

OIKOS

Ignite

Climate change may alter the signal of plant facilitation in Mediterranean drylands

Miguel Verdú¹✉, Esther Bochet¹, Tíscar Espigares², Jordi Margalef-Marrasé¹, José Manuel Nicolau³, Yu Yue^{1,4}, César Azorin-Molina¹ and Patricio Garcia-Fayos¹

¹Centro de Investigaciones sobre Desertificación (CSIC-UV-GV), Spain

²Facultad de Ciencias, Universidad de Alcalá, Spain

³Escuela Politécnica Superior, Universidad de Zaragoza, Spain

⁴Nanjing Meteorological Bureau, People's Republic of China

Correspondence: Miguel Verdú (miguel.verdu@ext.uv.es)

Oikos

2024: e10217

doi: [10.1111/oik.10217](https://doi.org/10.1111/oik.10217)

Subject Editor: Lohengrin Cavieres

Editor-in-Chief:

Gerlinde B. De Deyn

Accepted 15 March 2024



Facilitation is an ecological interaction that has allowed plant lineages to survive past climate aridification. This same interaction can be expected to buffer the effects of current climate change, which is tending to become more arid in the Mediterranean basin. However, facilitation may wane when stress conditions are extreme. Here we argue that the erosion of the facilitation signal between *Quercus ilex* and its nurses detected by García-Fayos et al. (2020) along 50 years in the eastern Iberian Peninsula may have been due to the reversion of facilitation to competition imposed by an increasingly arid climate. To support this speculation, we reconstructed the climatic niche of *Q. ilex* and its nurses as well as the local climate change occurring in the populations studied. We found that the decreasing trend in precipitation is pushing *Q. ilex* out of its climatic optimum in the stressful (semi-arid) but not in the mild (sub-humid) habitats. These results suggest that facilitation will be unable to mitigate the effects of climate change, especially those related to aridification. However, other scenarios linking climatic change with herbivory and rural abandonment should be considered to fully understand the past, present and future of facilitation interactions. Reconstructing past interactions can serve as an early warning signal about the future of populations in the face of climate change.

Keywords: aridification, climatic niche, competition, facilitation

Introduction

The current composition of plant communities cannot be understood without taking into account past climate and ecological interactions (Herrera 1992, Kraft and Ackerly 2014). The drastic climate change that occurred during the Cenozoic era (i.e. the last 66 Myr) led to abrupt vegetation shifts around the world (Pound et al. 2012, Lohmann et al. 2015). In particular, late Miocene vegetation in the Iberian Peninsula was dominated by warm mixed forests that were mostly replaced by xerophytic



www.oikosjournal.org

© 2024 The Authors. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

woods after the aridification of the past climate (Pound et al. 2012). This aridification caused the local extinction of ca 40 Paleotropical and Arctotertiary taxa and the diversification of drought-adapted species (Verdú and Pausas 2013, Verdú et al. 2019). Interestingly, not all Paleotropical and Arctotertiary lineages went extinct (Herrera 1992), as there was an ecological interaction that allowed them to survive climate change: facilitation (Valiente-Banuet et al. 2006). Nurse, drought-adapted plants, are able to mitigate the effects of climate change on Tertiary stress-sensitive lineages by allowing them to establish under the ameliorated micro-environmental conditions generated beneath their canopies (Valiente-Banuet et al. 2006). Similarly, species distribution models predict that threatened species may persist in future stressful climates due to the microclimatic buffering effect of dominant plant canopies (Stark and Fridley 2022).

The extent to which facilitation can mitigate the impacts of climate change will mostly depend on the severity of climate change itself. Although facilitation tends to increase with stress levels (Holzapfel et al. 2006), it may decline under extremely stressful conditions due to abiotic and biotic limitations leading to a shift from facilitation to competition (Maestre and Cortina 2004, Michalet et al. 2006). The decrease in facilitation at the dry extreme of the gradient can be explained by the non-linear physiological responses of plants to stress (Malkinson and Tielbörger 2010), as well as the interception of water by the nurse, preventing it from reaching the facilitated plant (Tielbörger and Kadmon 2000). Overall, the impact of neighboring species at the extreme of the stress gradient can be negative when both species share similar 'competitive' or 'stress-tolerant' life histories, and the abiotic stress gradient is influenced by a resource, such as water (Maestre et al. 2009).

Ultimately, the outcomes of facilitative interactions will depend on how far the current abiotic conditions deviate from the physiological optimum of each species. Gross et al. (2010) proposed the 'strain' framework to explain why species that are deviated from their physiological optima are those requiring facilitation. Climate change may be pushing species out of their physiological optima, making them more dependent on facilitation. The unprecedented rate at which climate is currently changing may compromise the buffering role of facilitation at particular aridity thresholds.

