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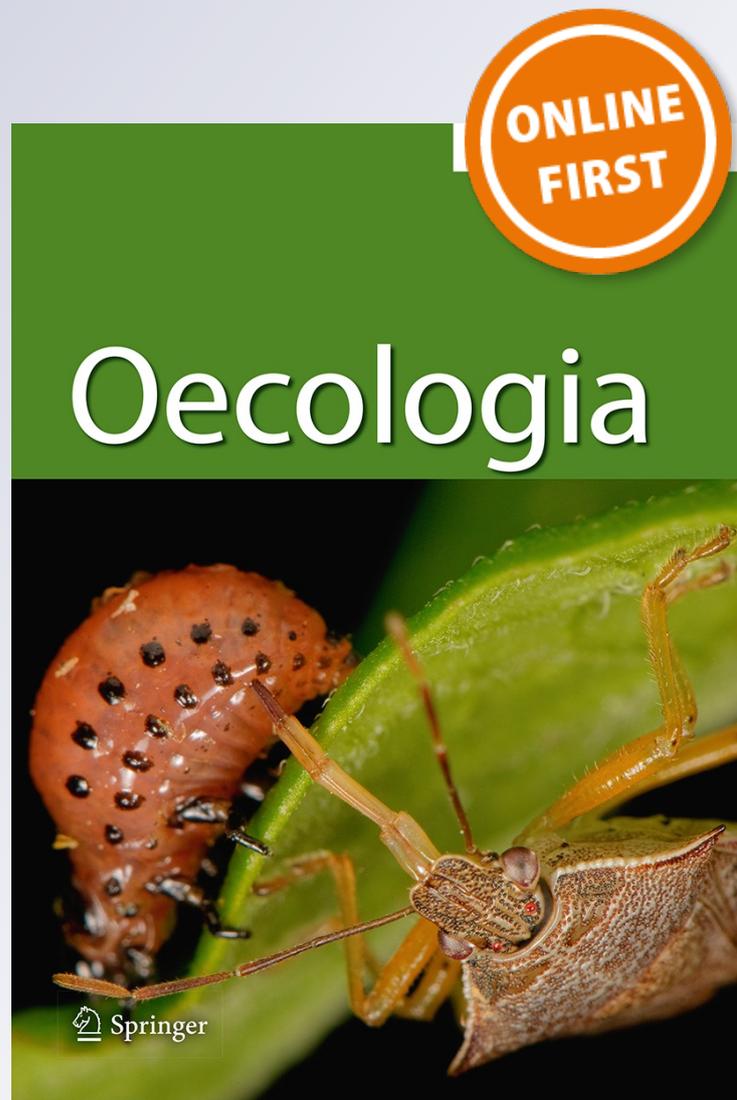
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Different intra- and interspecific facilitation mechanisms between two Mediterranean trees under a climate change scenario

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Abstract In harsh environments facilitation alleviates biotic and abiotic constraints on tree recruitment. Under ongoing drier climate change, we expect facilitation to increase as a driver of coexistence. However, this might not hold under extreme abiotic stress and when the outcome depends on the interaction with other drivers such as altered herbivore pressure due to land use change. We performed a field water-manipulation experiment to quantify the importance of facilitation in two coexisting Mediterranean trees (dominant *Juniperus thurifera* and coexisting *Quercus ilex* subsp. *ballota*) under a climate change scenario. Shifts in canopy dominance favouring *Q. ilex* could be based on the extension of heterospecific facilitation to the detriment of conspecific alleviation. We found that saplings of both species transplanted under the canopy of nurse trees had greater survival probability, growth and photochemical efficiency. Intra- and interspecific

facilitation mechanisms differed: alleviation of abiotic stress benefited both species during summer and *J. thurifera* during winter, whereas browsing protection was relevant only for *Q. ilex*. Facilitation was greater under the dry treatment only for *Q. ilex*, which partially agreed with the predictions of the stress gradient hypothesis. We conclude that present rainfall availability limits neither *J. thurifera* nor *Q. ilex* establishment. Nevertheless, under current global change scenarios, imposing increasing abiotic stress together with altered herbivore browsing, nurse trees could differentially facilitate the establishment of *Q. ilex* due to species-specific traits, i.e. palatability; drought, heat and cold tolerance, underlying species differences in the facilitation mechanisms and eventually triggering a change from pure juniper woodlands to mixed formations.

