


Do adult trees increase conspecific juvenile resilience to recurrent droughts? Implications for forest regeneration

ENRIQUE ANDIVIA ^{1,†} JAIME MADRIGAL-GONZÁLEZ,^{1,2} PEDRO VILLAR-SALVADOR,¹ AND MIGUEL A. ZAVALA¹

¹Forest Ecology and Restoration Group, Departamento de Ciencias de la Vida, Universidad de Alcalá, Campus Universitario, Ctra. Madrid-Barcelona, Km 33.6, Alcalá de Henares, 28805 Madrid, Spain

²Climate Change impacts and Risks in the Anthropocene (C-CIA), Institute for Environmental Sciences (ISE), University of Geneva, 66 Boulevard Carl Vogt, 1205 Geneva, Switzerland

Citation: Andivia, E., J. Madrigal-González, P. Villar-Salvador, and M. A. Zavala. 2018. Do adult trees increase conspecific juvenile resilience to recurrent droughts? Implications for forest regeneration. *Ecosphere* 9(6):e02282. 10.1002/ecs2.2282

Abstract. Recruitment is a bottleneck for forest regeneration especially in semi-arid Mediterranean environments. Ensuring natural forest regeneration is vital for preserving ecosystem function under climate warming and increased frequency and intensity of extreme droughts. Interspecific positive interactions are of paramount importance in these ecosystems. The net outcome of conspecific plant interactions in semi-arid forests, however, has been less explored, particularly the range of environmental conditions for which juveniles benefit from nursing effects. We evaluated the direction and magnitude of intraspecific relationships between adults and juveniles of *Pinus pinaster* in a dry continental Mediterranean forest in the Iberian Peninsula. We measured the longitudinal shoot elongation of the last 15 yr and foliar functional traits in pine saplings growing under the canopy of adult pines and in open habitats. We examined the growth response to precipitation and the resilience and resistance of growth to two extreme drought events in 2005 and 2012. Our results show likely facilitation of saplings by adult conspecifics. Nursed saplings had a greater size relative to age, longer needles, and faster shoot elongation than saplings in open habitats. In addition, saplings under the canopy were more resistant and resilient to the first severe drought event. However, saplings grown in open habitats were more resilient to the second drought event, which might suggest a shift in the net balance of conspecific interactions with increased drought frequency and with tree ontogeny. These results have a direct application for the adaptation and restoration of semi-arid forest ecosystems under climate change. Currently, adults are used as nurse plants to enhance survival and growth of juveniles. However, this positive effect on sapling performance might shift to negative under scenarios of increasing frequency and intensity of drought events.

Key words: climate change; drought; facilitation; forest restoration; growth stability; *Pinus pinaster*; plant–plant interactions; positive interactions; resilience; shelterwood.

Received 24 April 2018; **accepted** 2 May 2018. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2018 The Authors. 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.

† **E-mail:** e.andivia@gmail.com

INTRODUCTION

Recruitment is crucial for the regeneration and sustainable management of forests under climate change (Nyland 2016). Recruitment depends on multiple ecological processes, such as seed production and dispersal, seedling emergence and

survival, and sapling growth and mortality (Gómez-Aparicio 2008). Many environmental factors modulate these processes (Cuesta et al. 2010) and in semi-arid environments survival of juveniles to drought is a major bottleneck for forest regeneration (Puerta-Piñero et al. 2007). Thus, increased frequency and intensity of drought due

to climate warming might eventually compromise forest regeneration. In water-limited ecosystems, such as Mediterranean forests, plant–plant interactions (either positive or negative) drive the recruitment of forest tree species (Castro et al. 2004, Gómez-Aparicio et al. 2004, Andivia et al. 2017). Specifically, positive interactions at early plant ontogenetic phases might be decisive for forest maintenance and provisioning of ecosystem services under more intense and frequent droughts forecasted by climate change studies (Christensen et al. 2007).

Facilitation among plants is a positive interaction where the nurse plant increases the performance of another plant that grows under the nurse canopy compared to the plants growing outside the canopy (Holmgren et al. 1997). This often occurs because the nurse plant mitigates the abiotic (e.g., water stress) and/or biotic (e.g., herbivory) stresses that other plants experience outside the nurse canopy (Bertness and Callaway 1994, Gómez-Aparicio et al. 2008). Facilitative interactions usually involve different species and drive community structure and function (Bruno et al. 2003). Nonetheless, negative (competition) and facilitative interactions occur at the same time in plant communities, especially in arid and semi-arid environments (Padilla and Pugnaire 2006, Wright et al. 2014). The final performance of interacting plants depends on the balance between facilitation and competition, which at the same time depends on the environmental context (Brooker 2006). The *stress-gradient hypothesis* (SGH; Bertness and Callaway 1994) predicts that facilitative interactions become more important than competition as abiotic stress and herbivory increase. The validity of the SGH predictions has been examined in many species and under a wide range of environmental conditions (Maestre and Cortina 2004, Armas et al. 2011, Granda et al. 2012, Andivia et al. 2017). The magnitude of the shift from facilitation to competition largely depends on the indicator of plant fitness (survival, growth, or reproduction), the functional characteristics of the nurse and beneficiary plants, and the nature of the stress (Gómez-Aparicio et al. 2009, Maestre et al. 2009).

The use of interspecific facilitation as a tool in forest restoration relies mainly on nurse shrubs (Gómez-Aparicio et al. 2004). This idea stems from species coexistence theory throughout the secondary succession (Holzwarth et al.

2015), which predicts that functionally equivalent species are less likely to coexist due to niche overlapping. Accordingly, Verdu et al. (2012) show that the effectiveness of facilitation for restoration is increased with the phylogenetic distance between the nurse and the beneficiary species. Consistent with this prediction, no spatial association was observed between conspecific juveniles and adults in different Mediterranean tree species (Granda et al. 2012). However, facilitation between phylogenetically close species or between conspecifics does exist (Fajardo et al. 2006, Fajardo and McIntire 2010, Prinzing et al. 2017). In addition, conspecific facilitative interactions may only be apparent at specific development stages (Miriti 2006, Wright et al. 2014). For example, germination and early seedling survival can be enhanced under the canopy of conspecific adults (Ruano et al. 2009), especially in dry years (Lucas-Borja et al. 2016), but after establishment the relationship might shift to competition.

