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RESEARCH ARTICLE

Decrease in climatic disequilibrium associated with climate change and species abundance shifts in Mediterranean plant communities

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Abstract

1. Climate change induces changes in plant communities according to species' climatic requirements. These changes can be assessed by community climatic disequilibrium (CD), which corresponds to the difference between the climate inferred from the climatic requirements of the species in a community (community-inferred climate, CIC) and the local observed climate.
2. We assessed changes in CIC and CD during a long-term climatic manipulation (warming and drought treatments), embedded within the ongoing trends of climate change, in a Mediterranean shrubland (NE Iberian Peninsula) during 1999–2014. We used plant censuses, species distribution and climate layers since 1979 to create a multivariate environmental space where CIC and CD trends were estimated for 1999–2014.
3. CD consistently decreased, concomitant with an overall climate change-derived increase in aridity (higher temperature and lower precipitation). CIC significantly changed during 1999–2014, reflecting the reshuffling of the community composition due to an increase in the abundance of species distributed in warmer, drier and more seasonal localities. Overall, treatments simulating greater climate change did not accelerate the decrease in CD. However, a trend of steeper diminution of CD was observed under warming treatment. In turn, under drought treatment the species less adapted to seasonality and aridity became less abundant. This community tracking of climate did not follow yearly climatic variability; instead, it was detected by the CD trend at the decadal scale.
4. *Synthesis*. The procedure developed to measure CD reflects demographic behaviours, thus providing a reliable method to assess the impact of climate change on species and communities. The study demonstrates the current, rapid tracking of Mediterranean woody plant communities to climate change. This tracking results from changes in the abundance of species according to their climatic

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requirements, inferred from their distribution. However, inertia in demographic processes implies that plant communities do not immediately fit current climate change at local level, as supported by the minor effect of experimentally accentuated climate change.

KEYWORDS
biogeography and macroecology, climate change experiment, community assembly, community-inferred climate, global change ecology, Mediterranean shrubland, plant population and community dynamics, species climatic niche

1 | INTRODUCTION

Climate change is leading to detectable poleward and upward shifts in species distributions and to changes in community composition (Colwell et al., 2008; Feeley et al., 2011; Felde et al., 2012; Gottfried et al., 2012; Lenoir et al., 2008; Liang et al., 2016; Morueta-Holme et al., 2015; Peñuelas et al., 2007; Sigdel et al., 2018*)*. These changes, however, do not always indicate the rate or precision required to keep pace with climate change (Alexander et al., 2018; Bertrand et al., 2011; Dullinger et al., 2012; Lenoir et al., 2020; Svenning & Skov, 2007). Community composition thus may not accurately represent concurrent climatic conditions (Blonder et al., 2015; Davis, 1984; Lenoir & Svenning, 2015; Svenning & Sandel, 2013). This mismatch, also known as climatic disequilibrium (CD), corresponds to the amount of lag between the climate inferred from the climatic requirements of the species in a community and the local observed climate (Blonder, 2017; Devictor et al., 2012; Lenoir et al., 2020).

The magnitude of community CD depends on the capacity of the species to colonize favourable habitats experiencing new climate, the adaptation ability to the new climate of the existing species and the extinction delay of surviving species (Blonder et al., 2017; Svenning & Sandel, 2013). A community in equilibrium is assumed to be composed of species with climatic niche optima similar to the local observed climate (Bertrand et al., 2011; Blonder et al., 2017). When the climate of a locality changes, community composition is expected to change in accordance with the climate, but delayed responses producing transient disequilibrium are the rule (Blonder et al., 2017; Gaüzère et al., 2018; Svenning & Sandel, 2013). The presence of processes leading to delayed responses of community composition due to changes in climate would therefore increase the disequilibrium. These processes could particularly be associated with the following: (1) longer delays in the extinction of less suitable species due to species longevity, clonal reproduction or the presence of demographic compensatory processes (Bertrand et al., 2016; Doak & Morris, 2010; Jackson & Sax, 2010), (2) limitations in species plasticity and capacity to adapt, such as low rates of mutation or population isolation (Aguilar et al., 2019; Cheptou et al., 2017; Jump & Peñuelas, 2005; Valladares et al., 2007) or (3) the failure of more climatically appropriate species to immigrate due to the absence of more climatically suitable species in the regional pool (Blonder et al., 2015, 2017), low dispersal capacities (Svenning et al., 2015; Svenning & Skov, 2004) and reduced establishment or low rates of growth (Svenning & Sandel, 2013). Communities in disequilibrium with the climate would thus likely have some proportion of species poorly adapted to the climatic conditions with lower than expected abundances than more suitable species (Blonder et al., 2017; Svenning & Sandel, 2013).

Biotic and abiotic processes that lead to increases in the abundances of better-adapted species or decreases or extinction of less well-adapted species would therefore decrease CD (Lenoir & Svenning, 2015). So, CD is expected to decrease (i.e. community approaching an equilibrium with climate) in accordance with the magnitudes of environmental forcing (Richard et al., 2021). Extreme climatic events such as drought or heatwaves may thus induce abrupt changes in community composition promoting sudden decreases in CD (Pérez-Navarro et al., 2021; Serra-Diaz et al., 2018). In contrast, changes in climatic means, which act as progressive and constant environmental filters, would lead to gradual decreases in CD (Alexander et al., 2018), although fast decreases due to long-term accumulated changes would still be possible (Carnicer et al., 2011). Also, climate change indirectly affects community composition and CD by altering the availabilities of water and resources and the biotic interactions that underlie community assembly (Kraft et al., 2015). Therefore, we expect that plant species in regions with seasonally dry climate, such as the Mediterranean Basin (Giorgi & Lionello, 2008; Spinoni et al., 2018), would be favoured and their relative abundances would tend to increase under dry conditions triggered by climate change (Batllori et al., 2020).

Assessing the changes in the magnitude of CD requires characterizing the climate inferred from community composition (community-inferred climate, hereafter CIC). These changes could be estimated from the climatic requirements of the species in the community, defined by the values of the subset of climatic variables that determine the species' success. These values can be generally deduced from the distribution of the species (Elith et al., 2006; Franklin, 2010), which allows us to estimate the species-realized niche, although microlocal variability, demographic and adaptive legacies, and the effects of past land uses and disturbances also contribute to current patterns of species abundance (De Frenne et al., 2013; Thuiller et al., 2008).