Keywords *Juniperus thurifera* · Photochemical efficiency · Species interactions · *Quercus ilex* subsp. *ballota*

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Introduction

Plant-plant interactions shape community composition and dynamics (Michelet et al. 2006); for example, competitive exclusion limits species number and abundance during colonization whereas facilitation can expand the regeneration niche of a species (Callaway 1995; Vellend 2008; Martorell and Freckleton 2014). The relative importance of competition and facilitation in each realized community is modulated by environmental conditions: under low levels of abiotic stress, competition prevails over facilitation whereas under harsh abiotic conditions, facilitation dominates, as nurse plants alleviate the abiotic constraints underneath their canopy, especially in the case of early life stages

(Bertness and Callaway 1994; Brooker et al. 2008). Under current climate change scenarios imposing greater abiotic stress in large regions of the world (IPCC 2014), we would expect the importance of facilitation to increase in these regions (Callaway et al. 2002; Brooker 2006). However, the final outcome of plant–plant interactions is far from trivial since it has been reported to be context dependent (Maestre et al. 2009; Saccone et al. 2009). Michelet et al. (2006) suggested that the outcome of biotic interaction depends not only on the level of abiotic stress, but also on the competitive ability and stress tolerance of the interacting species. Later, Maestre et al. (2009) expanded this framework to include the type of imposed stress (resource or non-resource limiting) and predicted that facilitation would increase along a non-resource-limiting gradient (e.g. temperature) or when the facilitated species was stress tolerant. In contrast, facilitation would decline towards both ends of a resource-limited gradient (e.g. water), or when interacting species had similar competitive abilities (Holmgren and Scheffer 2010).

In addition to climate change, the impact of other global change drivers further complicates the ability to predict the outcome of plant–plant interactions. Currently, increasing levels of abiotic stress, due to climate change, co-occur with changes in land use and the corresponding shifts in herbivore pressure (Smit et al. 2009; Verwijmeren et al. 2013). This is the case in open woodlands of Spanish juniper (*Juniperus thurifera*), tertiary relict formations confined to the western Mediterranean Basin (Gauquelin et al. 1999). These iconic Mediterranean woodlands are semi-natural formations, maintained to some extent by human intervention (Olano et al. 2008) and often limit and coexist with holm oak (*Quercus ilex* subsp. *ballota*) woodlands (Gauquelin et al. 1999; Blanco 2005). Establishment of holm oak saplings in *J. thurifera* woodlands is limited by abiotic, i.e. cold temperatures and poor soils (Corcuera et al. 2004), and biotic constraints, i.e. propagule arrival and herbivory (DeSoto et al. 2010). Livestock grazing, in particular, plays a key role controlling the establishment of competing species with more palatable seedlings in *J. thurifera* woodlands. Indeed, previous studies have shown increased recruitment of *Quercus* and *Pinus* spp. following decreased domestic grazing pressure (DeSoto et al. 2010), which indicates canopy shifts in these woodlands. On the other hand, abandonment of traditional practices increases the available surface area for *J. thurifera* woodland expansion to the expense of old fields (Gimeno et al. 2012a).

Facilitation plays a crucial role in cold continental semi-arid Mediterranean steppes, where multiple co-occurring stresses constrain tree recruitment. Montesinos et al. (2007) and Gimeno et al. (2012b) have shown that in *J. thurifera* woodlands, adult trees effectively facilitate the establishment of conspecific saplings. In addition, Granda et al.

