climate).

filtering relevance on community assembly, thereby likely increasing climatic disequilibrium. On the other hand, there may be detrimental effects of vegetation canopy on understory plants; for instance, by light depletion under canopies or by competition for water and nutrients from established adults (Holmgren et al., 1997). All these opposing effects may counteract each other and hence reduce the explanatory power of our statistical model explaining multivariate CD. At

this time, we are not able to disentangle the respective contribution of these drivers. However, climatic disequilibrium provides an integrative estimation of their overall impact and further studies can address the role of different contributors other than climate to plant community assembly using this climatic framework.

We are aware of the methodological limitations of our study. For instance, the impossibility to represent the fundamental niche of the species from field species

occurrences (Pearman et al., 2008) which already include biotic interactions, dispersal limitations and also assume species equilibrium with climate, disregarding species mismatches with climate (Svenning & Sandel, 2013). Moreover, these niches assume species as uniform entities across their distribution ranges, not considering intra-species genetic variability or local adaptation, which may result in different climatic tolerances (Benito Garzón et al., 2011; Lloret & García, 2016). However, identifying these intra-specific levels with homogeneous ecological responses is not feasible yet for most plant cases. Also, given the lack of accurate information regarding species life-stage, the species climatic space used in our study more likely corresponds to adult individuals. Recruits and adults likely exhibit differences in their climatic niche (Jackson et al., 2009), but we assume that the climatic space of recruits is enclosed within the adult's one, so we do not expect a strong bias in our analyses regarding to niche centroid characterization. In addition, the predominance of adult records on species occurrence would imply that the climatic disequilibrium observed in our study might be more representative of future communities emerging from this recruit composition. Another limitation of our approach is that the spatial resolution of the climatic variables obtained from worldwide databases does not perfectly portray the climatic conditions closely experienced by plants (Zellweger et al., 2019), thus potentially neglecting the microclimatic conditions where species can survive the changing macro-climate (Lembrechts et al., 2019; Lenoir et al., 2017; Maclean & Early, 2023). True microclimatic data at high spatial resolution would capture more accurately the large environmental differences between microhabitats under nurses versus open ground (Haesen et al., 2023), though the use of large-scale and long-term microclimatic time series is still limited (Lembrechts & Lenoir, 2020). However, by using the same macro-climatic data for each pair of communities under canopy and in open ground, our approach allows us to deduce the macro-climatic amelioration effect of the canopy through the community climatic niche differences between open and understorey communities.

Despite disequilibrium was widely common both in open ground and under canopies, the higher disequilibrium of understorey recruits suggests the role of plant canopies affecting future community climatic lags, by allowing the establishment of less arid-adapted species in warm and dry conditions, but also favouring plant species that are suitable for warm climatic conditions in cold environments such as Mediterranean high mountains, then acting as a reservoir of species adapted for oncoming climate change. Future research assessing the magnitude of climatic disequilibrium in different ecosystems across the globe would help to predict the role of plant canopy on the fate of plant communities facing drastic climatic changes.

AUTHOR CONTRIBUTIONS

MPN, FL and MV conceived the idea. All authors collected field data, particularly JA and RMV sampled most of the sites. MPN characterized community disequilibrium and run statistical analyses. MPN and RMV produced the figures. All authors contributed to first draft and subsequent revisions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Climatic data used in this paper are already publicly available at <https://chelsea-climate.org/>. GBIF raw occurrence records can be download from: <https://doi.org/10.15468/dl.9c6h5v>. Rest of datasets and used R scripts are available in Dryad: <https://doi.org/10.5061/dryad.kh18932dg>, and Github: https://github.com/mangeles582/Recruit_disequilibrium respectively.

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REFERENCES

- Alcántara, J.M., Garrido, J.L., Montesinos-Navarro, A., Rey, P.J., Valiente-Banuet, A. & Verdú, M. (2019) Unifying facilitation and recruitment networks. *Journal of Vegetation Science*, 30, 1239–1249.
- Alexander, J.M., Chalmandrier, L., Lenoir, J., Burgess, T.I., Essl, F., Haider, S. et al. (2018) Lags in the response of mountain plant communities to climate change. *Global Change Biology*, 24, 563–579.
- Anthelme, F., Cavieres, L.A., Dangles, O., Simon, J., Rusch, G.M. & Dawson, W. (2014) Facilitation among plants in alpine