Long-term studies addressing the magnitude and change in community composition relative to changes in climate are particularly useful to understand processes leading to vulnerability or adaption of vegetation to climate change. Studies assessing the presence or accumulation of CD have recently become increasingly frequent, from global scales to finer spatial resolutions (Bertrand et al., 2011, 2016; De Frenne et al., 2019; Devictor et al., 2012; Duchenne et al., 2021; Dullinger et al., 2012; Esperon-Rodriguez et al., 2022; Gaüzère et al., 2017; Lenoir et al., 2013; Pérez-Navarro et al., 2021; Richard et al., 2021), but they are still more observational than experimental. To document the changes in the compositions of plant communities, detailed surveys conducted regularly over long periods are required, such as those provided by field experiments that manipulate climatic conditions (Elmendorf et al., 2015; Komatsu et al., 2019; Peñuelas et al., 2018). Although experimental effects are dependent on the number, intensity and duration of the treatments, experiments allow us to test whether trends of change are consistent or more pronounced in climate-forcing treatments (Komatsu et al., 2019) and to expand our capacity to predict the responses of communities to extrapolated climatic conditions. They also allow us to study the processes that determine the demographic responses of species, such as those involving plant ecophysiology (Peñuelas et al., 2018; Sandel et al., 2010). Some studies using experimental climatic manipulation have identified changes in species composition and the functional features of communities, especially in herbaceous ones (Komatsu et al., 2019; Ladouceur et al., 2022; Wellstein et al., 2017). But information is scarcer for woody communities (e.g. León-Sánchez et al., 2017; Liu et al., 2018; Matías et al., 2012), where the responses to climate change may be delayed by the demographic inertia that compensates for interannual environmental variability.

We tested the hypothesis asserting that climate change modifies the CD of plant communities by using an experiment that manipulated warming and drought for 15 years in a Mediterranean shrubland dominated by perennial woody species, combined with the climatic series of the previous decades. We assumed that changes in CD derived from interannual variation in species abundance would to some extent represent the tracking of communities to the new climatic conditions. This tracking will result from an increase or decrease in the abundance of more or less well-suited species, respectively, to the new climate. A constant CD would therefore indicate that species composition was tracking the new climatic conditions, where a decrease in CD would be a symptom of particularly effective community filtering by climate. Alternatively, an increase in CD over time would indicate that climatic variation would not correspond to the rate or direction of change in community composition. These trends of CD under the current climate would be intensified by climatic manipulations, increasing the intensity of climate change.

Specifically, we assessed the patterns of changes in CIC and CD during climatic experimental manipulation, embedded within the ongoing trends of climate change. First, we tested whether community composition shifted to a prevalence of species better suited to live in arid conditions by analysing changes in CIC considering the main axes of the climatic space, mostly defined by temperature, precipitation and seasonality. Second, we analysed changes in community dynamics based on CD by considering two descriptors of the current observed climate: (i) the average climate throughout the study period, thus calculating CD (hereafter CD*ave*) as the difference between the average climate recorded throughout the period and CIC derived from the species abundances recorded each year and (ii) yearly climatic data, thus calculating CD (hereafter CD*year*) as the difference between the climate recorded each year and CIC derived from the species abundances recorded that particular year. CD*ave* allowed us to estimate changes in species abundance based in the average climatic conditions over the entire considered period, and CD*year* allowed us to estimate the changes in the communities concurrent with the yearly climatic variability. While CD*year* informs on immediate reaction to current climate conditions (e.g. resulting from plant growth responding to the balance between water supply and demand), CD*ave* reflects community responses to overall larger-term climatic pressures and the lagged demographic responses to the climate (e.g. those resulting from seed or resources storage effects), buffering to some extent between-year climatic variability.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was carried out in Garraf Natural Park (southwestern Europe) (41.25° N, 1.75° E; 210 m a.s.l.). The climate is Mediterranean with hot, dry summers and mild winters; precipitation mostly occurs in spring and autumn. Mean annual temperature during the study period (1998–2014) was 15.5°C, ranging from 14.7 to 16.2°C. Summer temperature (June–August) averaged 23.4°C throughout the study period, and mean annual precipitation was 560.9 mm, ranging from 403.1 to 956.2 mm (Liu et al., 2018). Climate in the area has tended to be more arid since the beginning of the 20th century, indicated by the Standardised Precipitation-Evapotranspiration Index SPEI aridity index, a multiscalar drought-index based on precipitation and potential evapotranspiration (Vicente-Serrano et al., 2010), widely used in the literature (Figure S1). In particular, mean annual temperature has increased significantly by 0.8°C, and mean annual precipitation has decreased significantly by about 30%, during the last four decades (1979–2014). Temperature and precipitation, however, did not change significantly during the experiment (1999–2014 period), when the change in climate was less severe (Figure S2).

The dominant vegetation is Mediterranean shrubland, which grows in petrocalcic Calcixerept soil with a depth of 10–40 cm and a loamy texture with abundant calcareous nodules. The main species are shrubs and dwarf shrubs while herbs are less abundant (Prieto et al., 2009), as detailed in Table S1. This vegetation corresponds to a successional shrubland growing after two wildfires in summer 1982 and spring 1994, which burned *Pinus halepensis* forests established after agriculture was abandoned early in the 20th century (Lloret & Vilà, 2003).

2.2 | Experimental design

Treatments of moderate nocturnal warming, drought and a control were established during 1999–2014. Three plots of 20 m^2 (5 × 4 m) per treatment were randomly established on a south-facing aspect (13% slope). The warming treatment was applied by covering the plots at night with reflective curtains to reduce the escape of infrared radiation to the atmosphere, simulating global warming by increasing the minimum temperature at night (Beier et al., 2004; Peñuelas et al., 2018; Prieto et al., 2009) (Text S1). This warming treatment increased soil temperatures at a depth of 5 cm by an average of ca. 0.6°C, depending on the season and meteorological conditions (Liu et al., 2018). The drought treatment was applied in the spring and autumn, corresponding to the two main growing seasons; the drought plots performed as control plots during the rest of the year. The treatment consisted of a transparent waterproof plastic curtain that covered each plot (Beier et al., 2004; Peñuelas et al., 2007; Prieto et al., 2009) when rain fell. The drought treatment excluded ca. 40% of the precipitation and decreased soil moisture by ca. 20% during the study period. The control treatment had scaffolding similar to the warming and drought treatments, but without curtains, and run in parallel to the warming and drought treatments (Text S1).