Because forest regeneration is limited in dry areas, several management methods, such as the shelterwood system, are intended to facilitate seedling establishment and juvenile growth under the shelter of adult conspecifics. Understanding this adult–juvenile interaction is critical for the management and persistence of monospecific forests in water-limited sites and under future warmer drought scenarios. Resilience and resistance are two main components of tree functional stability and persistence in response to intense drought events (Lloret et al. 2011). In terms of growth, resistance is the ability to maintain growth during the intense drought event, while resilience is the capacity to restore pre-drought growth levels. The evaluation of the response of individuals to intense drought events in terms of growth stability is essential to anticipate forest structure changes and the effectiveness of forest management methods under scenarios of increasing aridity. This is especially important for juveniles because they are more vulnerable than adults to droughts (Herrero and Zamora 2014, Madrigal-González and Zavala 2014).

In this study, we address the net balance of intraspecific interactions between adults and juveniles of maritime pine (*Pinus pinaster* Aiton). Specifically, we explore whether the proximity to adults increases sapling resilience and resistance to consecutive intense drought events. Natural

regeneration of this species in Mediterranean-climate locations is becoming challenging, especially toward the dry end of its distribution range (González-Alday et al. 2009, Calama et al. 2017). The study site is in an area of inland sand dunes in central-northern Iberian Peninsula. Soils have very low fertility and water retention capacity (García Fernández 2004), which together with the low precipitation, strongly constrains tree growth and regeneration (Gomez-Sanz and Garcia-Vinas 2011). Under these stressful conditions, we measured annual shoot growth over the last 15 yr in saplings growing in two contrasting microhabitats: beneath adult canopies and in open habitats and assessed sapling resilience and resistance after two severe drought events in 2005 and 2012. As the net outcome of biotic interactions may ultimately filter functional traits distribution (McIntire and Fajardo 2014), we also measured foliar traits and biomass allocation at the branch level in these saplings. With this information, we tested which relation, facilitative or competitive, better explained the interaction between adults and juveniles of *P. pinaster*. Following the facilitation paradigm, adult trees will enhance juvenile performance as well as the resilience and resistance to intense drought events. In addition, saplings growing under the canopy of adult trees will show a more resource-acquisitive strategy than those growing in open areas (García-Cervigón et al. 2015).

METHODS

Study area

The study system is a Mediterranean continental-climate open forest in central Iberian Peninsula (Fig. 1; 41°22'11" N, 4°15'22" W). It is located in a homogeneous flat territory of about 7500 ha at 841 m a.s.l. The site is on inland sand dunes, which have sandy soils, highly unstructured, extremely poor in nutrients and with low water retention capacity (Gomez-Sanz and Garcia-Vinas 2011). The sandy layer usually reaches 10 m in depth, but in some cases, it can reach up to 20 m (García Fernández 2004). Mean annual temperature is 12°C, and annual precipitation oscillates between 430 and 470 mm with maximum rainfall during winter and spring. Winter is cold due to the high continental influence, and summer is dry and warm with a drought period of 4–5 months, from June to September or

October. The dominant tree species is the maritime pine (*Pinus pinaster* Ait.), which has a mean density of 76 tree/ha. We explored the spatial configuration of adult and juvenile pines by recording all individuals in a 0.25 ha square plot established at the core of our study site in a flat and homogenous area. The sampling showed a marked spatial aggregation of adults and juveniles (Appendix S1: Fig. S1). Because of the extreme soil and climatic conditions, tree density is low and maximum tree height is 7–12 m in healthy individuals. Some individuals, nonetheless, show a shrubby appearance with maximum heights of 2 m (Fig. 1). The understory vegetation is formed by sparse vegetation dominated by a few chamaephytes such as *Helichrysum stoechas* (L.) Moench or *Thymus mastichina* L. and a rich community of annual herbs and soil lichens.

The shelterwood cutting system is the typical forest management in the area, which is performed in permanent plots with moderate thinning and natural regeneration over a 100-yr rotation period. Last cutting in the area occurred in 2016. Timber and resin extraction constitute the main use in the area, which have had a considerable economic impact in the region for centuries.

Growth analysis in pine saplings

In early May 2017, we randomly selected 20 adults in a flat area of about 400 ha. These adult trees were different from those sampled to explore the spatial arrangement of pine trees in the area (Appendix S1: Fig. S1). For each adult tree, we randomly selected two saplings growing under the canopy of an adult tree and two saplings growing in open habitats. For each microhabitat (under the canopy and in open habitats), one sapling was oriented to the north and the other one to the south, relative to the adult tree. We considered as saplings the non-reproductive individuals, which in most cases were <3 m in height and <35 yr old. As *P. pinaster* shows one shoot flush of growth per year in the study area, we estimated the age of saplings by counting the number of annual bud scars or branch whorls (Herrero and Zamora 2014). In May 2017, we measured the longitudinal shoot growth in the leader shoot of the 80 selected saplings. Annual shoot growth spanning from 2001 to 2016 was measured as the elongation of stem segments between consecutive annual bud scars or branch