Facilitation interactions have been shown to turn into competition with the ontogeny of the plants and the occurrence of this ontogenetic shift can be influenced by environmental stress conditions (Schiffers and Tielbörger 2006, Le Roux et al. 2013). This ontogenetic shift from facilitation to competition can result in a spatial pattern where juveniles are spatially associated with nurses while adults grow in isolation. This pattern could also be attributed to isolated plants excelling across all ontogenetic stages. Miriti et al. (2006) tested these two hypotheses in the desert shrub *Ambrosia dumosa*, validating the ontogenetic shift scenario. *Quercus ilex* is a Mediterranean species strongly dependent on facilitation in the recruitment stage, as described by a multitude of experimental and observational studies measuring spatial association

of *Q. ilex* saplings with nurses (reviewed by Verdú et al. 2021). However, García-Fayos et al. (2020) showed a spatial pattern consistent with an ontogenetic shift from facilitation to competition. Specifically, these authors tracked the signal of facilitation (i.e. a significant association with nurses) in *Q. ilex* for saplings (≤ 15 years) and juveniles (16–50 years) plants in 17 sub-humid and semi-arid Mediterranean drylands. They found that *Q. ilex* saplings were associated with nurse plants both in sub-humid and semi-arid communities but, interestingly, such association was erased in juvenile plants only in the semi-arid communities. Here, we explored whether current climate change is reverting initial facilitation interactions into competition at particular aridity thresholds. To do this, we reconstructed the climatic (precipitation) niches of *Q. ilex* and its potential nurses to verify how they adjust to changing climate conditions in both semi-arid and sub-humid communities. We hypothesized that climate change has caused the initial facilitation signal to disappear in semi-arid populations because under this climate both *Q. ilex* and its nurses are moving well outside their climatic optima. We also provide alternative explanations related to species lifespan, nurse mortality, herbivory or rural abandonment, which warrant further critical research.

Material and methods

In testing the hypothesis that climatic change has transformed facilitation into competition, we leverage the findings of García-Fayos et al. (2020), who observed that the spatial signal of facilitation diminishes in semi-arid but not in sub-humid communities in eastern Spain. If climatic change has specifically eroded the signal of facilitation in semi-arid communities, then the climatic factor limiting the interaction should manifest primarily in these communities. To address this, we initially reconstruct the climatic temporal trends in both community types and assess whether the climatic requirements of *Q. ilex* and its nurses are still met in recent times, as we describe below.

Study area and facilitation assessment

Here we briefly describe the methodology and results from García-Fayos et al. (2020) that ignited the current study.

The study area was located in the Iberian mountain range (eastern Spain), where 17 plots of 231 × 231 m were sampled along a 130 km east-west transect. Plots were selected and used in a previous study with vegetation remote-sensing data and their size was determined by the pixel size of the UTM re-projected MODIS Terra satellite MOD13Q1-product (Moreno-de las Heras et al. 2018). All the plots have calcareous soils and are located at high and flat areas between 1060 and 1400 m a.s.l. Eleven plots were located in areas with semi-arid climate and six plots in sub-humid climate areas.

The spatial association between *Q. ilex* and its potential nurse plants was estimated by recording the number of nurse individuals close (< 50 cm) to each *Q. ilex* recruit. Forty-six

random points per plot were sampled to quantify the presence of nurse plants. The age of all the *Q. ilex* recruits was estimated with the help of an allometric model built with 171 plants relating the diameter of the root collar with the age of the plant determined from tree-ring counts. Recruits were classified as saplings (up to 15 years old) and juveniles (16 to 50 years old) because the effect of deep shade on recruits turns from positive to negative at approximately 15 years of age (Espelta et al. 1995). García-Fayos et al. (2020) selected potential nurses among those species with morphological traits attracting dispersers, deterring predators or enhancing the microhabitat for *Q. ilex* seedling establishment (i.e. plant size and shape, leaf size and leaf density, spinescence, etc). Among all these potential nurses, they selected seven long-lived trees or shrubs: *Pinus nigra*, *Juniperus thurifera*, *J. communis*, *J. phoenicea*, *J. sabina*, *Quercus faginea* and *Q. ilex*. We then conducted statistical tests to check for spatial associations of each nurse species and *Q. ilex* saplings or juveniles in semi-arid and sub-humid communities. While spatial correlation does not definitively imply facilitation (Liancour and Doležal 2023) the extensive experimental data showing that *Q. ilex* requires nurses to recruit under (Verdú et al. 2021) enables us to confidently classify the observed spatial relationships as facilitation interactions. The association between *Q. ilex* and nurses was analyzed by fitting a logistic regression relating the log of the odds of *Q. ilex* recruit presence to the presence of a nurse plant within 50 cm around the recruit or random point. Random plot effects for both the intercept and slope parameters were included in the model. García-Fayos et al. (2020) showed that *Q. ilex* saplings (≤ 15 years) were significantly associated with nurses, being the odds of finding a sapling associated with a nurse ca 30 times larger than those of finding a lack of association. The pattern was the same for semi-arid and sub-humid populations. However, the association pattern between *Q. ilex* juveniles (16–50 years) and nurses differed between areas: while the association pattern was significant in the sub-humid populations (with odds ratio ca 7 times larger in association than in non-associated plants), in the semi-arid there was no significant association.