2.3 | Vegetation survey

Species were recorded in the central 12 m^2 (4 × 3 m) of all treatments, where five parallel transects 3 m long were permanently set 0.8 m from each other. Species composition and abundance were recorded following the point-intercept method at points 5 cm apart along the five transects (305 points in each plot) (Prieto et al., 2009). Surveys were conducted annually in the dry season (July and August) from 1999 to 2014, covering 16 years of the experiment. Species contacts in each plot were summed to estimate species relative abundance in the plot community and, then, to calculate CIC and CD values. A total of 31 species were monitored in this study (Table S1). Field data records are available at CORA.RDR and Figshare (https://figshare.com/articles/dataset/Garraf_centroid_distances_new_csv/24552751) repositories. The surveys were reported to the Garraf Natural Park authorities, according to the established requirements.

2.4 | Community disequilibrium CD

2.4.1 | Data for species occurrence

Data for species occurrences along their geographical distributions for the 31 species were obtained from the database of the Global Biodiversity Information Facility GBIF 2019 (www.gbif.org) The occurrence records were then filtered to remove taxonomic inconsistencies (i.e. inaccurate synonyms and wrong species) and inappropriate records (fossil, herbarium and planting records, and geographic inconsistencies). To avoid possible sampling bias and reduce spatial climatic autocorrelation, we randomly thinned the data sets of occurrences by retaining only one occurrence within a radius at which occurrences were not spatially autocorrelated. Filtering the spatial autocorrelation allows minimizing the overrepresentation of sampling areas more accessible to humans and extremely similar climatic conditions by geographic proximity. We used the ecospat.mantel.correlogram function from the ecospat R package (di Cola et al., 2016) to identify the minimum distance at which occurrences were not spatially autocorrelated. When the minimum non-autocorrelation distance was <1 km^2, we randomly thinned the species records to one observation per km^2, equivalent to the grid resolution of the climatic data set, to maintain the agreement between occurrences and environmental layers. The final data sets contained from 5,003 to 66,656 observations per species (Table S1).

2.4.2 | Climatic data

Thirteen climatic variables for the reference period 1979–2013 (average of 35 years) at 1-km^2 resolution (CHELSA v.1.2 database; Karger et al., 2017, 2018) were used to characterize the climatic optima of the species niches (Text S2). This average period of 35 years was chosen as representative of the longevity of shrubland species. The selected 13 climatic variables—instead of the 19 biovariables commonly used—were chosen to avoid implicit climatic interactions between temperature and precipitation (e.g. temperature of the driest quarter), which may correlate differently between different species distributions, thus hindering subsequent interpretation (Pérez-Navarro et al., 2021).

To characterize observed climate at the study site, we downloaded the same set of climatic variables for each year of the experimental period (1999–2014) (CHELSA v.1.2 database; Karger et al., 2017, 2018). We obtained two alternative data sets from this 16-year database: (1) one with the climatic average of the 16-year period, used to estimate the change in climatic filtering for a reference average climate (CD*ave*) and (2) one with yearly information to characterize CD each year (CD*year*). Given the field distribution of the experimental plots and the spatial resolution of the climatic layers (1 km^2), all plots were included in the same pixel and shared the same macroclimatic conditions, implying that differences in CD were driven directly by differences in community composition between plots and treatments.

2.4.3 | Community climate estimation

To calibrate the common climatic space for estimating both climatic optima and community CD for the species, we applied a principal component analysis (PCA) to reduce the dimensionality of the 13 climatic variables to the first two PCA axes. The PCA used climatic data for the average period (1979–2013) from all sites of the occurrences of all 31 species after scaling the variables (PCA-occ sensu; Broennimann et al., 2012). The first two axes explained

75.4% of the variability of the 13 climatic variables (Figure 1). We chose this multivariate climatic approach to integrate all climatic information to determine the overall climate of the community and its disequilibrium. The PCA axes were also used separately to estimate univariate CD, because they compiled a comprehensive set of variables and facilitated the interpretation of the results. The first PCA axis (explaining 52.1% of the variance) was correlated positively with the temperature variables and negatively with the precipitation variables, so it could be used as a gradient of aridity. Likewise, the second PCA axis (explaining 23.3% of the variance) was correlated positively with the precipitation variables and some of the temperature variables and negatively with the seasonality of temperature, so it could be used as a gradient of humidity and seasonality, where positive values were correlated with high humidity and low seasonality and low values were correlated with low humidity and high seasonality.

We translated the species occurrences from the geographic space into the two-dimensional climatic space defined by the two PCA axes, based on the 13 climatic values (using the *suprow* function in the ade4 package (v1.7-16; Dray & Dufour, 2007)), and we obtained the two corresponding PCA coordinates for the occurrence of each species. We then applied a two-dimensional kernel density function to the species occurrences in the climatic space, which allowed us to determine the densities of the presence of each species for each cell in the environmental space (i.e. species niches). Specifically, we applied Gaussian kernel functions, with optimal bandwidths selected by cross-validation (Duong & Hazelton, 2005), and removed densities below the 0.05 percentile. After obtaining the species niches, we estimated the centroid of each species niche (i.e. the climatic optimum) as the centre of gravity of the niche (i.e. estimating the mean of the climatic values in each climatic axis, weighted by the species densities in each climatic axis) (available at CORA.RDR and Figshare https://figshare.com/articles/dataset/Garraf_centroid_distances_new_csv/24552751 data repositories). We then estimated CIC for each of the 144 communities (3 replicates × 3 treatments × 16 years). CIC was calculated as the centre of gravity of all centroids of the species niches (i.e. the mean of the centroids of the species niches on each climatic axis, weighted by the relative abundance of each species) (Blonder et al., 2015).

We also translated the observed climate at the study site and for the average of the experimental period 1999–2014 and for each year into the two-dimensional climatic space previously defined. The community climatic framework, including the observed climate, the centroids of the species niches and CIC, are shown in Figure 2. Finally, we estimated the average and yearly CD for each plot as the Euclidean distance in the climatic space between CIC of the census year and the average local climate of the experimental period (CD*ave*) and CIC of the census year and the observed climate in the same year (CD*year*). CD ranged from 0 (tight equilibrium) to any positive value, where higher values indicated a higher overall CD. CD*ave* estimates the capacity of a community to keep pace with climate change at an approximately decadal scale, that is climatic filtering, and CD*year* represents the community rate to track yearly climatic variability. We consequently obtained one CD*ave* and one CD*year* per plot replicate, treatment and year. Since the previous calculation of CD*ave* and CD*year* were absolute values which does not inform on the direction of the CD relative to the observed climate, we also calculated CD*ave* and CD*year* for each PCA axis separately.