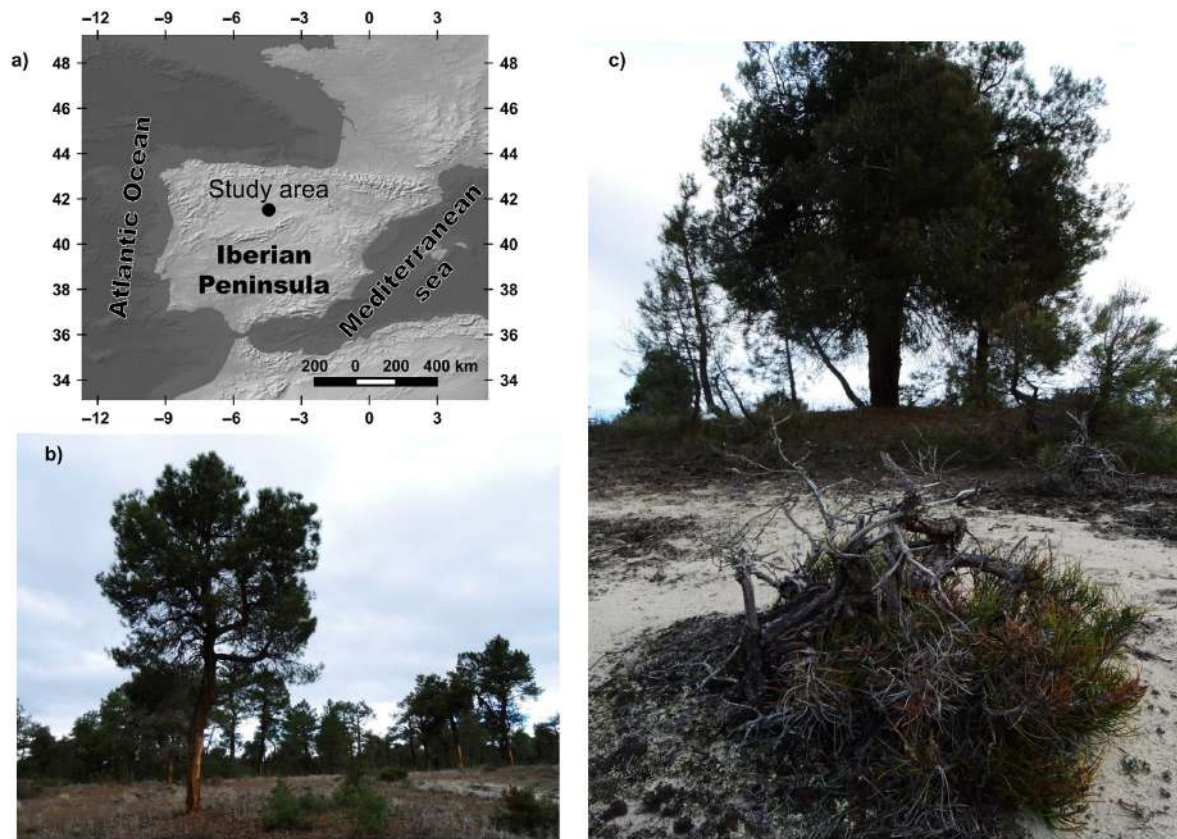


Fig. 1. (a) Geographical location of the study site. (b) Image of the study area showing adults and juveniles of *Pinus pinaster*. (c) Detail of a pine with a shrubby appearance.

whorls. The elongation of annual shoot segments has been widely used to evaluate the response of plants to environmental conditions and to drought events (Herrero and Zamora 2014). We also measured the stem diameter at breast height (dbh) and 10 cm aboveground (Db), sapling height, the number of other pine saplings in a 5 m radius to the focal sapling, and the distance to the closest adult pine. We estimated sapling stem volume (SV) as the product of plant height and $1/3$ basal area.

Needle morphology and biomass allocation at the branch level

In all selected saplings, two branches oriented to the south and north from the upper third of the sapling canopy were cut and the number of needle cohorts was counted. We avoided branches located under other branches to prevent any confounding effects due to shade (Rolo et al. 2015).

From each branch, the current-year shoot segment (i.e., year 2016) was cut and needles were removed, scanned (ScanJet 300 HP, Palo Alto, California, USA), and the projected area was measured with ImageJ. We also measured the needle length (NL) in 10 current year needles per pine sapling. All plant material was oven-dried at 65°C for 48 h and weighed. Needle mass per area (LMA) was calculated by dividing total needle mass by projected needle area. The leaf area ratio (LAR) of the current-year shoot segment was determined by dividing the needle area by the shoot segment mass (needle + stem mass). Needle mass fraction (LMF) was calculated dividing needle mass by shoot segment mass. Needle length is a good indicator of tree response to water availability (Herrero and Zamora 2014), whereas LMA, LAR, and LMF reflect biomass allocation and resource-use strategies in response to environment conditions (Lambers et al. 2008).

Data analysis

To evaluate whether pine saplings from different microhabitats differ in age and morphological parameters (height, Db, dbh, and SV), we fitted a linear mixed model (LMM) for each parameter considering microhabitat as a fixed effect, and plot (i.e., each adult pine) as a random term. A *t* test was conducted to evaluate whether differences between microhabitats were significantly different from zero.

To analyze the shoot growth pattern of pine saplings, we used a LMM in which sapling age (as a second-degree polynomial), microhabitat (under canopy and in open habitats), annual precipitation, sapling size (Db), and competition (as number of sapling in a 5 m radius) were considered as main effects. We also included the interaction between microhabitat and age, and between microhabitat and precipitation to test whether the response of sapling growth to these covariates differed between microhabitats. We computed annual precipitation using climatic records from the two closest meteorological stations of the Spanish National Agency of Meteorology (AEMET). Annual precipitation was computed from September of the previous year to August of the present year to account for the previous winter conditions up to the end of the growing season. Continuous variables were standardized to allow comparisons across model-estimated parameters and testing interactions (Zuur et al. 2009). Multicollinearity was evaluated using the variance inflation factor (VIF). The response variable (i.e., shoot elongation rate) was log-transformed to achieve normality and homoscedasticity.

We applied a mixed model because our experimental design resulted in spatial and temporary autocorrelation due to (1) the fact that we sampled four pine saplings per plot (i.e., pine adult); and (2) growth series results in non-independency among observations within the same pine sapling (i.e., repeated measurements). For these reasons, we considered pine sapling identity nested within plot identity as a random term in the model. We also tested different autoregressive correlation structures for growth measurements. To do this, we adjusted models by restricted maximum likelihood (REML) using different orders for the temporary autocorrelation structure and selected the one with the lowest value of the Akaike's information criterion adjusted for sample size (AIC_c).

Once the best random structure was selected, we identified the best-supported fixed effect structure by following a backward model selection procedure. First, we fitted the full model including all main effect and the abovementioned interactions, and we compared it with reduced models in which each pairwise interaction was dropped (Round 1). Then, we compared the selected model after round 1 with models that ignored the main effects. If the difference in AIC_c between two models was ≤ 2 , then the simpler model was selected (Burnham and Anderson 2002). All alternative models were fitted by the maximum likelihood method (ML), whereas the parameters of the selected model were estimated by REML.

To evaluate the resistance and resilience of pine saplings to drought events of 2005 and 2012, we followed the procedure described by Madrigal-González et al. (2017). Briefly, we first fitted a linear mixed model in which age (as a second-degree polynomial) and the pine sapling identity nested within plot identity were considered as fixed and random effects, respectively. Then, Pearson's residuals were extracted and scaled to 1–2 values according to the following formula:

$$\text{scaled residual} = \left[\frac{x_i - \min(x)}{\max(x) - \min(x)} \right] + 1$$

where x_i is the residual value for the observation i , and $\max(x)$ and $\min(x)$ are the maximum and minimum residual. These scaled residuals are values of elongation rate without the effects of sapling age. This scaling procedure allows the calculation of resistance and resilience indexes avoiding negative and zero values (Madrigal-González et al. 2017).

Resistance (R_t) and resilience (R_s) indexes were calculated following Lloret et al. (2011) on the scaled Pearson's residuals:

$$R_t = Dr/PreDr$$

$$R_s = PostDr/PreDr$$

Resistance is the capacity to maintain the pre-drought (PreDr) shoot elongation rate during the year of the drought event (Dr), whereas resilience is the capacity to reach pre-drought elongation rates after the drought event (PostDr). R_t and R_s indices were calculated for each sapling from the

scaled residual growth corresponding to the drought events 2005 and 2012. We selected these years because they were the most intense drought events during the study period with an annual precipitation of 271 and 284 mm, respectively. Pre-drought and post-drought growth values were the mean scaled residuals of growth in the 2 yr before and after 2005 and 2012, respectively. To evaluate whether pine saplings from different microhabitats differ in their resistance and resilience to drought events, we fitted a linear model for the resistance and resilience indexes for each drought event (2005 and 2012) considering microhabitat as a fixed effect. A *t* test was conducted to evaluate whether differences between microhabitats were significantly different from zero.