Observed climatic trends

Climate changes that occurred at these sites over the last decades were quantified using quality controlled and homogenized meteorological observations from high spatial resolution databases (González-Hidalgo et al. 2011, 2022); highlighting the marked spatial and temporal variability of air temperature and precipitation changes across the Iberian Peninsula. Benetó and Khodayar (2023) also found remarkable interseasonal and regional-to-local differences in precipitation changes in eastern Spain.

Climatic niche reconstruction

We characterized the climatic niche of *Q. ilex* by using a univariate climatic space approach based on annual precipitation.

We focus on rainfall because it is a limiting factor for its spatial distribution, especially below 460 mm annual rainfall (Villar-Salvador et al. 2013). In addition, water is a very limiting resource, and competition for it has been shown to reverse facilitation into competition (Maestre and Cortina 2004).

First, we obtained species occurrences from the Global Biodiversity Information Facility (GBIF) database (www.gbif.org) and climatic data from the CHELSA database (Karger et al. 2017, <https://chelsa-climate.org>). Then, we extracted mean annual precipitation of the 1979–2013 period from all the obtained occurrences of *Q. ilex* subsp. *rotundifolia*- the subspecies that corresponds to the studied *Q. ilex* populations- to build the univariate niche.

Second, we characterized the univariate niche and the niche-derived indices by following Broennimann et al. (2021) and Perez-Navarro et al. (2022). Briefly, to construct the species niche, a one-dimensional density function was adjusted, based on all the outcomes of the climate (mean annual precipitation) of *Q. ilex* subsp. *rotundifolia* occurrences. Species climatic suitability was then calculated by dividing the values of kernel density estimates by the maximum density estimate of the species niche, obtaining an index ranging between 0 and 1 (Perez-Navarro et al. 2021). We identified the niche optimum as the climatic space with species climatic suitability higher than 0.50, that is the environmental space with higher probability of appearance. We also estimated the univariate species niche centroid as the mode of these two variables.

Finally, we characterized the climatic niche of the seven nurse species in the study area (*J. communis*, *J. phoenicea*, *J. sabina*, *J. thurifera*, *P. nigra*, *Q. faginea*, and *Q. ilex*) that are in our studied plots by applying the same aforementioned procedure.

Adjustment of the climate niche to the observed climate

General linear models (GLM) were used to study annual precipitation change across time in our studied plots, to find whether the *Q. ilex* and nurse species populations were surpassing species climatic optima along the studied period. Mean annual precipitation (log-transformed) was used as the dependent variable. Time, defined as years after 1950, was used as an independent variable. Type of climate (sub-humid and semi-arid) was also included as a factor. To consider whether the precipitation is changing distinctly across climates, we added the interaction between time and climate (factor). Durbin–Watson index was calculated to test the autocorrelation of the residuals of the built model.

Results

Based on the findings of García-Fayos et al. (2020), who dated the age of associated and non-associated *Q. ilex* saplings and juveniles, we can infer that in the sub-humid communities, all species that were positively associated with *Q. ilex* saplings (*P. nigra*, *J. communis*, *Q. faginea*, and *J. thurifera*) maintained

the spatial association with juveniles. Conversely, species that lacked associations with saplings in the sub-humid area (*J. sabina*, *J. phoenicea* and *Q. ilex*) also demonstrated no such associations with juveniles (Table 1). The sole instance of a negative association was observed with *Q. ilex* and its own species' juveniles (odds ratio significantly lower than 1 in Table 1).

In the semi-arid zone, species that previously displayed positive associations with *Q. ilex* saplings (*J. thurifera* and *J. phoenicea*) drastically reduced (*J. thurifera*; odds reduced from 45.0 to 5.8) or even lost their association (*J. phoenicea*; odds reduced from 12.0 to 1.6) with juveniles (Table 1). *Quercus ilex*, on the other hand, did not exhibit any significant associations with either its saplings or juveniles in these semi-arid regions (Table 1).

The reconstructed precipitation niche of *Q. ilex* indicates that its optimum annual precipitation ranges between 447 and 720 mm (Fig. 1).