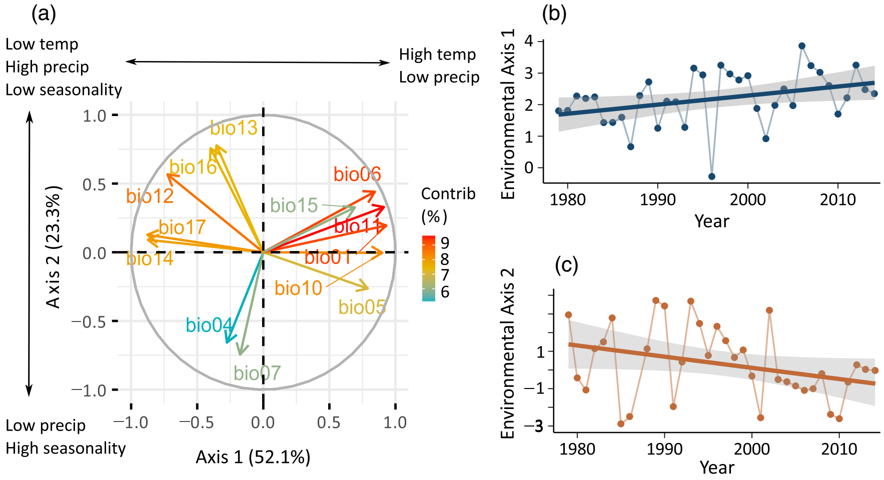

FIGURE 1 (a) Correlation circle of the principal component analysis of 13 bioclimatic variables (see Text S1 for explanation), defining the environmental climatic space for which species centroids, observed climate, community-inferred climate and community climatic disequilibrium were calculated. The main climatic features corresponding to axes 1 and 2 are also depicted. (b) Recent trend of yearly observed climate in the study site, represented by its coordinates on axis 1 of the environmental climatic space, showing conditions of generally increasing temperatures and decreasing precipitation. The blue line and shading correspond to a linear fit ($p = 0.039$) and the confidence interval 95%, respectively. (c) Recent trend of yearly observed climate, represented by its coordinates on axis 2 of the environmental climatic space, showing conditions of generally decreasing precipitation and increasing seasonality. The brown line and shading correspond to a linear fit ($p = 0.043$) and to the confidence interval 95%, respectively. Note that despite the overall period showing significant climatic trends, in the study period 1999–2014, the climatic trend is not significant for any of the axes (see also Figures S1 and S2).

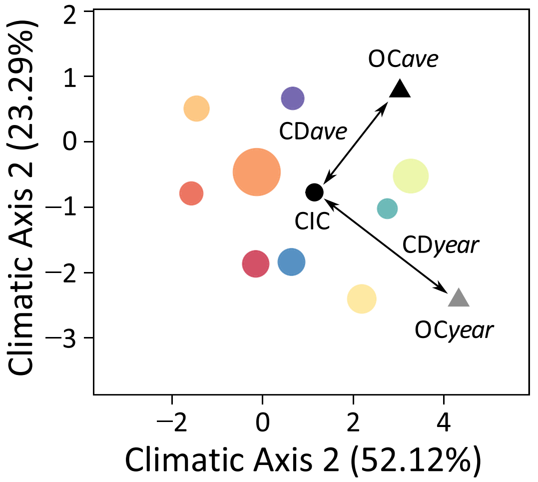

FIGURE 2 Example diagram representing the 2-dimensional climatic framework used to estimate community-inferred climate (CIC) and climatic disequilibrium (CD). Colour dots represent the climatic optima (niche centroids) of each species in the community, and dot size represents species relative abundance in the community. Black dot represents the CIC as the community centre of mass, while black and grey triangles represent the observed climate (OC) of the average reference period (in our case, 1999–2014, OC*ave*) and the study year (OC*year*). CD was correspondingly estimated as the Euclidean distance between CIC and the corresponding observed climate (OC*ave* and OC*year*).

Univariate CIC and observed climate for each PCA axis were also estimated following the same procedure as previously described for two dimensions but applied to one dimension.

2.5 | Statistical analyses

We first tested potential shifts in community composition by analysing changes in CIC over time. We considered the yearly coordinates of CIC on the first two axis of the PCA climatic space, which are defined mostly by temperature and precipitation (see the section Community climate estimation). We applied two mixed-effects models: one with CIC on axis 1 (CIC$_{X1}$) as the response variable and one with CIC on axis 2 as the response variable (CIC$_{X2}$). In both cases, treatment, year and their interaction were used as explanatory variables, and plot was used as a random effect. See models 1 and 2 in Table S2 for further details.

To verify whether changes in CIC were due to changes in the abundance of species with a determined climatic profile, we established three climatic groups of species considering each PCA axis: (i) species with niche centroids in the top 15.9 percentile of the distribution of all species in the corresponding PCA axis (i.e. above the mean plus one standard deviation of the distribution), representing species highly tolerant to climatic conditions for the corresponding PCA axis, (ii) species with niche centroids in the bottom 15.9 percentile of the distribution of the axis (i.e. below the mean minus one standard deviation), representing species with the lowest tolerance to the climatic conditions represented by the corresponding PCA axis and (iii) the remaining species, which were discarded for these analyses. In the case of PCA axis 1, species in the top percentile were considered 'more arid' species, and species in the bottom percentile were considered as 'less arid' species. In the case of PCA axis 2, species in the top percentile were considered as 'less seasonal and more wet-tolerant' species, and species in the bottom percentile were considered as 'more seasonal and more dry-tolerant' species. Changes throughout the study period in the abundances of these climatic groups of species were tested separately for each PCA axis using linear mixed-effects models with random intercepts. In both cases, the sum of the total number of contacts of species belonging to each group logarithmically transformed was included as the response variable, and year, treatment (control, warming and drought), climatic group (top or bottom tolerant percentile) and their pairwise interactions were included as explanatory variables, with plot as a random factor (Models 3 and 4, Table S2).

Changes in multivariate CD (both CD*ave* and CD*year*) during 1999–2014 were also analysed using linear mixed-effects models with random intercepts. We applied two models, with CD*ave* and CD*year* as response variables. In both models, treatment, year and their interaction were explanatory variables, and plot was a random factor (models 5 and 6, Table S2). Finally, we also analysed the relationship between the change in CD*ave* in relation to the change in observed climate relative to average climate (climatic anomaly) to compare the rate of community tracking of climate (CD*ave*) and the rate of yearly change in climate. We preferred the use of CD*ave* instead CD*year* to assess changes in CD relative to climatic variability since yearly observed climate is included in the calculation of CD*year*, and between-year variability is basically due to changes in species composition. In this case, CD*ave* was the response variable, and the observed climate anomaly, considered as the difference between yearly observed climate and mean observed climate for the study period, treatment and their interaction were the explanatory variables, and year and plot were crossed random effects (model 7, Table S2). Similarly, we also tested the relationship between CD year, observed climate treatment and their interaction (model 8, Table S2). In all cases, post hoc pairwise contrast tests were applied using the emmeans package (Lenth, 2022) to identify differences in treatment slopes and intercepts. All analyses were run using R-4.2.1 (R Core Team, 2022).