For each foliar trait (NL, LMA, LAR, and LMF), we fitted a mixed model in which microhabitat and sapling age were considered fixed effects, and the plot identity was included as a random term to account for spatial autocorrelation of observations. Model selection was also performed following a backward procedure based on the AIC_c . All statistical analyses were performed R v3.2.5.

RESULTS

Growth patterns of pine saplings

Sampled saplings were between 17 and 35 yr old. Pine saplings grown under the canopy of a pine adult were younger (mean \pm SE; 25.7 ± 0.7 and 28.6 ± 0.9 yr old, respectively; $P = 0.01$), taller (219 ± 12 and 95 ± 8 cm, respectively; $P < 0.001$), and showed lower dbh than saplings in open habitats (3.3 ± 0.3 vs. 4.3 ± 0.4 cm, respectively; $P = 0.02$). However, they did not differ significantly in terms of Db (8.0 ± 0.5 vs. 9.3 ± 0.7 cm, respectively; $P = 0.12$) and stem volume (4.5 ± 0.6 and 3.8 ± 1.1 dm³, respectively; $P = 0.59$). Mean distance to the bole of the closest adult pine tree was 3.9 ± 0.6 m and 19.8 ± 1.4 m for saplings grown under the canopy and in open habitats, respectively.

The second-order autoregressive structure was selected as the random term structure for the LMM used to analyze the shoot elongation pattern of saplings (Appendix S1: Table S1). This means that a given observation within the same individual shows a temporary autocorrelation

with the two previous measurements. The best supported model for the structure of the fixed effects includes the interaction between the microhabitat and the sapling age, and the main effect of the annual precipitation (Table 1). The selected model meets the homoscedasticity assumptions (Appendix S1: Fig. S2), and VIF values were lower than four units, indicating an acceptable degree of collinearity.

Saplings growing in different microhabitats showed a different pattern of shoot elongation with age (Fig. 2a). On the one hand, the shoot elongation rate of the saplings under adults initially increased linearly with age and then slowed to a constant value. On the other hand, saplings in open habitats showed low elongation rates during the first years of life but strongly accelerated at latter ages. These different patterns of growth over time resulted in a greater mean shoot elongation rate under the canopy of adults than in open habitats (10.3 ± 0.9 and 4.3 ± 0.6 cm/yr, Fig. 2b). In fact, shoot elongation rate was always greater in saplings under

Table 1. Comparison of linear mixed models to assess the effects of explanatory variables on the annual stem elongation of *Pinus pinaster* saplings.

Evaluated model	AIC_c	ΔAIC_c
Round 1		
–Full model	2229.8	0.6
–Microhabitat \times age	2235.0	4.6
–Microhabitat \times precipitation	2230.4	0
Round 2		
–Precipitation	2331.8	103.3
–Size	2229.4	0.9
–Competition	2228.9	0.4
–Precipitation and size	2331.9	103.4
–Precipitation and competition	2330.5	102.0
–Size and competition	2228.5	0
–Precipitation, size and competition	2330.5	102.0
Selected model	Microhabitat \times age + precipitation	

Notes: The full model included the interaction between microhabitat and age (as a second-degree polynomial), and between microhabitat and precipitation, as well as the main terms size (sapling Db and competition [number of saplings in a 5 m radius]). Models in round 1 excluded the pairwise interaction terms while models in round 2 excluded main terms. Model selection was performed based on the corrected Akaike's information criteria (AIC_c). ΔAIC_c refer to the difference in AIC_c between the assessed model and the model selected in each Round (i.e., $\Delta AIC_c = 0$). The final models show the selected explanatory variables for the fixed-effect terms.