During the 1950 to 2010 period, the studied populations underwent a significant decrease in precipitation (estimate \pm SE = -0.0017 ± 0.0007 ; $t = -2.28$ $p = 0.02$, general linear model) across time. Besides, the residuals of the built model did not show autocorrelation (Durbin–Watson test = 1.96, $p = 0.29$). This is translated into a drop of 9.98 mm mean annual precipitation per decade, that is a total loss of 60.89 mm rainfall at the end of the study period (2010). Furthermore, we observed that the same negative trend is experienced in both climates, since no interaction between time and type of climate was found (0.0007 ± 0.0010 ; $t = 0.69$; $p = 0.48$, Fig. 2). As, obviously, semi-arid communities had, in average, lower precipitation than sub-humid ones (0.1577 ± 0.0362 ; $t = 4.35$; $p < 0.0001$), the decreasing temporal trend led semi-arid, but not sub-humid *Q. ilex* populations to the limit of their optimum precipitation niche (Fig. 2).

The precipitation optima differed between nurse species (Fig. 1). Annual rainfall in sub-humid populations did not decrease below the lower limit of the nurses' precipitation optima (*P. nigra*, *J. communis*, *J. thurifera* and *Q. faginea* in Fig. 3). Similarly, the decreasing trend of rainfall in semi-arid populations has led to a total annual precipitation that is still compatible with the nurses' precipitation optima (*J. phoenicea* and *J. thurifera* in Fig. 3).

Discussion

Our results show that the *Q. ilex* populations studied in the Iberian Peninsula have suffered a decrease in precipitation over the last decades. By reconstructing the climatic niche of the species, we have detected that the decreasing precipitation experienced so far is a limiting factor for some, but not all, *Q. ilex* populations. In particular, the climate change over the last decades has pushed Iberian semi-arid populations towards the limit of its precipitation optimum. Although the trend is the same for sub-humid populations, these latter are still within their optimal range of precipitation. The climatic trend is not currently jeopardizing the survival of *Q. ilex* nurses because all of them have optima well within the current precipitation levels experienced in their populations.

The differential effects of climatic change in semi-arid vs. sub-humid populations may explain why the signal of initial facilitation – the association between *Q. ilex* and its nurses – has been erased in the former but not in the latter populations as described in García-Fayos et al. (2020). We argue that the facilitation signal has been lost in older plants (>15 years) from the semi-arid populations because *Q. ilex* is far from its precipitation optimum and facilitation is reversing to competition. Evidence exists that plant facilitation may turn into competition along the ontogeny of a plant or in response to temporal fluctuations in the environment (Verdú et al. 2004, Valiente-Banuet and Verdú 2008). These authors identified that the signal of the facilitation interaction disappeared in the species that tended to compete more. Similarly, Maestre and Cortina (2004) showed a shift from the initial facilitation to competition when the annual precipitation was so low that the benefits provided by the nurse (*Stipa tenacissima*) to the facilitated species (*Pistacia lentiscus*) did not overcome its own resource uptake.

Alternative explanations for the loss of spatial association between nurses and beneficiaries in the semi-arid communities can be explored. First, the differences in their lifespans: under this scenario, nurses might experience a comparatively shorter lifespan, dying earlier than their facilitated plants. We discard this possibility because this pattern would not explain why the spatial association signal disappears only in semi-arid climates and not in sub-humid ones. In addition, both *Q. ilex* and all its nurses are long-lived species without substantial

Table 1. Species-specific nurse effects. Data show the odds of finding a *Quercus ilex* sapling or a juvenile associated with a nurse species in the semi-arid and the sub-humid communities. Odds significantly higher than 1 indicates positive association. 95% Confidence intervals are shown in brackets, and values significantly higher than 1 are highlighted in bold. NA indicates the absence of a species from the respective community.

Nurse species	Saplings (3–15 years)		Juveniles (16–50 years)	
	Semi-arid	Sub-humid	Semi-arid	Sub-humid
<i>Pinus nigra</i>	NA	8 [4, 13]	NA	6 [4, 9]
<i>Juniperus communis</i>	NA	14 [9, 21]	NA	6 [3, 9]
<i>Quercus faginea</i>	NA	3 [2, 4]	NA	4 [3, 6]
<i>Juniperus sabina</i>	NA	1.4 [0.7, 3.1]	NA	1.1 [0.6, 2.0]
<i>Juniperus thurifera</i>	45 [11, 173]	20 [8, 50]	5.8 [3, 11]	21 [9, 47]
<i>Juniperus phoenicea</i>	12 [3, 42]	0.8 [0.3, 1.9]	1.6 [0.6, 4.1]	0.6 [0.3, 1.2]
<i>Quercus ilex</i>	1.9 [0.8, 5.3]	0.7 [0.5, 0.1]	0.8 [0.5, 1.2]	0.4 [0.3, 6]