3 | RESULTS

3.1 | Change in observed climate

Trajectories of observed climate along environmental PCA axes 1 and 2 in recent decades, including the experimental period and 20 years before its initiation, had significantly increasing values of the coordinates in axis 1—indicating higher temperature and lower precipitation—and significantly decreasing values of the coordinates in axis 2—indicating lower precipitation and higher seasonality

(Figure 1b,c). These climatic trends were nonetheless not significant for the experimental period (Figure S2).

3.2 | Shift in community composition

CIC_{X1} increased significantly throughout the study period in all three treatments (year estimate = 0.03, $p < 0.001$; ANOVA $F_{1,135} = 115.13$, $p < 0.001$) (Figure 3a; Table S3), indicating an increase in aridity, inferred from community composition. The climatic treatments and year also significantly interacted (ANOVA $F_{2,135} = 3.77$, $p = 0.026$), because the increase in CIC_{X1} was slightly more pronounced in the warming treatment than in the drought and control treatments, although it was only significantly higher than the drought treatment (Figure 3a; Table S3). The observed climate always had higher coordinate values on PCA axis 1 of the environmental climatic space than did CIC_{X1} (Figure 3a), corresponding to warmer and drier climate than the inferred from community composition. The observed climate (OC), however, fluctuated greatly between years, with no clear pattern of increase (Figure 1c), so the difference between CIC and OC, corresponding to CD, generally tended to decrease (see below). This result is consistent with an increase in the abundances of the species living under warmer and drier conditions, that is the group of more arid species, belonging to the top percentile of the species niche optima for PCA axis 1, which tended to become more abundant over time (estimate of year: more arid group interaction = 0.09, $p = 0.001$) (Figure 3b). A contrast test indicated that the abundance of the group of more arid species increased over time, particularly for the warming treatment but also for the controls, although this increase was not significant in the drought treatment (Table S4). In contrast, the less arid species did not have a significant overall trend in spite of a marginal reduction in drought treatments, and their abundance did not differ between the treatments (Table S3).

CIC_{X2} decreased significantly throughout the study period (year estimate = −0.0235, $p < 0.001$; ANOVA $F_{1,135} = 33.58$, $p < 0.001$), indicating a shift of the community to a higher prevalence of species better adapted to less precipitation and higher seasonality (Figure 3c). This result is consistent with an increase

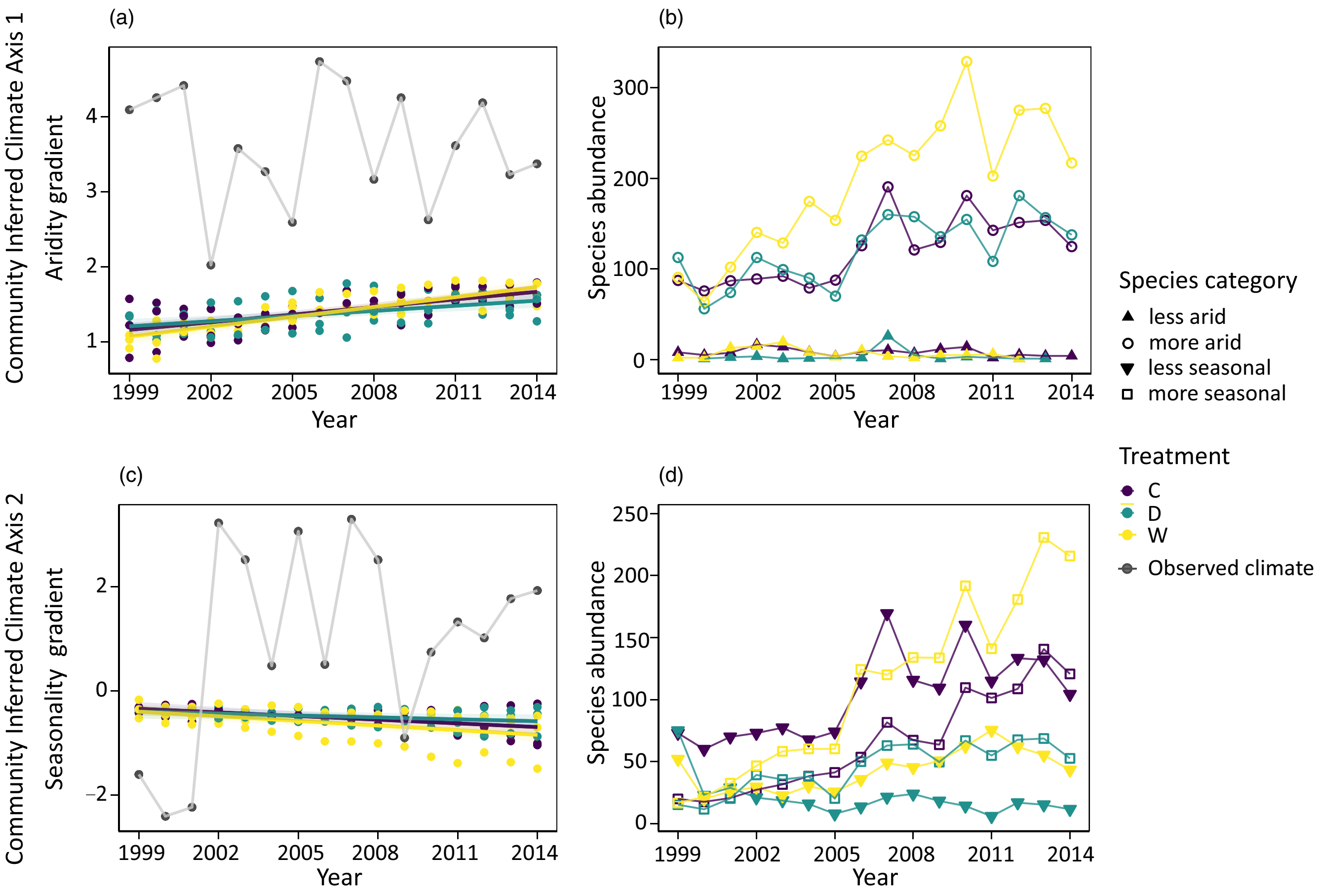

FIGURE 3 (a, c) Yearly community inferred climate for axis 1 (CIC_{X1}) and axis 2 (CIC_{X2}) throughout the study period in the three treatments (warming 'W', drought 'D' and control 'C'). The coloured lines depict the treatment fits, and the grey lines depict the coordinates of yearly observed climate on the principal component analysis (PCA) axes characterizing the environmental climatic space. Note that observed climate is almost always above CIC, meaning that, despite the existing variability, the observed climate was more arid and seasonal during the whole study period than expected according to the community composition. (b, d) Yearly abundances of the climatic groups of species (i.e. number of contacts), based on the percentile distribution on the PCA axes: (b) species living in a more or less arid, warmer climate defined by axis 1 and (d) species living in a more or less dry and seasonal climate defined by axis 2.