- environments in the face of climate change. *Frontiers in Plant Science*, 5, 1–15.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. Available from: <https://doi.org/10.18637/jss.v067.i01>
- Batlloori, E., Lloret, F., Aakala, T., Anderegg, W.R.L., Aynekulu, E., Bendixsen, D.P. et al. (2020) Forest and woodland replacement patterns following drought-related mortality. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 29720–29729.
- Benito Garzón, M., Alía, R., Robson, T.M. & Zavala, M.A. (2011) Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*, 20, 766–778.
- Bennett, A.E. & Classen, A.T. (2020) Climate change influences mycorrhizal fungal–plant interactions, but conclusions are limited by geographical study bias. *Ecology*, 101, e02978.
- Berdugo, M., Vidiella, B., Solé, R.V. & Maestre, F.T. (2022) Ecological mechanisms underlying aridity thresholds in global drylands. *Functional Ecology*, 36, 4–23.
- Bernabé Chazarra, A., Flórez García, E., Peraza Sánchez, B., Tohá Rebull, T., Lorenzo Mariño, B., Criado Pinto, E. et al. (2018) Mapas climáticos de España (1981–2010) y ETo (1996–2016). Mapas climáticos España y ETo.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C. et al. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, 479, 517–520.
- Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., de Ruffray, P., Gégout, J.-C.C. et al. (2016) Ecological constraints increase the climatic debt in forests. *Nature Communications*, 7, 12643.
- Blonder, B., Moulton, D.E., Blois, J., Enquist, B.J., Graae, B.J., Macias-Fauria, M. et al. (2017) Predictability in community dynamics. *Ecology Letters*, 20, 293–306.
- Blonder, B., Nogués-Bravo, D., Borregaard, M.K., Donoghue, J.C., Jørgensen, P.M., Kraft, N.J.B.B. et al. (2015) Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology*, 96, 972–985.
- Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G. et al. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography*, 21, 481–497.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. et al. (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96, 18–34.
- Callaway, R.M. (2007) Positive interactions and community organization. In: *Positive interactions and interdependence in plant communities*. Netherlands: Springer, pp. 295–333.
- Cavieres, L.A. (2021) Facilitation and the invasibility of plant communities. *Journal of Ecology*, 109, 2019–2028.
- Davis, M.B. (1984) Climatic instability, time, lags, and community disequilibrium. In: Diamond, J.M. & Case, T.J. (Eds.) *Community ecology*. New York: Harper and Row, pp. 269–284.
- de Castanho, C.T. & Prado, P.I. (2014) Benefit of shading by nurse plant does not change along a stress gradient in a coastal dune. *PLoS One*, 9, e105082.
- de Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M. et al. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 18561–18565.
- de Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M. et al. (2019) Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3, 744–749.
- Duchenne, F., Martin, G. & Porcher, E. (2021) European plants lagging behind climate change pay a climatic debt in the North, but are favoured in the South. *Ecology Letters*, 24(6), 1178–1186.
- Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A. et al. (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2, 619–622.
- Eriksson, O. (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations—ScienceBase-catalog. *Oikos*, 77, 248–258.
- Fukami, T. (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, 46, 1–23.
- GBIF.org. (2020) GBIF occurrence download. <https://doi.org/10.15468/dl.9c6h5v>
- Gómez-Aparicio, L., Gómez, J.M., Zamora, R. & Boettinger, J.L. (2005) Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *Journal of Vegetation Science*, 16, 191–198.
- Grimmond, C.S.B., Robeson, S.M. & Schoof, J.T. (2000) Spatial variability of micro-climatic conditions within a mid-latitude deciduous forest. *Climate Research*, 15, 137–149.
- Haesen, S., Lembrechts, J.J., de Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M.B. et al. (2023) ForestClim—bioclimatic variables for microclimate temperatures of European forests. *Global Change Biology*, 29, 2886–2892.
- Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The interplay of facilitation and competition in plant communities. *Ecology*, 78, 1966–1975.
- Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 19659–19665.
- Hutchinson, G.E. (1957) Concluding remarks—the demographic symposium as a heterogeneous unstable. *Population*, 53, 415–427.
- Jackson, S.T., Betancourt, J.L., Booth, R.K. & Gray, S.T. (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 19685–19692.
- Jackson, S.T. & Sax, D.F. (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, 25, 153–160.
- Jordano, P., Bascompte, J. & Olesen, J.M. (2003) Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters*, 6, 69–81.
- Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. (2013) Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes. *Functional Ecology*, 27, 1244–1253.
- Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W. et al. (2017) Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122.
- Lembrechts, J.J. & Lenoir, J. (2020) Microclimatic conditions anywhere at any time! *Global Change Biology*, 26, 337–339.
- Lembrechts, J.J., Nijs, I. & Lenoir, J. (2019) Incorporating microclimate into species distribution models. *Ecography*, 42, 1267–1279.
- Lenoir, J., Gégout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E. et al. (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, 33, 295–303.
- Lenoir, J., Graae, B.J., Aarrestad, P.A., Alsos, I.G., Armbruster, W.S., Austrheim, G. et al. (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, 19, 1470–1481.
- Lenoir, J., Hattab, T. & Pierre, G. (2017) Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography*, 40, 253–266.
- Lenoir, J. & Svenning, J.-C. (2015) Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography*, 38, 15–28.