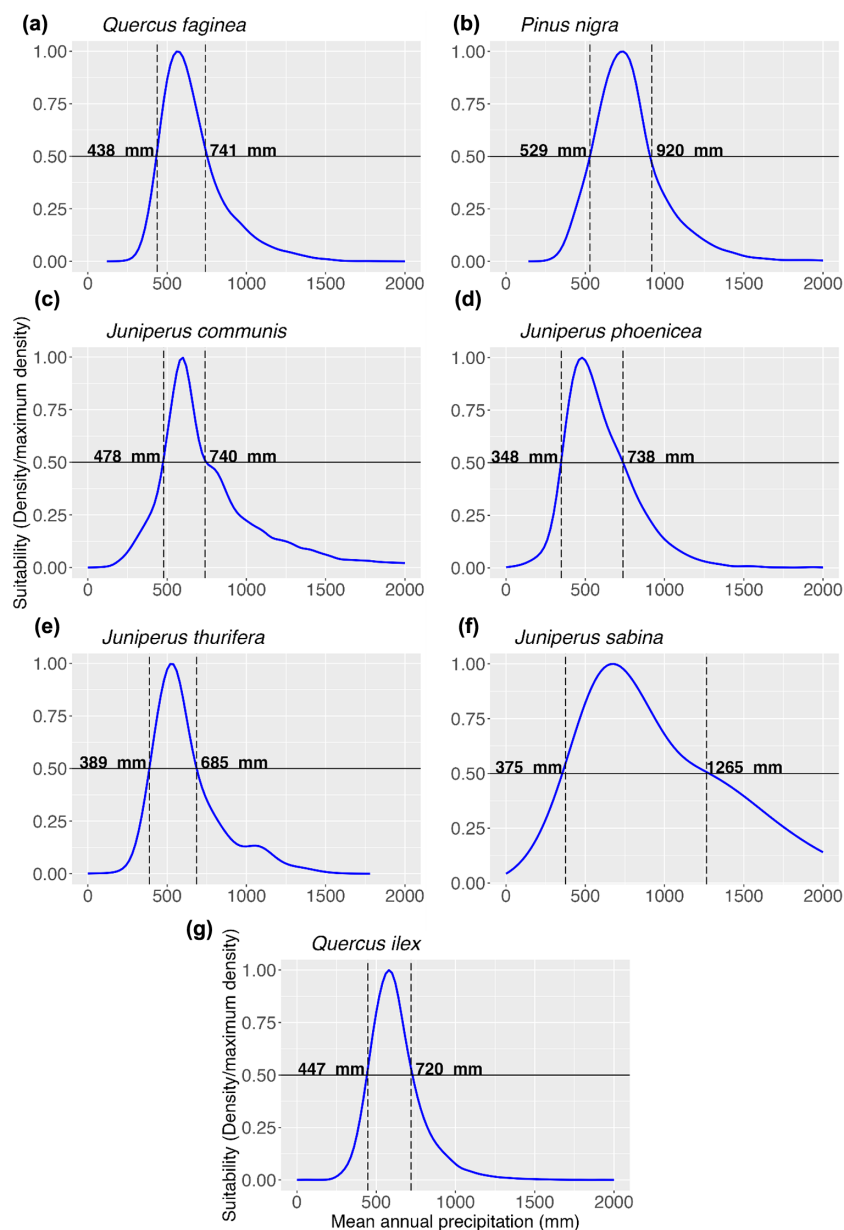


Figure 1. Representation of the species niche based on univariate space (mean annual precipitation) as a density function weighted by its maximum density, that is climatic suitability. Dashed vertical black lines delimit the niche optima, established as the climatic space with a climatic suitability higher than 0.50.

lifespan differences. Second, increased mortality of nurses: climate change may be pushing the most suitable nurse species out of semi-arid regions, leading to increased mortality independently of their spatial association with *Q. ilex*. This scenario is plausible and would also compromise the future of regeneration through facilitation unless new species could take the nurse, although we ignore the limitation in nurse effects induced by a lack of time consecutive to accelerated warming (Zimmer et al. 2018). Third, decreased protection from predation: herbivory combined with drought stress has been shown to alter the outcome of facilitation interactions (Michalet et al. 2014, Verwijmeren et al. 2019). In our

semi-arid communities, elevated water stress could also have 1) reduced food availability, intensifying herbivory pressure on both nurse plants and their supported plants, which are typically more palatable than isolated individuals and/or 2) diminished the protective function of nurse plants against herbivores by causing leaf loss and increasing the detectability of facilitated plants (Verwijmeren et al. 2019). An alternative scenario related to herbivory could be that rural abandonment triggered the facilitation process, previously hindered by intense landuse in semi-arid regions. In places where regeneration faced challenges not just due to climate but also due to substantial herbivore pressure, the facilitation