over time in the abundance of species living in drier, more seasonal localities (Figure 3d; Table S4) (estimate of the interaction between year: group of drier and more seasonal species = 0.085, $p < 0.001$). Drought treatment showed an overall reduction in CIC$_{X2}$ throughout the study period, although within categories contrast test for drought treatment only showed marginally significant reduction of less seasonal and arid-adapted species and significant increases of species living in more seasonal-dry environment. Control and warming treatments showed significantly different trends with respect to drought, with increases in time of both more and less seasonal-adapted species. (Table S3). These results imply that drought treatment was the only one in which the increase through time of arid-seasonal-adapted species was accompanied by a decrease in the less dry, seasonal-adapted group of species (Table S3).

3.3 | Changes in CD

CD*ave* generally decreased significantly over time (time estimate = −0.01, $p = 0.02$; ANOVA $F_{1,135} = 14.6$, $p < 0.001$) (Figure 4a; Table S5) but did not differ significantly between the treatments. The climatic treatments did not significantly interact with year, but CD*ave* decreased significantly in the control and warming treatments throughout the study period. CD*ave* also decreased in the drought treatment, but not significantly.

Despite an important interannual variability, CD*year* also tended to consistently decrease in all treatments throughout the study period (year estimate = −0.05, $p = 0.02$; ANOVA $F_{1,135} = 16.64$, $p < 0.001$) but did not differ significantly between the treatments. Time did not significantly interact with treatment (Figure 4b; Table S5).

Finally, models correlating CD*ave* with observed climate anomaly did not identify a significant effect of observed climate anomaly. This effect, however, was positive and significant for the warming treatment, which also differed significantly from the other treatments, suggesting a larger accumulation of CD*ave* in years when the observed climate anomaly was larger (Table S6). In turn, CD*year*, exhibited a significant, positive relationship with observed climate anomaly, without contrasting differences between treatments (Table S7).

4 | DISCUSSION

Our study found that CD decreased in Mediterranean shrubland at a decadal scale, concomitant with current regional trends of increasing aridity associated with climate change (Giorgi & Lionello, 2008; Spinoni et al., 2018). This finding supports previous records of CD reduction with extreme drought (Pérez-Navarro et al., 2021), indicating that CD is also decreasing even in the absence of extreme climatic events. This decrease in CD reflects the effect of climate on the requirements of the species and the magnitude and direction of interactions with other species (Kraft et al., 2015). This effect is consistent with changes in CIC, associated with the increased abundance of species that can tolerate drier and warmer conditions (Figure 3b) and species living in a more seasonal climate (Figure 3d). These changes agree with previous studies conducted under the same or similar experimental conditions that reported increasing abundances of species distributed in drier regions with experimental drought (Bilton et al., 2016; Liu et al., 2018). The changes also agree with many reported observations of shifts in species distribution associated with climate change (Lenoir & Svenning, 2015; Walther et al., 2002). This community filtering should be ultimately accounted for by the functional and demographic traits of species (Lloret et al., 2016; Paniw et al., 2021), although we did not consider species traits in our study. The responses of the population distributions and abundances of plant species to climate change have been widely documented, but scaling up the effects of climate change to

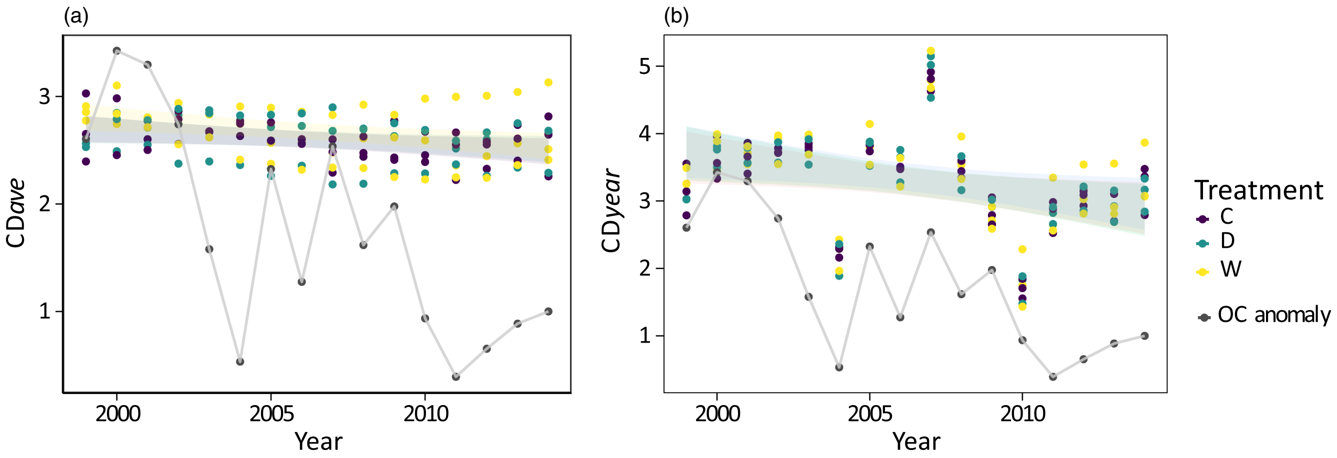

FIGURE 4 (a) Trends in yearly CD*ave* throughout the study period in the treatments. The coloured lines depict the treatment fits, and the shaded areas correspond to confidence interval 95%. (b) Yearly CD*year* throughout the study period in the treatments. The coloured lines depict the treatment fits, and the shaded areas correspond to confidence interval 95%. The grey line corresponds to the distance in the environmental space between yearly observed climate and average observed climate during the study period (i.e. observed climate anomaly).

the community level is less common (Anderson-Teixeira et al., 2013; Franklin et al., 2016; Matías et al., 2012).