- Lenth, R.V. (2021) *emmeans: estimated marginal means, aka least-squares means*. R package version 1.7.
- Lloret, F. & García, C. (2016) Inbreeding and neighbouring vegetation drive drought-induced die-off within juniper populations. *Functional Ecology*, 30, 1696–1704.
- Lloret, F., Peñuelas, J., Prieto, P., Llorens, L. & Estiarte, M. (2009) Plant community changes induced by experimental climate change: seedling and adult species composition. *Perspectives in Plant Ecology, Evolution and Systematics*, 11, 53–63.
- Maclean, I.M.D. & Early, R. (2023) Macroclimate data overestimate range shifts of plants in response to climate change. *Nature Climate Change*, 13, 484–490.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97, 199–205.
- Maestre, F.T. & Cortina, J. (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society B: Biological Sciences*, 271, 331–333.
- Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I. et al. (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 9, 767–773.
- Molina-Venegas, R., Aparicio, A., Lavergne, S. & Arroyo, J. (2018) Soil conditions drive changes in a key leaf functional trait through environmental filtering and facilitative interactions. *Acta Oecologica*, 86, 1–8.
- Nicotra, A., Atkin, O., Bonser, S., Davidson, A., Finnegan, E., Mathesius, U. et al. (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, 15, 684–692.
- Odorico, P.D., He, Y., Collins, S., de Wekker, S.F.J., Engel, V. & Fuentes, J.D. (2013) Vegetation–microclimate feedbacks in woodland–grassland ecotones. *Global Ecology and Biogeography*, 22, 364–379.
- Pausas, J.G. & Bond, W.J. (2018) Humboldt and the reinvention of nature. *Journal of Ecology*, 107, 1031–1037.
- Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008) Niche dynamics in space and time. *Trends in Ecology & Evolution*, 23, 149–158.
- Perez-Navarro, M.A., Broennimann, O., Esteve, M.A., Bagaria, G., Guisan, A. & Lloret, F. (2022) Comparing climatic suitability and niche distances to explain populations responses to extreme climatic events. *Ecography*, 2022, 1–12.
- Perez-Navarro, M.A., Lloret, F., Ogaya, R., Estiarte, M. & Peñuelas, J. (2023) Decrease in climatic disequilibrium associated with climate change and species abundance shifts in Mediterranean plant communities. *Journal of Ecology*, 112, 291–304. Available from: <https://doi.org/10.1111/1365-2745.14233>
- Perez-Navarro, M.A., Serra-Diaz, J.M., Svenning, J.C., Esteve-Selma, M.Á., Hernández-Bastida, J., Lloret, F. et al. (2021) Extreme drought reduces climatic disequilibrium in dryland plant communities. *Oikos*, 130, 1–11.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2009) *Nlme package*. R Package version 3.
- Poorter, L. (2007) Are species adapted to their regeneration niche, adult niche, or both? *The American Naturalist*, 169, 433–442.
- Pritchard, J.M. & Comeau, P.G. (2004) Effects of opening size and stand characteristics on light transmittance and temperature under young trembling aspen stands. *Forest Ecology and Management*, 200, 119–128.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, 3, 349–361.
- R Core Team. (2023) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: <https://www.R-project.org>
- Rey, P.J., Alcántara, J.M., Manzaneda, A.J. & Sánchez-Lafuente, A.M. (2016) Facilitation contributes to Mediterranean woody plant diversity but does not shape the diversity–productivity relationship along aridity gradients. *The New Phytologist*, 211, 464–476.
- Richard, B., Dupouey, J.-L., Corcket, E., Alard, D., Archaux, F., Aubert, M. et al. (2021) The climatic debt is growing in the understorey of temperate forests: stand characteristics matter. *Global Ecology and Biogeography*, 30, 1474–1487.
- Serra-Diaz, J.M., Franklin, J., Dillon, W.W., Syphard, A.D., Davis, F.W. & Meentemeyer, R.K. (2016) California forests show early indications of both range shifts and local persistence under climate change. *Global Ecology and Biogeography*, 25, 164–175.
- Serra-Diaz, J.M., Franklin, J., Ninyerola, M., Davis, F.W., Syphard, A.D., Regan, H.M. et al. (2014) Bioclimatic velocity: the pace of species exposure to climate change. *Diversity and Distributions*, 20, 169–180.
- Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10, 1115–1123.
- Stahl, U., Reu, B. & Wirth, C. (2014) Predicting species' range limits from functional traits for the tree flora of North America. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13739–13744.
- Svenning, J.C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T. et al. (2014) The influence of interspecific interactions on species range expansion rates. *Ecography*, 37, 1198–1209.
- Svenning, J.C. & Sandel, B. (2013) Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, 100, 1266–1286.
- Valiente-Banuet, A. & Verdú, M. (2007) Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, 10, 1029–1036.
- Zellweger, F., de Frenne, P., Lenoir, J., Rocchini, D. & Coomes, D. (2019) Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution*, 34, 327–341.
- Zhu, K., Woodall, C.W., Ghosh, S., Gelfand, A.E. & Clark, J.S. (2014) Dual impacts of climate change: Forest migration and turnover through life history. *Global Change Biology*, 20, 251–264.

SUPPORTING INFORMATION

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