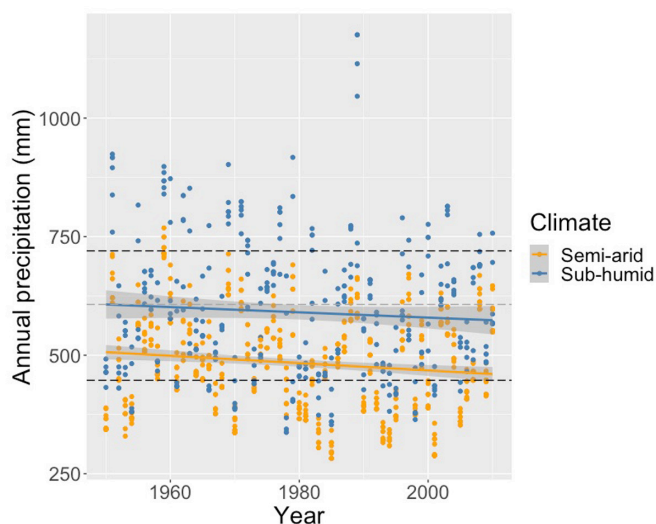


Figure 2. Temporal trend of the mean annual precipitation in the studied populations of *Quercus ilex* for 1950–2010. Each dot represents the observed mean annual precipitation of a studied plot in semi-arid (yellow) and sub-humid (blue) populations. Grey dashed line represents the centroid of the niche based on mean annual precipitation (607 mm). Black dashed lines represent the niche optima of *Q. ilex*, set as the precipitation range (447–720 mm) located within the space with climatic suitability greater than 0.50.

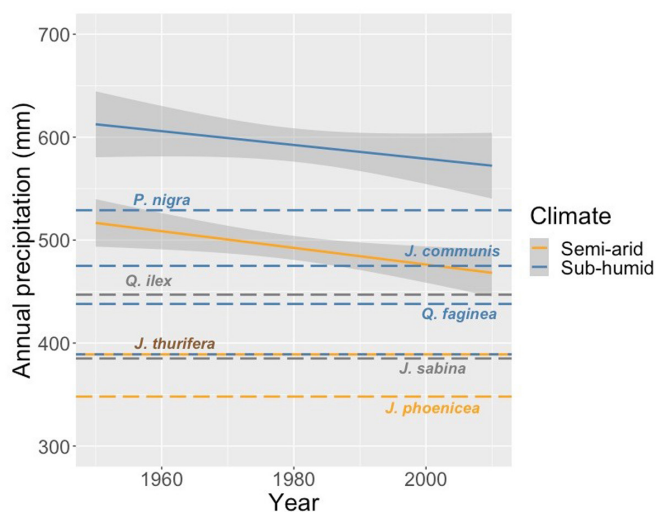


Figure 3. Annual precipitation trends in the semi-arid (orange line) and sub-humid (blue line) studied populations for 1950–2010. The lower limit of the niche optima for each species is represented by a horizontal line, depicted in blue for nurses inhabiting only in the subhumid (*Pinus nigra*, *Juniperus communis* and *Quercus faginea*), orange for the nurse living only in the semiarid (*Juniperus phoenicea*), bicolor for the nurse inhabiting both in the subhumid and the semiarid (*Juniperus thurifera*) and grey for non-nurses (*Quercus ilex* and *Juniperus sabina*).

pattern might have been eradicated. Later on, the significant reduction in livestock resulting from rural abandonment stopped erasing the facilitation pattern, making it discernible in recent years.

With all these alternatives in mind that deserve further research, our analysis suggests that climate change is favouring the disruption of positive interactions between adults in semi-arid populations. If the trend towards aridification continues, as predicted by climate change models (Giorgi and Lionello 2008, Somot et al. 2008, Miró et al. 2021), it is possible that initial facilitative interactions will also be compromised as nurses move further and further away from their climatic optimum. The difference between the climatic optimum of a species and the actual climate can be visualized as a climatic debt that measures the time lag in the response of the plants to the climate (Bertrand et al. 2016). If climate change pushes nurse and/or facilitated plants to either taxonomic or functional extinction, plants should pay the debt that, in extreme situations, could lead them to coextinction. We suspect that *Q. ilex* is already paying the climatic debt in semi-arid communities where climate change is preventing the maintenance of facilitation interactions. This is a case in which the extinction of interactions precedes the species extinction and dramatically affects ecosystem functioning (Valiente-Banuet et al. 2015). As Janzen (1974) claimed almost half a century ago, ‘what escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions’. Reconstructing past interactions and climates, as we have done here, should serve as an early warning signal of the biodiversity loss that climatic change may produce.

Acknowledgements – We thank Pedro Villar for the discussions on the alternative scenarios that could explain our observed spatial pattern of *Q. ilex*.

Funding – Financial support was provided by the project PID2020-113157GB-I00 (funded by MCIN/AEI/10.13039/501100011033 and ‘ERDF A way of making Europe’) and CIPROM/2021/63 (Generalitat Valenciana).