Our study supports the use of CD as an estimate of community compositional change, even at local spatial scales and under experimental conditions, where changes in the composition may be smaller than at broader temporal scales. Throughout the characterization of species' climatic requirements, this approach allowed us to detect changes in the abundances of species with different climatic tolerances. Species distributed under more arid and seasonal conditions tended to increase (*Fumana thymifolia*, *Helianthemum syriacum*, *Lithodora fruticosa* and *Ulex parviflorus*), but species living under less arid and less seasonal conditions (*Teucrium polium*, *Cuscuta epithymum* and *Odontites luteus*) tended to become less abundant, particularly under drought treatment. These species are likely to have a set of traits that account for their dynamics associated with climate (Lloret et al., 2016; Prieto et al., 2009). Current responses of plant communities to climate change have been explored in sensitive regions, such as high mountains (Dullinger et al., 2012; Steinbauer et al., 2022), and Mediterranean regions, located between arid and wet biomes (Cornwell & Ackerly, 2009; Guiot & Cramer, 2016; Thuiller et al., 2011). Our study supports this empirical evidence, showing that these current changes in plant communities can be interpreted at the stand level based on the climatic characterization of species (Liu et al., 2018; Martin et al., 2019). These changes are consistent with a trend in these communities of decreasing plant biodiversity for both recruits (Lloret et al., 2004) and adults (Prieto et al., 2009), particularly in the drought treatment, thus likely conducting to a homogenization of the community and revealing the risk for the maintenance of some species.

The number of studies analysing changes in CD at the community level, particularly the effect of microclimatic buffering, has recently increased (De Frenne et al., 2019; Lenoir et al., 2013; Maclean et al., 2015; Zellweger et al., 2020), reporting the existence of climatic debt in plant communities—increasing CD in time—(e.g. Bertrand et al., 2016). Our finding of decreasing CD would imply a reduction of this debt, likely due to a combination of rapid change in the plant community composition and a period of relatively stable climate. While studies on CD are often based on presence–absence records at regional scale and deal with colonization and extinction processes, commonly associated with the edge of species' distribution range, our work addresses local population dynamics and associated processes inside of a species range (i.e. establishment, growth and mortality driven by biotic interaction), for which abundance data are more informative. Vegetation is expected to adapt to the climate in the long term, but factors such as topo-climatic heterogeneity and interactions between soils and species will also play important roles in determining the actual distribution of vegetation (e.g. Thuiller et al., 2008; Van der Putten et al., 2010). In fact, the decoupling between microclimate and macroclimatic conditions may contribute to expand the apparent ranges that species occupy in the environmental climatic space. This trend occurs because populations tend to occupy sites where individuals can persist suboptimally due to suitable microhabitats (Davis et al., 2019; De Frenne et al., 2013), positive interactions with other species, such as facilitation (Svenning & Sandel, 2013) or adaptions to local conditions (Benito Garzon et al., 2011). The colonization and persistence of populations in local suboptimal climates under conditions of fluctuating stability would therefore tend to increase community CD, moving the community far from an equilibrium with climate. When environmental constraints become stronger, such as aridity associated with climate change, species filtering tends to reduce CD, moving the community to a new equilibrium with climate. Although species ranges rarely shift as fast as climate change (Devictor et al., 2012; Lenoir et al., 2020; Zellweger et al., 2020), in the Mediterranean region, a positive relationship has been documented between species occurrence and warming within species ranges (Duchenne et al., 2021). Mediterranean ecosystems, nonetheless, also face threats other than climate change, such as habitat fragmentation, modifications of nitrogen cycling, or the loss of pollinators, which may be key determinants for species distribution and future community CD, regardless of the rate of climate change (Maxwell et al., 2016; Peñuelas et al., 2020).

Importantly, the observed tracking of plant communities to climate change was linked to the temporal scale. The trajectories of the CIC in recent decades were consistent with the trend of climate, but the climate was inherently variable at a yearly scale. In fact, temperature and precipitation did not significantly increase or decrease during the experimental period. Thus, we found that the changes in CD at this yearly scale did not follow the between-year climatic variability (Figure 4). Yearly CD and yearly anomaly of observed climate were not correlated in the drought or control treatments, suggesting that short-term CD dynamics did not strictly respond to yearly climatic conditions (Table S6). Nevertheless, the observed climate anomaly was positively correlated with CD in the warming treatment, suggesting that an accumulation of CD is likely to occur with hot years. These findings indicate the limitations of the communities living under warm conditions to tightly track climate change (Table S3). Nevertheless, the dynamics of CD at a larger, decadal scale show a consistent decreasing trend, as indicated by the calculation using both the average climate recorded throughout the study period (CD*ave*) and the climate recorded each year (CD*year*) (Figure 4).

These patterns of CD indicate that the dynamics of CIC were inertial; CIC consistently and progressively followed a trend of aridification, in contrast with the high stochasticity of yearly recorded climate. This difference is likely due to the demographic inertia of plant populations, which allows them to buffer this environmental variability (Alexander et al., 2018; Büntgen et al., 2014), except in extreme situations. Survival and growth often depend on the climate of previous years, because they rely on accumulated reserves and bud banks, which may buffer instantaneous stress, and the establishment of new plants relies on seed banks, built over successive years (Del Cacho et al., 2012). Lagged responses buffering yearly climatic variability are particularly evident when perennial species are dominant, as in our study case (Prieto et al., 2009). This demographic inertia would also account for the consistent increase in CIC_{X1} during 1999–2014, although the observed climate did not tend to increase aridity during this period. The observed climate, in fact, consistently remained above CIC, thus contributing to the decrease in CD during 1999–2014. An increase in CIC will, thus, represent changes in plant communities responding to the pressure of average decadal climate, which was always more arid and warmer than the climate inferred from the community composition.

The experimental drought and warming plots in our study failed to clearly provide a more pronounced decrease in CD than did the control plots. The warming treatment, however, indicated a trend of larger increases in the abundance of species living under drier and warmer conditions than in the other treatments, in agreement with the findings of a previous study in which species were grouped by their tolerance to two bioclimatic variables (summer temperatures and spring precipitation) (Liu et al., 2018). We found that the species belonging to the 'drier and more seasonal' group were more abundant in the drought treatment, in which the increase in the abundances of these species coincided with a slight decrease in the abundance of the 'less seasonal and drier' group of species. These results suggest that the drought treatment could have had a positive effect on species that are more prone to experience seasonal patterns of temperature. The absence of a clear trend of more pronounced CD*ave* decrease in the drought treatment may be attributed to the smaller weight of these 'less seasonal and drier' groups, mainly recorded in PCA axis 2.