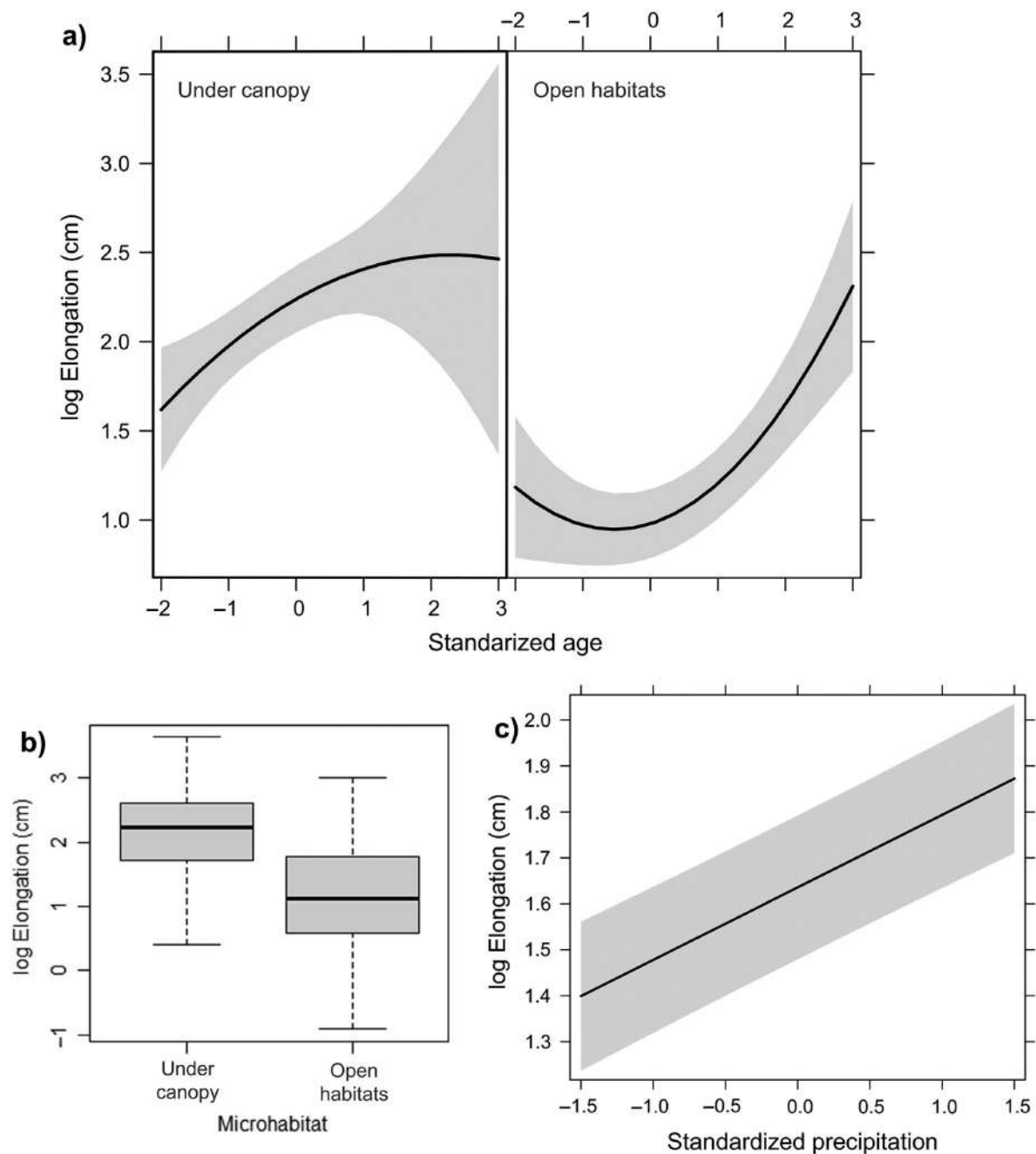


Fig. 2. Model prediction for (a) the effect of the interaction between microhabitat and sapling age, (b) the effect of microhabitat, and (c) the effect of annual precipitation on the annual shoot elongation of *Pinus pinaster* saplings.

adult canopies than in those in open habitats (Appendix S1: Fig. S3). Pine saplings positively responded to annual precipitation (Fig. 2c) with no differences between microhabitats.

Resilience and resistance to intense drought events

The drought of 2005 strongly reduced the sapling shoot elongation rate irrespective of the

microhabitat (Appendix S1: Fig. S3). However, saplings under the canopy of adults recovered the pre-drought elongation rate 2 yr after the drought event, whereas saplings in open habitats recovered it 6 yr later (Fig. 3). In response to the 2005 drought, saplings under canopy were more resistant (0.91 ± 0.01 vs. 0.86 ± 0.01 , $P = 0.03$) and resilient (0.98 ± 0.01 vs. 0.91 ± 0.01 , $P < 0.001$) than saplings in open habitats (Fig. 4). The drought of 2012 also reduced sapling shoot elongation (Appendix S1: Fig. S3). Unlike the drought of 2005, saplings in an open habitat recovered faster than those under canopy (Fig. 3), which were less resistant (0.93 ± 0.01 vs. 0.97 ± 0.01 , $P = 0.07$) and resilient (0.91 ± 0.01 vs. 1.00 ± 0.02 , $P < 0.001$) than the saplings in open habitats (Fig. 4). Thus, the microhabitats modulated the resistance and resilience capacity of saplings to the two most intense drought events during the study period in the opposite way.

Differences between microhabitats in needle and shoot morphological attributes

Sapling age and microhabitat did not significantly affect LMA, LAR, or LMF (Appendix S1:

Table S2). Mean \pm SE values for LMA, LAR, and LMF were 0.363 ± 0.001 kg/m², 2.11 ± 0.03 m²/kg, and $75.9 \pm 0.77\%$, respectively. However, needle length was positively related to sapling age (estimated slope = 0.09 ± 0.02) and was significantly greater in saplings grown under canopy than in open habitats (7.2 ± 0.2 and 5.9 ± 0.3 cm, respectively; $P < 0.001$). In addition, saplings under canopy had a higher number of needle cohorts per branch of the same age than saplings in open habitats (median = 4 and 2, respectively).

DISCUSSION

Our results support the facilitation hypothesis of saplings by adult conspecifics of *Pinus pinaster* in the study forest. Most performance and functional variables showed higher values in the saplings recruited beneath the canopy of adult conspecifics than in open spaces as evidenced by their greater size, needle length, shoot elongation rate, and resilience after the first intense drought (2005). However, resilience to the second intense drought event (2012) was lower in saplings under the canopy, suggesting a shift in the net balance of

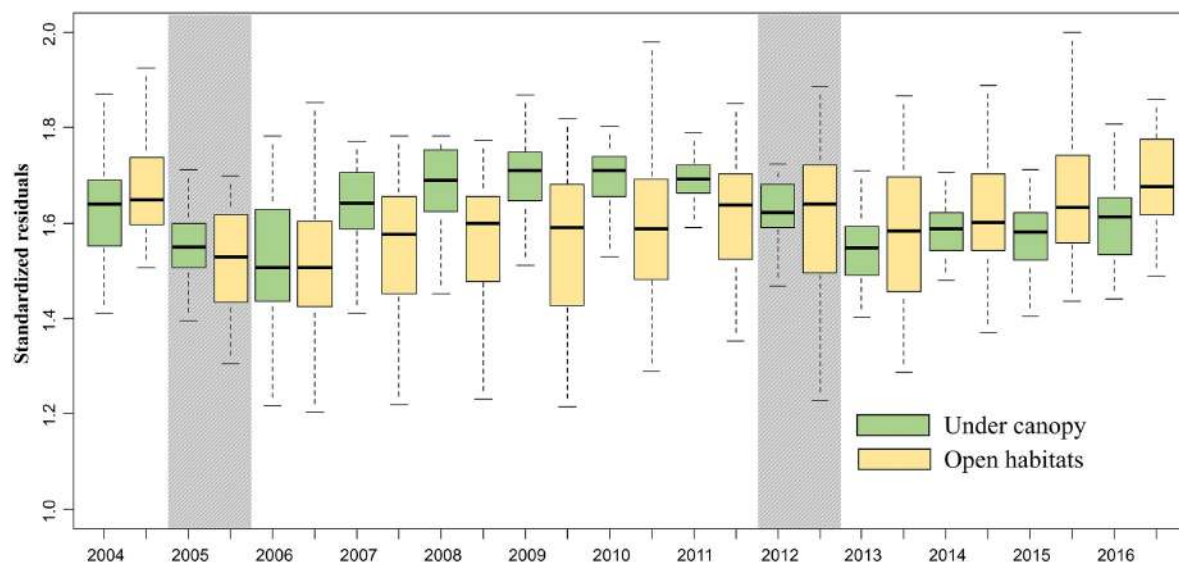


Fig. 3. Standardized residuals for annual shoot elongation of *Pinus pinaster* saplings growing under the canopy of adult pines and in open habitats. Residuals were obtained after fitting a linear mixed-effects model which included sapling age (as a second-degree polynomial). The shaded areas depict values during the drought events of 2005 and 2012, respectively. Boxes are 95% and 5% percentile values, while the solid lines indicate the median.