(2012) found that heterospecific seedlings occurred under the canopy of *J. thurifera* adults, suggesting effective interspecific facilitation. Yet, we expect intra- and interspecific facilitation mechanisms to greatly differ due to species' physiological tolerance and functional traits (Liancourt et al. 2005; Maestre et al. 2009; Saccone et al. 2009). Juniper canopies facilitate establishment by providing a milder microclimate and richer soils that benefit both conspecific and competing saplings (Gomez-Aparicio et al. 2005; Smit et al. 2008; Valladares et al. 2008). In addition, *J. thurifera* foliage is loaded with secondary metabolites (Barrero et al. 2004) that detract herbivores and protect more palatable species (*Quercus* spp.) from browsing. Abandonment of traditional practices decreases browsing by domestic herbivores (goats and sheep) but this effect is partially counterbalanced by increased populations of wild herbivores such as wild boar and roe deer (Mangas and Rodriguez-Estival 2010). This occurs under a climate change scenario imposing more intense abiotic stress of two kinds: resource limiting (reduced precipitation during the spring and summer) and non-resource limiting [warmer and more extreme temperatures (IPCC 2014)]. Under increasing abiotic stress, the importance of facilitation should increase even more in scenarios with significant herbivore pressure (Smit et al. 2009; Verwijmeren et al. 2013), although the converse has been found for some herbaceous species in mowing experiments (Maalouf et al. 2012; Le Bagousse-Pinguet et al. 2014). Yet, the extent of facilitation would be limited under extreme abiotic stress (Michelet et al. 2006; Maestre et al. 2009; Holmgren and Scheffer 2010; Verwijmeren et al. 2013). Overall, current global change scenario profoundly affects the interaction between these two tree species, and predictions regarding the composition and functioning of these Mediterranean continental woodlands are very uncertain, especially when taking into account that in the particular case of holm oak, a certain level of negative density dependence during earlier life stages has been suggested (Granda et al. 2012).

Both competition and facilitation are often inferred from the analyses of their imprints on the spatial structure of the population (Franco and Nobel 1989). In the past decade, this approach has experienced a great boom due to the refinement of spatial analyses techniques (Wiegand et al. 2003). Nevertheless, analyses of spatial structure usually lack insights into the underlying mechanism of plant–plant interactions. On the other hand, experiments under controlled conditions allow one to test for specific mechanisms underlying competition [e.g. allelopathy (McKinley and Van Auken 2004)] and facilitation [e.g. soil amelioration (Rodriguez-Echeverria et al. 2013)], but lack realism. Field experiments lie in between purely observational and experimental studies and allow for more realistic hypothesis testing (Gomez-Aparicio et al. 2005; Montesinos et al. 2007;

Matesanz et al. 2009; Soliveres et al. 2010). Here, we performed a water-manipulation experiment in a *J. thurifera* woodland, to compare the early performance of *J. thurifera* with potentially competing holm oak, under different levels of a key resource (water) that is expected to be severely modified by climate change. We tested for the role of facilitation by experimentally considering microhabitat heterogeneity related to *J. thurifera* canopies to understand potential changes in community composition in these woodlands under ongoing global change. We hypothesised that: (1) adult trees facilitate the recruitment of both *Q. ilex* subsp. *ballota* and *J. thurifera* by increasing their survival probability and physiological status; but (2) with differences in the underlying mechanisms of intra- and interspecific facilitation linked to species-specific morphological (palatability) and physiological traits (heat, cold and drought tolerance); and finally (3) the facilitation intensity increases with decreasing water availability in both species.

Materials and methods

Study sites and species

The Spanish juniper, *Juniperus thurifera* L. (Cupressaceae) is a dioecious tree species with a relict Tertiary distribution of the western Mediterranean Basin. It is usually the dominant species in low-density woodlands on poor, shallow, rocky soils (both acidic and calcareous, although more abundant in the latter), at a variety of altitudes (300–3200 m a.s.l.) in climates that range from arid to sub-humid Mediterranean types (Gauquelin et al. 1999).

Holm oak, *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. (Fagaceae), is an evergreen, drought-adapted tree-shrub, found throughout the western Mediterranean Basin (Castroviejo et al. 1993). Holm oak is found from cold semi-arid to temperate humid Mediterranean climates and it coexists with deciduous oaks and some conifers in the coldest and moistest limits of its distribution. In most parts of the Iberian Peninsula, holm oak is largely indifferent to soil type (Terradas 1999).