Author contributions

Miguel Verdú: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Esther Bochet:** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Investigation (equal); Visualization (equal); Writing – review and editing (equal). **Tiscar Espigares:** Data curation (equal); Investigation (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Jordi Margalef-Marrasé:** Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (lead); Supervision (equal); Validation (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **José Manuel Nicolau:** Data curation (equal); Investigation (equal); Validation (equal);

Writing – review and editing (equal). **Yu Yue:** Data curation (equal); Formal analysis (lead); Investigation (equal); Writing – review and editing (equal). **César Azorin-Molina:** (molina) Data curation (equal); Formal analysis (equal); Validation (equal); Writing – review and editing (equal). **Patricio Garcia-Fayos:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h9w0vt4rj> (Margalef-Marrase et al. 2024).

References

- Benetó, P. and Khodayar, S. 2023. On the need for improved knowledge on the regional-to-local precipitation variability in eastern Spain under climate change. – *Atmos. Res.* 290: 106795.
- Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., De Ruffray, P., Gégout, J. C. and Loreau, M. 2016. Ecological constraints increase the climatic debt in forests. – *Nat. Commun.* 7: 12643.
- Broennimann, O., Petitpierre, B., Chevalier, M., González-Suárez, M., Jeschke, J. M., Rolland, J., Gray, S. M., Bacher, S. and Guisan, A. 2021. Distance to native climatic niche margins explains establishment success of alien mammals. – *Nat. Commun.* 12: 2353.
- Espelta, J. M., Riba, M. and Javier, R. 1995. Patterns of seedling recruitment in west-Mediterranean *Quercus ilex* forest influenced by canopy development. – *J. Veg. Sci.* 6: 465–472.
- García-Fayos, P., Monleón, V. J., Espigares, T., Nicolau, J. M. and Bochet, E. 2020. Increasing aridity threatens the sexual regeneration of *Quercus ilex* (holm oak) in Mediterranean ecosystems. – *PLoS One* 15: e0239755.
- Giorgi, F. and Lionello, P. 2008. Climate change projections for the Mediterranean region. – *Global Planet. Change* 63: 90–104.
- González-Hidalgo, J. C., Brunetti, M. and De Luis, M. 2011. A new tool for monthly precipitation analysis in Spain: MOPRE-DAS database (monthly precipitation trends December 1945–November 2005). – *Int. J. Climatol.* 31: 715–731.
- González-Hidalgo, J. C., Beguería, S., Peña-Angulo, D. and Sandonis, L. 2022. Variability of maximum and minimum monthly mean air temperatures over mainland Spain and their relationship with low-variability atmospheric patterns for period 1916–2015. – *Int. J. Climatol.* 42: 1723–1741.
- Gross, N., Liancourt, P., Choler, P., Suding, K. N. and Lavorel, S. 2010. Strain and vegetation effects on local limiting resources explain the outcomes of biotic interactions. – *Perspect. Plant Ecol. Evol. Syst.* 12: 9–19.
- Herrera, C. M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. – *Am. Nat.* 140: 421–446.
- Holzappel, C., Tielbörger, K., Parag, H. A., Kigel, J. and Sternberg, M. 2006. Annual plant–shrub interactions along an aridity gradient. – *Basic Appl. Ecol.* 7: 268–279.
- Janzen, D. H. 1974. The deflowering of Central America. – *Nat. Hist.* 83: 48–53.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P. and Kessler, M. 2017. Climatologies at high resolution for the earth's land surface areas. – *Sci. Data* 4: 170122.
- Kraft, N. J. B. and Ackerly, D. 2014. The assembly of plant communities. – In: Monson, R. K. (ed.), *Ecology and the environment*. – Springer, pp. 67–88.
- Le Roux, P. C., Shaw, J. D. and Chown, S. L. 2013. Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. – *New Phytol.* 200: 241–250.
- Liancourt, P. and Doležal, J. 2023. Overgrowth competition or facilitation from cushion plants: implication for the role of plant–plant interactions. – *Ecology* 104: e3989.
- Lohmann, G., Butzin, M. and Bickert, T. 2015. Effect of vegetation on the Late Miocene ocean circulation. – *J. Mar. Sci. Eng.* 3: 1311–1333.
- Maestre, F. T. and Cortina, J. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. – *Proc. R. Soc. B* 271: S331–S333.
- Maestre, F. T., Callaway, R. M., Valladares, F. and Lortie, C. J. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. – *J. Ecol.* 97: 199–205.
- Malkinson, D. and Tielbörger, K. 2010. What does the stress-gradient hypothesis predict? Resolving the discrepancies. – *Oikos* 119: 1546–1552.
- Margalef-Marrase, J. et al. 2024. Climate change may alter the signal of plant facilitation in Mediterranean drylands. – *Dryad*, <https://doi.org/10.5061/dryad.h9w0vt4rj>
- Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., Valiente-Banuet, A. and Callaway, R. M. 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? – *Ecol. Lett.* 9: 767–773.
- Michalet, R., Le Bagousse-Pinguet, Y., Maalouf, J.-P. and Lortie, C. J. 2014. Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. – *J. Veg. Sci.* 25: 609–613.
- Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. – *J. Ecol.* 94: 973–979.
- Miró, J. J., Estrela, M. J., Olcina-Cantos, J. and Martin-Vide, J. 2021. Future projection of precipitation changes in the Júcar and Segura river basins (Iberian Peninsula) by CMIP5 GCMs local downscaling. – *Atmosphere* 12: 879.
- Moreno-de las Heras, M., Bochet, E., Monleón, V., Espigares, T., Nicolau, J. M., Molina, M. J. and García-Fayos, P. 2018. Aridity induces nonlinear effects of human disturbance on precipitation-use efficiency of Iberian woodlands. – *Ecosystems* 21: 1295–1305.
- Perez-Navarro, M. A., Broennimann, O., Esteve, M. A., Bagaria, G., Guisan, A. and Lloret, F. 2022. Comparing climatic suitability and niche distances to explain populations responses to extreme climatic events. – *Ecography* 11: e06263.
- Perez-Navarro, M. A., Broennimann, O., Esteve, M. A., Moya-Perez, J. M., Carreño, M. F., Guisan, A. and Lloret, F. 2021. Temporal variability is key to modelling the climatic niche. – *Divers. Distrib.* 27: 473–484.
- Pound, M. J., Haywood, A. M., Salzmann, U. and Riding, J. B. 2012. Global vegetation dynamics and latitudinal temperature gradients during the Mid to Late Miocene (15.97–5.33 Ma). – *Earth Sci. Rev.* 112: 1–22.
- Schiffers, K. and Tielbörger, K. 2006. Ontogenetic shifts in interactions among annual plants. – *J. Ecol.* 94: 336–341.
- Somot, S., Sevault, F., Déqué, M. and Crépon, M. 2008. 21st century climate change scenario for the Mediterranean using a