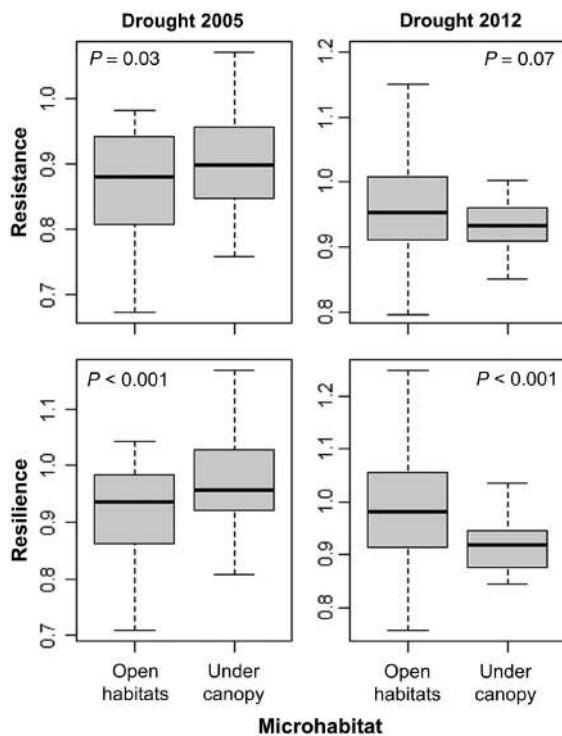


Fig. 4. Resistance and resilience to the drought events of 2005 (left panels) and 2012 (right panels) for *Pinus pinaster* saplings growing under the canopy of conspecific adults and in open habitats. Boxes are 95% and 5% percentile values, while the solid lines indicate the median. The P -value of the t test that evaluates whether differences between microhabitats were significantly different from zero is shown within each panel.

conspecific tree–tree interactions with increased drought frequency and with tree ontogeny.

Pine saplings grown under canopy and in open habitats were different in size after controlling for age. These differences may be attributed to (1) a strong photo-inhibition in response to direct irradiation and thus limited carboxylation (Puerta-Piñero et al. 2007), (2) increased stem elongation in response to shade (Lafuente-Laguna et al. 2012) and/or greater soil water availability (Gómez-Aparicio et al. 2008, Prieto et al. 2011), and (3) limitations associated with a less stable environment, more exposed to climatic variability including drought events (Madrigal-González and Zavala 2014). Air temperature, humidity, and soil fertility are more stable and at levels that increase the growth of beneficiary species under the nurse individuals compared to open spaces

(Moro et al. 1997, Gómez-Aparicio et al. 2005, Cuesta et al. 2010). Consistently, needle length and the number of needle cohorts, which negatively correlate with the water stress to which trees are exposed (Jonasson et al. 1997, Herrero and Zamora 2014), were greater in saplings under the influence of adults. Contrary to our expectations, nonetheless, the rest of leaf and shoot traits did not differ between microhabitats. Acclimation of plants to shade involves lower LMA, and greater LAR and LMF to optimize light harvesting (Lambers et al. 2008, Rolo et al. 2015). Similarly, facilitated saplings would show a more resource-acquisitive strategy than those growing in open areas (García-Cervigón et al. 2015). Thus, the lack of differences in current year shoot and leaf morphological traits between microhabitats suggests that the distinct environmental conditions in both microhabitats do not affect the mass allocation at current year shoot level, but saplings of open spaces adjust leaf size and number to minimize water loss (Ogaya and Peñuelas 2006). Further studies should incorporate the evaluation of water relation parameters, root traits, as well as differences in environmental conditions between microhabitats to disentangle the underlying mechanisms behind the observed facilitation process.

Despite the growth rate being higher in saplings under the canopy than in open habitats, saplings had similar growth responses to precipitation in both microhabitats indicating no synergy between precipitation and microhabitat. Additionally, saplings in open areas showed exponential growth with very low growth during the first years after emergence. The low aboveground growth rate of saplings in open habitats at very early development stages might reflect a plastic biomass allocation response that prioritizes the root growth at the expense of shoot growth at early development stages, especially in plants exposed to water stress (Schenk and Jackson 2002, Olmo et al. 2014, Ledo et al. 2017). Greater root to shoot development can reduce plant water loss while increasing water uptake capacity (Grossnickle 2012). These results support the idea of stressful environmental conditions outside the canopy protection and that plants show greater sensitivity to stress at early ontogenetic stages. Previous studies in this forest ecosystem have also observed positive effects of adult pine trees on the herbaceous layer diversity

at the landscape level (Madrigal-González et al. 2010). Similarly, germination and early survival of *P. pinaster* seedlings decreases with harvested basal area under Mediterranean conditions (González-Alday et al. 2009, Ruano et al. 2009).

The intense drought events strongly reduced sapling growth. Interestingly, the response of pine saplings varied not only between microhabitats but also between drought events. Saplings in open habitats showed the lowest growth resistance and resilience to the 2005 intense drought. In fact, saplings in open areas recovered their pre-drought growth rates 6 yr later than saplings under adults. These results reinforce our hypothesis about the facilitative role of conspecific adults in harsh environments. However, resilience to the 2012 drought was greater in saplings in open habitats than in those under adults. Ontogeny can determine the direction of plant–plant interactions (Miriti 2006). Our results suggest a shift from facilitative to negative interactions between conspecific adults and juveniles. Further evidence of this is that sapling growth rate saturated at a younger age under adults than in gaps. Facilitation usually prevails at early ontogenetic stages (Miriti 2006), where plants are more vulnerable to abiotic stress due to shallow roots and low carbon reserves (Niinemets 2010). Conversely, large plants demand more resources, which may increase competition (Wright et al. 2014).

Few studies have demonstrated the mechanisms underlying positive interactions between conspecifics in stressful environments (see Weltzin and McPherson 1999, Fajardo et al. 2006, Fajardo and McIntire 2010, Gimeno et al. 2015). Niche differences for avoiding the functional similarity among individuals of the same species rely on differences in size and other functional traits that change with ontogeny such as leaf size or gas exchange (Mediavilla and Escudero 2003). Tree size increases continuously, which modulates their future growth (Stephenson et al. 2014), and the productivity (Coomes et al. 2014) and interactions (Aakala et al. 2013) in forest communities. Size differences might imply niche differentiation in resource use (Zang et al. 2012). For instance, in situations where strong above-ground competition is predominant, size stratification in combination with distinct light yield strategies may lead to greater resource use efficiency and, therefore, greater packaging of

biomass and productivity (Forrester and Albrecht 2014). Nonetheless, size heterogeneity in monospecific forests can reduce stand productivity due to strong intraspecific asymmetric competition (Bourdier et al. 2016). This apparent contradiction might be solved by incorporating environment stress as a bottom-up force that hinders dominance through the reduction of above-ground biomass. Our results therefore highlight the importance of environmental stress for explaining the coexistence of adult and juvenile conspecifics in populations at the ecological limit of their distribution. In parallel, these results highlight an interesting paradox. In a scenario of increased frequency of intense droughts, benefits provided by adults during early ontogenetic stages might jeopardize the long-term performance of saplings. Greater sapling growth under adults might reduce root investment, which can compromise the ability of saplings to withstand repeated intense drought events (McDowell et al. 2008). In addition, a higher juvenile density below adult canopies than in open habitats (Appendix S1: Fig. S1) might also exacerbate the negative effect of repeated intense droughts due to greater competition. Future studies in similar harsh environments using spatially explicit approaches are needed to evaluate the long-term impacts of drought events on other demographic processes, such as mortality, to understand plant carbon dynamics and their importance in forest regeneration under scenarios of increased frequency of extreme drought.