The study was conducted at the Alto Tajo Natural Park, and surroundings, in Central Spain. On the study area, the soils are shallow, poorly developed and formed from Cretaceous and Jurassic limestone. The climate is continental Mediterranean with hot and dry summers and cold and cloudless winters. Mean \pm SE annual rainfall is 499.7 ± 14.4 mm and the mean annual temperature is 10.2 ± 0.1 °C (Molina de Aragón, $40^{\circ}50'40''\text{N}$, $1^{\circ}53'07''\text{W}$, 1063 m a.s.l., 1951–2009 period; data provided by the Spanish Agencia Estatal de Meteorología). In this area, the lower altitudes (700–950 m a.s.l.) are dominated by open woodlands of *Q. ilex* subsp. *ballota*, on south-facing slopes,

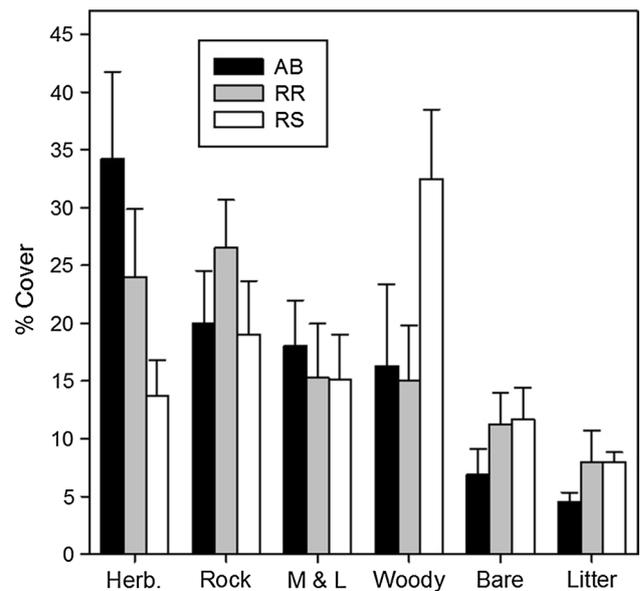


Fig. 1 Mean \pm SE ($n = 10$) percentage surface covered by herbaceous species (*Herb.*), rock, mosses and lichens (*M & L*), woody species, bare soil and litter at each of the study sites: Ablanque (*AB*), Ribarredonda (*RR*) and Río Salado (*RS*)

and by *Pinus nigra* Arn., on north-facing slopes. These woodlands are delimited by open woodlands of *J. thurifera* that dominate the upper plateaus [950–1400 m a.s.l. (Valldares et al. 2008)].

Experimental design and plant material

We selected three sites in mature woodlands where *J. thurifera* was the dominant species (Gimeno et al. 2012b): Ablanque (*AB*; $40^{\circ}53'32''\text{N}$, $2^{\circ}13'34''\text{W}$, 1110 m a.s.l.), Ribarredonda (*RR*; $40^{\circ}52'10''\text{N}$, $2^{\circ}17'47''\text{W}$, 1030 m a.s.l.) and Río Salado (*RS*; $40^{\circ}50'32''\text{N}$, $2^{\circ}18'1''\text{W}$, 975 m a.s.l.). At each site, we established study plots in two types of microhabitat: open interspaces with no trees within a radius of 4 m (open treatment), and under the canopy of adults (height >2 m) of *J. thurifera* (canopy treatment). In February 2008, we transplanted 304 *J. thurifera* saplings and 149 *Q. ilex* subsp. *ballota* saplings. We transplanted five saplings at each open plot and three to five saplings at each canopy plot. Within each plot, plants were 50–75 cm from each other. The number of plots varied among study sites due to differences in microtopography and sizes of available nurse trees (Table 1). Planting holes were dug manually and were 30-cm depth \times 30-cm diameter.