- couple atmosphere–ocean regional climate model. – *Global Planet. Change* 63: 112–126.
- Stark, J. R. and Fridley, J. D. 2022. Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. – *Global Ecol. Biogeogr.* 31: 562–575.
- Tielbörger, K. and Kadmon, R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. – *Ecology* 81: 1544–1553.
- Valiente-Banuet, A. and Verdú, M. 2008. Temporal shifts from facilitation to competition occur between closely related taxa. – *J. Ecol.* 96: 489–494.
- Valiente-Banuet, A., Rumebe, A. V., Verdú, M. and Callaway, R. M. 2006. Modern Quaternary plant lineages promote diversity through facilitation of ancient tertiary lineages. – *Proc. Natl Acad. Sci. USA* 103: 16812–16817.
- Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M. and Zamora, R. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. – *Funct. Ecol.* 29: 299–307.
- Verdú, M. and Pausas, J. G. 2013. Syndrome-driven diversification in a Mediterranean ecosystem. – *Evolution* 67: 1756–1766.
- Verdú, M., Villar-Salvador, P. and García-Fayos, P. 2004. Gender effects on the post-facilitation performance of two dioecious *Juniperus* species. – *Funct. Ecol.* 18: 87–93.
- Verdú, M., Pausas, J. G., Postigo-Mijarra, J. M., Barrón, E., Casas-Gallego, M., Arroyo, J. and Carrión, J. S. 2019. Phylogenetic diversity in the Iberian flora through the Cenozoic. – *Environ. Exp. Bot.* 170: 103888.
- Verdú, M., Gómez, J. M., Valiente-Banuet, A. and Schöb, C. 2021. Facilitation and plant phenotypic evolution. – *Trends Plant Sci.* 26: 913–923.
- Verwijmeren, M., Smit, C., Bautista, S., Wassen, M. J. and Rietkerk, M. 2019. Combined grazing and drought stress alter the outcome of nurse: beneficiary interactions in a semi-arid ecosystem. – *Ecosystems* 22: 1295–1307.
- Villar-Salvador, P., Nicolás Peragón, J. L., Heredia Guerrero, N. and Uscola Fernández, M. 2013. *Quercus ilex* L. – In: Pemán, J., Navarro-Cerrillo, R. M., Nicolás, J. L., Prada, M. A. and Serada, R. (eds), *Producción y manejo de semillas y plantas forestales*, Vol. 2. Organismo Autónomo Parques Nacionales, pp. 226–250.
- Zimmer, A., Meneses, R. I., Rabatel, A., Soruco, A., Dangles, O. and Anthelme, F. 2018. Time lag between glacial retreat and upward migration alters tropical alpine communities. – *Perspect. Plant Ecol. Evol. Syst.* 30: 89–102.