Management implications and conclusions

Our results are interesting for the evaluation of the potential increase of intense drought events linked to climate change on the regeneration and restoration of pine forests under harsh environments. These ecosystems are vulnerable to tree cover loss because seedling recruitment strongly depends on facilitation by adult conspecific (González-Alday et al. 2009, Ruano et al. 2009, Rodríguez-García et al. 2011). Specifically, pre-existing adult trees can enhance survival and growth of juveniles after disturbances, such as intense droughts, fires, or tree harvesting, but also the success of active restoration measures such as seedling planting. However, our results also show a shift in the net effect of adults on sapling resilience to repeated intense drought events.

Higher frequency of intense droughts in such already water-limited forests might represent novel hazards that exceed our ability to manage regeneration through adult positive interactions. In this regard, the shelterwood thinning should be adapted to the reality of extreme event legacies on tree productivity through a spatially explicit planning that maximizes growth, short-term resilience, and recovery capacity after repeated perturbations. Further studies are therefore needed on the spatially explicit nature of the outcome of adult-juveniles plant interactions in a scenario of increased magnitude and frequency of drought.

ACKNOWLEDGMENTS

This work was supported by the project FUNDIVER (Spanish Ministry of Economy and Competitiveness, MINECO, Spain; CGL2015-69186-C2-2-R) and the network Remedinal-3 (S2013/MAE-2719) of the Community of Madrid. EA was supported by the postdoctoral grants “Ayudas para contratos para la formación postdoctoral” (FPDI-2013-15573) from the Ministry of Economy of the Spanish Government. We thank Liliana Ramos and Daniel Gómez-Sánchez for their valuable field assistance, and Kristen Grinager (official translation service of the Universidad de Alcalá) for the revision of the English language. The authors declare no conflict of interest.

LITERATURE CITED

- Aakala, T., S. Fraver, A. W. D’Amato, and B. J. Palik. 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. *Forest Ecology and Management* 308:128–135.
- Andivia, E., P. Villar-Salvador, L. Tovar, S. Rabasa, and J. M. Rey Benayas. 2017. Multiscale assessment of woody species recruitment in Mediterranean shrublands: facilitation and beyond. *Journal of Vegetation Science* 28:639–648.
- Armas, C., S. Rodríguez-Echeverría, and F. I. Pugnaire. 2011. A field test of the stress-gradient hypothesis along an aridity gradient. *Journal of Vegetation Science* 22:818–827.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:187–191.
- Bourdier, T., T. Cordonnier, G. Kunstler, C. Piedallu, G. Lagarrigues, and B. Courbaud. 2016. Tree size inequality reduces forest productivity: an analysis combining inventory data for ten European species and a light competition model. *PLoS ONE* 11: e0151852.
- Brooker, R. W. 2006. Plant–plant interactions and environmental change. *The New phytologist* 171:271–284.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Calama, R., R. Manso, M. E. Lucas-Borja, J. M. Espelta, M. Piqué, F. Bravo, C. del Peso, and M. Pardos. 2017. Natural regeneration in Iberian pines: a review of dynamic processes and proposals for management. *Forest Systems* 26:02.
- Castro, J., R. Zamora, J. A. Hódar, J. M. Gómez, and L. Gómez-Aparicio. 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restoration Ecology* 12:352–358.
- Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, R. Held, R. Jones, R. K. Kolli, W. K. Kwon, and R. Laprise. 2007. Regional climate projections. Pages 847–940 in S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller, editors. *Climate Change 2007: the physical science basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, University Press. Cambridge University Press, Cambridge, UK, and New York, New York, USA.
- Coomes, D. A., O. Flores, R. Holdaway, T. Jucker, E. R. Lines, and M. C. Vanderwel. 2014. Wood production response to climate change will depend critically on forest composition and structure. *Global Change Biology* 20:3632–3645.
- Cuesta, B., P. Villar-Salvador, J. Puértolas, J. M. Rey Benayas, and R. Michalet. 2010. Facilitation of *Quercus ilex* in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs. *Journal of Ecology* 98:687–696.
- Fajardo, A., J. M. Goodburn, and J. Graham. 2006. Spatial patterns of regeneration in managed uneven-aged ponderosa pine/Douglas-fir forests of Western Montana, USA. *Forest Ecology and Management* 223:255–266.
- Fajardo, A., and E. J. B. McIntire. 2010. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology* 99:642–650.
- Forrester, D. I., and A. T. Albrecht. 2014. Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. *Forest Ecology and Management* 328:94–102.