Limitations due to low amount of replication, surveys based on transect contacts instead individual census, reduced duration of the experiment, lack of a combined warming and drought treatment, stochasticity associated with irregular functioning of warming equipment and rain covers, and artefacts associated with the experimental conditions likely contributed to the inconclusive the effects of treatments. An absence of differences in observed climate across treatments may also occur because this parameter was calculated considering that the observed climate was common to all three treatments, but not relative to the microclimate generated by the experimental conditions in each plot, due to missing data in some years. Differences in CD between treatments thus only correspond to distinct changes in species abundance, likely underestimating CD in treatments. Estimates of CD also corresponded to the multivariate space of several bioclimatic variables, while warm and drought treatments concentrated on one or a few correlated variables associated with temperature and precipitation, respectively. When changes in a community based on species abundance are translated into multivariate space (CIC), the effect of the single climatic variable induced by the experiment may become weaker.

Our approach to calculating CD was also subject to the limitations recognized in species distribution models (SDMs) when describing the species-realized climatic niche (Guisan & Thuiller, 2005; Mod et al., 2016; Wisz et al., 2013). The realized niches represented in our study were derived from contemporary observational occurrences of species (implicitly including sampling biases, biotic interactions and anthropogenic impacts) (Kearney, 2006; Feeley & Silman, 2011), so they may not perfectly portray the physiological optima of the species (Blonder et al., 2015; Murphy et al., 2006). Frequently used large-scale climatic databases, at the continental level in our case—1 km^2 resolution—also neglect finer climatic geographic heterogeneity and microclimate conditions, which can determine species occurrence and population success (De Frenne et al., 2013; Haesen et al., 2023; Lembrechts et al., 2019). In addition, niche size and climatic optima may be imperfectly represented due to the lack of consideration of spatiotemporal plasticity and the adaptation of species (Benito Garzon et al., 2011). In addition, the role of species functional traits of these communities was not considered here to interpret shifts in species abundance, although they have revealed to respond to climatic gradients (Garnier et al., 2019). Finally, CIC is calculated from the centroids of the species-realized niche; this procedure may underestimate the role of non-optimal conditions to explain the performance of populations, thus preventing to detect equilibrium with climate and overestimating CD.

In conclusion, our study demonstrates the climate change tracking of Mediterranean plant communities dominated by woody perennials. This tracking is illustrated by a decrease in community CD, estimated using the distance in the climatic space between observed climate and CIC and obtained from the abundance of species and their bioclimatic distribution. Climatic filtering was generally operating in these communities, increasing the abundance of species living in more arid conditions and decreasing the abundance of species better adapted to wetter conditions. This tracking was detected at the decadal scale, while yearly climatic variability and demographic inertia would likely mask immediate responses to climate in the absence of extreme climatic events. Climatic experimental conditions inducing warming, and particularly drought, are consistent with these patterns, although they do not produce large changes in the climatic profiles of species when these are referred to multidimensional climatic space, likely due to the simplicity of the experimental setting in manipulating the climate.

AUTHOR CONTRIBUTIONS

María Angeles Pérez-Navarro and Francisco Lloret conceived the idea and designed the analytical methodology. Josep Peñuelas designed the experiment. Romà Ogaya, Marc Estiarte and Josep Peñuelas carried out the experiment and collected the data. María Angeles Pérez-Navarro performed the analysis of data. Francisco Lloret and María Angeles Pérez-Navarro led the writing of the manuscript. All authors contributed critically to the drafts.

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CONFLICT OF INTEREST STATEMENT

The authors disclose any potential sources of competing interest.

DATA AVAILABILITY STATEMENT

Field data and species centroid coordinates in the built environmental climatic space are available at CORA.RDR (https://doi.org/10.34810/data956) and Figshare: https://figshare.com/articles/dataset/Garraf_centroid_distances_new_csv/24552751 repositories (Ogaya, 2023). Species occurrences used for calibrating species niches before cleaning can be downloaded from GBIF through the link https://doi.org/10.15468/dl.qzhd6n (GBIF, 2020). Climatic data can be downloaded from CHELSA database v.1.2 https://chelsa-climate.org/downloads/ (Karger et al., 2017, 2018).

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SUPPORTING INFORMATION

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

Text S1: Experimental design.

Text S2: The climatic variables selected to characterize the climatic optima of the species niches were: mean annual temperature (bio 1), seasonality of temperature (standard deviation × 100) (bio 4), maximum temperature of the warmest month (bio 5), minimum temperature of the coldest month (bio 6), annual range in temperature (bio7), mean temperature of the warmest quarter (bio 10), mean temperature of the coldest quarter (bio 11), annual precipitation (bio 12), precipitation of the wettest month (bio 13), precipitation of the driest month (bio 14), seasonality of precipitation (coefficient of variation) (bio 15), precipitation of the wettest quarter (bio 16) and precipitation of the driest quarter (bio 17).

Figure S1a: Yearly total precipitation and average temperature in the study area from 20 years before the start of the experiment to the last year of the experiment, i.e. mid-term climatic representation (1979–2014).

Figure S1b: Yearly total precipitation and average temperature in the study area for the experimental period (1999–2014).

Figure S2: Example of community climatic framework in plot 2 for the three experimental treatments (C, control; D, drought; and W, warming) for 2004.

Table S1: List of recorded species, indicating the species code used in the climatic diagrams (see Figure S2), family, growth form, filtering distance used to reduce spatial bias and autocorrelation, final number of total occurrences used to calibrate the species niches and the climatic group corresponding to the species distribution on PCA axes 1 (PCA1) and 2 (PCA2), as detailed in Section 2.5.

Table S2: Results of the linear mixed-effects models (LMM), model ANOVAs, post hoc tests for individual treatment slopes and pairwise contrast between treatment slopes of CIC_{X1} and CIC_{X2}.

Table S3: Results of the linear mixed-effects models (LMM) and post hoc tests for individual treatment slopes of the models correlating the relative abundance of species with the category of climatic tolerance for PCA axes 1 and 2.

Table S4: Results of the linear mixed-effects models (LMM), ANOVAs, post hoc tests for treatment slopes and contrast between treatment slopes of year relative to CD*ave* and CD*year*.

Table S5: Results of the linear mixed-effects models (LMM), ANOVAs and post hoc tests and contrast between treatments for CD*ave* and CD*year*, with treatment as the only explanatory variable and year and plot as random factors.

Table S6: Results of the linear mixed-effects models (LMM), ANOVAs, post hoc tests for individual treatment slopes and pairwise contrast between treatment slopes of the relationship between OC anomaly and CD*ave* (CI*Cyear* − OC*ave*).

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