J. thurifera saplings were 3 years old and were obtained from Viveros El Fleix (Buñol, Valencia). Plants were grown in an open-air nursery ($39^{\circ}25'4.9''\text{N}$, $0^{\circ}47'29.1''\text{W}$, 365 m a.s.l.) exposed to a mean annual temperature of 13 °C and a mean annual total rainfall of 536 mm. Seeds were sown in a

mixture of peat (60 %) and coconut rind (40 %) in forestry trays and were treated with Alagmix (LIDA Química, Almussafes, Valencia). *Q. ilex* subsp. *ballota* saplings were obtained from a previous glasshouse experiment. Saplings were grown from acorns collected in six different localities in Spain. Seven months before being transplanted, they had been subjected to three different experimental treatments [see Gimeno et al. (2009) for a detailed characterization of the growth conditions, origins and experimental treatments]. Plants from different origins and subjected to different experimental treatments were randomly allocated to different study sites and microhabitats.

In spring 2009, we applied a watering treatment with two different levels: mesic (watered plants) and dry (non-watered plants). Since spring and summer 2009 were exceptionally dry, non-watered (dry treatment) plants received ambient rainfall, equivalent to future drier scenarios (due to very dry spring conditions), and watered plants (mesic treatment) received ambient rainfall plus the added water, equivalent to that of a typical year (Matesanz et al. 2009). The watering treatment was performed during May and June 2009. We chose these months for two reasons: first, the projections of the most likely future climate scenario for the Mediterranean region indicate significant reductions in the mean annual rainfall, primarily with decreasing precipitation during spring and summer (IPCC 2014). Actually, 2009 was warmer and drier than a usual year in the study area, particularly during the spring and summer (Fig. S1). Second, spring is the season during which most species inhabiting the Mediterranean areas acquire most of their resources for growth and reproduction (Mitrakos 1980). In particular, *J. thurifera* growth peaks during these months (Camarero et al. 2010) and it is sensitive to spring precipitation (Bertaudiere et al. 1999; Rozas et al. 2009; Gimeno et al. 2012c; Olano et al. 2013). For *Q. ilex*, successful establishment is determined by survival up to the first months after emergence (in the spring), due to their high vulnerability to drought (Villar-Salvador et al. 2004). The watering treatment was performed only in sites RR and RS, due to the null survival of holm oak observed in site AB after 2008. At each study site we randomly assigned each plot to one watering treatment. Irrigation consisted of adding 1–1.5 L of water per plant at each irrigation event (see Fig. S2 for a detailed description of the irrigation experiment), water addition was reduced by 25 % in canopy plots to simulate canopy rainfall interception (Breshears et al. 1997; Valladares et al. 2008). Since our approach was dependent on current weather conditions we checked daily for rainfall events and consequently adjusted our watering treatments. Water was carefully added with a watering can to avoid runoff and to maximize absorption by the soil. A 50 × 50-cm rigid frame was placed around each

plant so that the entire surface was watered; each application was equivalent to 4- to 6-mm rainfall events. Irrigation was carried out at 3- to 5-day intervals.

Abiotic characterization of the experimental treatments

We visually estimated percentages of ground surface components (bare soil, rock, lichen and moss, litter, woody species and herbaceous species) in ten random squares (0.25-m² surface area) placed in open inter-spaces with no trees within a 4-m radius, at each site (Fig. 1). Climatic conditions from 2008 to 2009 at the study area were monitored continuously with a HOBO weather station close to the study sites (40°49′08″N, 2°12′47″W, 1200 m a.s.l.). The station incorporated a rain gauge (RGA-MOXX), a photosynthetically active radiation (PAR) sensor (S-LIA-M003) and a temperature sensor (12-bit Temperature Smart Sensor). Readings of each sensor were recorded every 30 min with a data logger (HOBO H21-001; all components from HOBO Onset Computer Corporation, Bourne, MA).

Light availability was estimated at each plot with hemispherical photographs (Rich 1990; Valladares and Guzman 2006). Photographs were taken at 40-cm height (similar to that of the plants) with a digital camera (CoolPix 995; Nikon, Tokyo), set horizontally on a tripod, coupled to a fish-eye lens of 180° field of view (FCE8; Nikon). Photographs were processed with the software Hemiview version 2.1 (Delta-T Devices, Burwell, UK). We estimated the proportion of direct (direct site factor; DSF), indirect (or diffuse, indirect site factor; ISF) and total (global site factor; GSF) radiation reaching each plot, relative to a location with no sky obstruction. Mean daily solar irradiance (mol PAR m⁻² day⁻¹) at each plot was calculated by multiplying GSF by measured daily PAR (Valladares and Guzman 2006).