- García Fernández, J. 2004. La explotación tradicional en "La Tierra de Pinares" segoviana. *Investigaciones geográficas* 35:5–24.
- García-Cervigón, A. I., J. C. Linares, P. Aibar, and J. M. Olano. 2015. Facilitation promotes changes in leaf economics traits of a perennial forb. *Oecologia* 179:103–116.
- Gimeno, T. E., A. Escudero, and F. Valladares. 2015. Different intra- and interspecific facilitation mechanisms between two Mediterranean trees under a climate change scenario. *Oecologia* 177:159–169.
- Gómez-Aparicio, L. 2008. Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. *Journal of Ecology* 96:1128–1140.
- Gómez-Aparicio, L., J. M. Gómez, R. Zamora, and J. L. Boettinger. 2005. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *Journal of Vegetation Science* 16:191–198.
- Gómez-Aparicio, L., R. Zamora, J. Castro, and J. A. Hódar. 2008. Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivores? *Journal of Vegetation Science* 19:161–172.
- Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14:1128–1138.
- Gómez-Aparicio, L., M. A. Zavala, F. J. Bonet, and R. Zamora. 2009. Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients. *Ecological Applications* 19:2124–2141.
- Gómez-Sanz, V., and J. I. García-Vinas. 2011. Soil moisture spatio-temporal behavior of *Pinus pinaster* stands on sandy flatlands of central Spain. *Forest Systems* 20:293–302.
- González-Alday, J., C. Martínez-Ruiz, and F. Bravo. 2009. Evaluating different harvest intensities over understory plant diversity and pine seedlings, in a *Pinus pinaster* Ait. natural stand of Spain. *Plant Ecology* 201:211–220.
- Granda, E., A. Escudero, M. de la Cruz, and F. Valladares. 2012. Juvenile-adult tree associations in a continental Mediterranean ecosystem: no evidence for sustained and general facilitation at increased aridity. *Journal of Vegetation Science* 23:164–175.
- Grossnickle, S. C. 2012. Why seedlings survive: influence of plant attributes. *New Forests* 43:711–738.
- Herrero, A., and R. Zamora. 2014. Plant responses to extreme climatic events: a field test of resilience capacity at the southern range edge. *PLoS ONE* 9:e87842.
- Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975.
- Holzwarth, F., N. Ruger, and C. Wirth. 2015. Taking a closer look: disentangling effects of functional diversity on ecosystem functions with a trait-based model across hierarchy and time. *Royal Society Open Science* 2:140541.
- Jonasson, S., H. Medrano, and J. Flexas. 1997. Variation in leaf longevity of *Pistacia lentiscus* and its relationship to sex and drought stress inferred from leaf $\delta^{13}C$. *Functional Ecology* 11:282–289.
- Lafuente-Laguna, D., L. Rodríguez-Núñez, and J. P. Majada Guijo. 2012. *Pinus pinaster* Aiton. Pages 900–927 in J. Pemán García, R. Navarro Cerrillo, J. L. Nicolás Peragón, M. A. Prada Sáez and R. Serrada Hierro, editors. *Producción y manejo de semillas y plantas forestales*. Organismo Autónomo Parques Nacionales, Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, Spain.
- Lambers, H., F. S. Chapin, and T. L. Pons. 2008. *Plant physiological ecology*. Springer, New York, New York, USA.
- Ledo, A., et al. 2017. Tree size and climatic water deficit control root to shoot ratio in individual trees globally. *New Phytologist* 217:8–11.
- Lloret, F., E. G. Keeling, and A. Sala. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120:1909–1920.
- Lucas-Borja, M. E., D. Candel-Pérez, F. A. García Morote, T. Onkelinx, P. A. Tíscar, and P. Balandier. 2016. *Pinus nigra* Arn. ssp. *salzmannii* seedling recruitment is affected by stand basal area, shrub cover and climate interactions. *Annals of Forest Science* 73:649–656.
- Madrigal-González, J., J. A. García-Rodríguez, A. Puerto-Martín, B. Fernández-Santos, and P. Alonso-Rojo. 2010. Scale-dependent effects of pines on the herbaceous layer diversity in a semi-arid Mediterranean ecosystem. *Community Ecology* 11:77–83.
- Madrigal-González, J., A. Herrero, P. Ruiz-Benito, and M. A. Zavala. 2017. Resilience to drought in a dry forest: insights from demographic rates. *Forest Ecology and Management* 389:167–175.
- Madrigal-González, J., and M. A. Zavala. 2014. Competition and tree age modulated last century pine growth responses to high frequency of dry years in a water limited forest ecosystem. *Agricultural and Forest Meteorology* 192–193:18–26.
- Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97:199–205.

- Maestre, F. T., and J. Cortina. 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society B: Biological Sciences* 271:S331–S333.
- McDowell, N., et al. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* 178:719–739.
- McIntire, E. J. B., and A. Fajardo. 2014. Facilitation as a ubiquitous driver of biodiversity. *New Phytologist* 201:403–416.
- Mediavilla, S., and A. Escudero. 2003. Mature trees versus seedlings: differences in leaf traits and gas exchange patterns in three co-occurring Mediterranean oaks. *Annals of Forest Science* 60:455–460.
- Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94:973–979.
- Moro, M. J., F. I. Pugnaire, P. Haase, and J. Puigdefabregas. 1997. Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. *Ecography* 20:175–184.
- Niinemets, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* 260:1623–1639.
- Nyland, R. D. 2016. *Silviculture: concepts and applications*, Third edition. Waveland Press, Long Grove, Illinois, USA.
- Ogaya, R., and J. Peñuelas. 2006. Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*. *Biologia Plantarum* 50:373–382.
- Olmo, M., B. Lopez-Iglesias, and R. Villar. 2014. Drought changes the structure and elemental composition of very fine roots in seedlings of ten woody tree species. Implications for a drier climate. *Plant and Soil* 384:113–129.
- Padilla, F. M., and F. I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment* 4:196–202.
- Prieto, I., F. M. Padilla, C. Armas, and F. I. Pugnaire. 2011. The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics* 13:181–187.
- Prinzing, A., W. A. Ozinga, M. Brändle, P.-E. Courty, F. Hennion, C. Labandeira, C. Parisod, M. Pihain, and I. V. Bartish. 2017. Benefits from living together? Clades whose species use similar habitats may persist as a result of eco-evolutionary feedbacks. *New Phytologist* 213:66–82.
- Puerta-Piñero, C., J. M. Gómez, and F. Valladares. 2007. Irradiance and oak seedling survival and growth in a heterogeneous environment. *Forest Ecology and Management* 242:462–469.
- Rodríguez-García, E., G. Gratzner, and F. Bravo. 2011. Climatic variability and other site factor influences on natural regeneration of *Pinus pinaster* Ait. in Mediterranean forests. *Annals of Forest Science* 68:811–823.
- Rolo, V., E. Andivia, and R. Pokorný. 2015. Response of *Fagus sylvatica* and *Picea abies* to the interactive effect of neighbor identity and enhanced CO₂ levels. *Trees - Structure and Function* 29:1459–1469.
- Ruano, I., V. Pando, and F. Bravo. 2009. How do light and water influence *Pinus pinaster* Ait. germination and early seedling development? *Forest Ecology and Management* 258:2647–2653.
- Schenk, H. J., and R. B. Jackson. 2002. Rooting depths, lateral root spreads and belowground aboveground allometries of plants in water limited ecosystems. *Journal of Ecology* 90:480–494.
- Stephenson, N. L., et al. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507:90–93.
- Verdu, M., L. Gomez-Aparicio, and A. Valiente-Banuet. 2012. Phylogenetic relatedness as a tool in restoration ecology: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences* 279:1761–1767.
- Weltzin, J. F., and G. R. McPherson. 1999. Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones. *Ecological Monographs* 69:513–534.
- Wright, A., S. A. Schnitzer, and P. B. Reich. 2014. Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecology* 95:2213–2223.
- Zang, C., H. Pretzsch, and A. Rothe. 2012. Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees - Structure and Function* 26:557–569.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, New York, USA.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2282/full>