In June 2009 we collected three soil sub-samples, between 5- and 15-cm depth, of ca. 200 g from each plot, with a spade (avoiding major rocks); these were thoroughly mixed, air-dried and sieved (2-mm grain). To measure total N and P content, soil samples were first digested according to the Kjeldhal method and then the N and P content measured with an automatic wet chemistry analyser (Skalar 4000 SAN System, Segmented Flow Analyzer; Skalar, Breda, the Netherlands). Organic C content was estimated from the soil organic matter, determined by combustion in a muffle furnace (Walkley and Black 1934). Na, K, Ca and Mg were first extracted with ammonium acetate at pH 7 and then determined spectrophotometrically. These analyses were performed with an elemental analyser (PLASMA ICP Optima 4300 DV; Perkin-Elmer, Waltham, MA) at the service of general analyses of the Institute of Agricultural Sciences (ICA-CSIC, Madrid).

Ecophysiological and morphological measurements

Survival censuses were performed every 15 days for the first 9 months, monthly for the following 15 months, and in June and September 2010. We labelled as dead those individuals presenting no photosynthetically active leaves and exhibiting loss of flexibility in the branches. We also recorded the cause of mortality: plants either dried out or were browsed by macro-herbivores. Maximum plant height was measured three times for all plants: right after transplant (H1), at the beginning (H2) and at the end (H3) of the spring 2009 (when the watering experiment was performed). Three growth rates were calculated: growth during 2008 (H2-H1), growth during the spring 2009 (H3-H2) and total growth (H3-H1). Only positive growth in height was considered for the analyses: data from browsed, broken or dry plants were excluded.

Predawn maximum photochemical efficiency of photosystem II (F_v/F_m) was measured at four different measuring campaigns (beginning and end of the spring and summer and mid-summer) in 2 consecutive years (2008, 2009). F_v/F_m is a dynamic estimator of plant physiological status that indicates photoinhibitory damage in response to temperatures, light and/or water stress (Valladares and Pearcy 1997; Maxwell and Johnson 2000). F_v/F_m was measured with a FMS-2 fluorometer (Hansatech, UK) in 20–25 *J. thurifera* and in ten to 15 *Q. ilex* subsp. *ballota* saplings per combination of study site and microhabitat. For each campaign, measured plants were randomly selected within each treatment combination.

Statistical analyses

Differences in F_v/F_m among study sites and between microhabitats and species were analysed with linear models with the following factors: study site, species, microhabitat and the interaction between the latter two. Only the data from the three first measuring campaigns of F_v/F_m from site AB were used due to the null survival of *Q. ilex* subsp. *ballota* saplings in this site. To test for differences in growth (only sites RR and RS), we performed a similar model, but controlled for the effect of plant size by including plant height (at the start of the experiment) as an additional fixed predictor. A similar model was used to test for the effect of the watering treatment (data only from 2009 and sites RS and RR) and its interactions with microhabitat and species on F_v/F_m and growth. We used type III sum of squares and the maximum likelihood estimator; significant differences among groups were analysed with post hoc Tukey's honest significant differences test.

To test for differences in survival we estimated the survival probability curves of each combination of species and microhabitat with the Kaplan–Meier product limit method.

Differences among them were assessed with a χ^2 multiple comparison test. Log-rank tests were used afterward to test for significant differences in survival between treatment combinations and study sites for all possible pairwise comparisons (Pyke and Thompson 1986). Cumulative survival (at the plot level, at the end of the first summer and at the end of the experiment) and browsing frequency (among dead plants) were analysed with generalized non-linear models. We adjusted a binomial distribution and used the logit as link function. We modelled survival and browsing including the following predictors: study site, species, microhabitat and the interaction between the latter two.

Since *Q. ilex* subsp. *ballota* seedlings came from a previous experiment (Gimeno et al. 2009), we performed additional main effects ANOVAs to test for the effect of the locality of origin saplings and the previous experimental treatment on the different response variables (F_v/F_m , growth and survival); we could not test for the interactive effects with the different field treatments (study site, microhabitat and watering) due to reduced sample size. We did not find any significant effect ($P > 0.05$) of the population of origin or of the previous experimental treatment (data not shown). All analyses were performed with Statistica 6.0 (StatSoft, Tulsa, OK).

Results

Abiotic environment: light and soil nutrient concentration

The three study sites had similar percentages of surface area covered by bare soil, rock, lichen and moss, litter, woody and herbaceous species (Fig. 1; $F < 2.5$ and $P > 0.2$, for all types of cover). Open and canopy microhabitats differed significantly in light availability: ISF, DSF and mean daily solar irradiance were higher in the open than under the canopy ($F > 1000$, $P < 0.001$). We found no significant differences in light availability among study sites or between planted microsites of species (Table S2). Nutrient concentrations were consistently higher under the canopy than in the open in all sites and for both species. Soils from *J. thurifera* and *Q. ilex* plots differed in [Na], [Mg] and [P] and in the C/N ratio. Soil [Na], [Mg], [Ca], [N], [P], [C_{org}] varied among localities (Tables S1, S2).

Survival and growth

Given the low mortality rates observed after the watering treatment (1.0 ± 0.3 dead plants per treatment combination 1 year after the watering treatment, mean \pm SE, $n = 16$) we did not analyse the effect of the watering treatment on the survival function. Survival curves differed between species and microhabitats (overall test, $\chi^2 = 53.28$, $P < 0.001$).

Fig. 2 **a** Survival probability functions through time and **b** mean (+SE) probability of being browsed for *Juniperus thurifera* (squares) and *Quercus ilex* subsp. *ballota* (circles) in the open (open symbols) and under the canopy (closed symbols). **a** Different letters indicate significant differences ($P < 0.05$) among treatment combinations

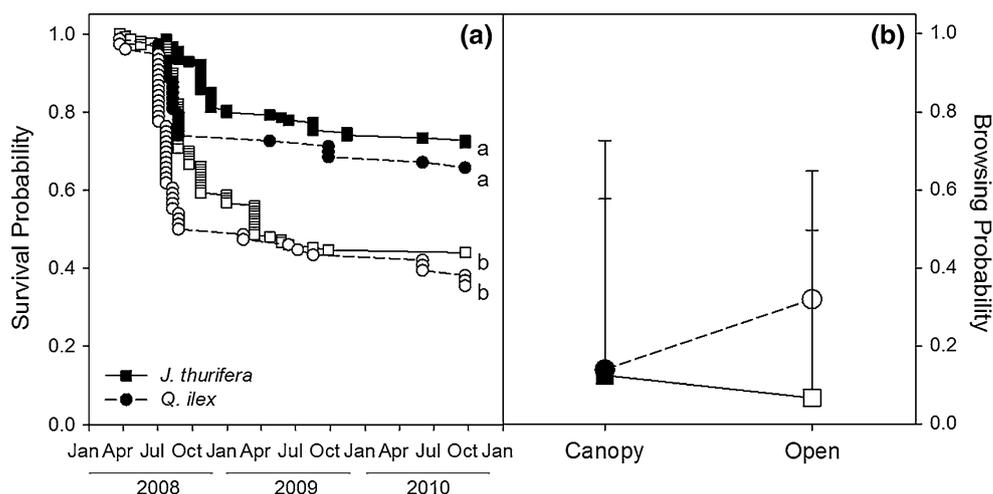


Table 1 Number of plots and plants of each microhabitat type (canopy, open) and species per site

Site	Microhabitat	Species	Plots	Plants
Ablanque	Canopy	<i>Juniperus thurifera</i>	19	51
		<i>Quercus ilex</i>	9	20
	Open	<i>J. thurifera</i>	10	50
		<i>Q. ilex</i>	5	25
Ribarredonda	Canopy	<i>J. thurifera</i>	17	53
		<i>Q. ilex</i>	9	26
	Open	<i>J. thurifera</i>	10	51
		<i>Q. ilex</i>	5	26
Rio Salado	Canopy	<i>J. thurifera</i>	10	50
		<i>Q. ilex</i>	7	26
	Open	<i>J. thurifera</i>	10	49
		<i>Q. ilex</i>	5	26

Pairwise log-rank tests showed that saplings of both species died faster in the open than under the canopy ($\chi^2 = 35.7$, $P < 0.001$; Fig. 2). Survival probability decreased drastically after the first summer, particularly in the open: survival probability at the end of the first summer was significantly higher under the canopy ($86 \pm 2\%$) than in the open ($60 \pm 2\%$, $\chi^2 = 31.9$, $P < 0.001$). *J. thurifera* survival probability at the end of the first summer was significantly higher ($\chi^2 = 20.1$, $P < 0.001$, $84 \pm 2\%$ for *J. thurifera* vs. $63 \pm 2\%$ for *Q. ilex* subsp. *ballota*). The shape of the survival curves and final survival probabilities (at the end of the first summer and at the end of the experiment) differed among sites ($\chi^2 > 50$ and $P < 0.001$ in all cases). This was due to null survival of *Q. ilex* subsp. *ballota* saplings in one of the study sites (Ablanque). The majority of plants died because they dried out (84.2%). The probability of being browsed was higher for *Q. ilex* subsp. *ballota* than for *J.*

thurifera ($\chi^2 = 9.8$, $P = 0.002$; Fig. 2). We found that there was a significant interaction between species and microhabitat in the proportion of dead browsed plants ($\chi^2 = 4$, $P = 0.045$; Fig. 2): the probability of being browsed decreased from open to canopy microhabitats only for *Q. ilex* subsp. *ballota*.

We found significant differences in growth in height in 2008 between species (Table 1). *J. thurifera* saplings grew more, when controlling for plant size (effect of plant size, $F = 6.45$, $P = 0.012$), although *Q. ilex* subsp. *ballota* saplings grew more in absolute terms (*Q. ilex*, 1.84 ± 0.25 ; *J. thurifera*, 1.68 ± 0.20 cm, mean \pm SE, $n = 84$ and 168 , respectively). There was a significant interaction of species \times microhabitat: species differences in growth in 2008 were higher in the open than under the canopy (Table 1). In spring 2009, watered saplings grew more than non-watered saplings (mesic, 2.01 ± 0.33 ; dry, 0.87 ± 0.14 cm, $n = 101$ and 88). Noteworthy, the effect of the watering treatment on growth in spring 2009 varied between microhabitats and species, i.e. there was a significant microhabitat \times watering interaction and a marginally significant species \times watering interaction (Table 2). Between microhabitats, the overall effect of the watering treatment was greater for saplings under the canopy (mesic, 2.77 ± 0.49 ; dry, 0.90 ± 0.18 cm, $n = 64$ and 59). Between species, *Q. ilex* subsp. *ballota* (mesic, 3.23 ± 0.63 ; dry, 1.03 ± 0.24 cm, $n = 40$ and 33) responded more positively to water addition than *J. thurifera* (mesic, 1.22 ± 0.31 ; dry, 0.77 ± 0.16 cm, $n = 61$ and 55). Total growth in height was highest in watered plants (Fig. 3; Table 1) and under the canopy (Fig. 3; Table 1). The effect of the microhabitat on total growth was species dependent: differences between microhabitats were higher in *Q. ilex* subsp. *ballota* than in *J. thurifera* (Fig. 3; Table 1). Study sites RR and RS did not differ significantly in plant growth (Table 1).

Table 2 Results of the statistical analyses of the effects of the different study sites, species, microhabitat and watering treatment and their interactions on growth in height and on maximum photochemical efficiency (F_v/F_m), on different dates

Variable	Study site	Species (Sp.)	Microhabitat (MH)	Watering (W)	Sp. × MH	Sp. × W	MH × W	Sp. × MH × W		
Growth	2008	<i>F</i>	1.96	3.94	0.57	5.74				
		<i>P</i>	0.163	<i>0.048</i>	0.45	<i>0.017</i>				
	Spring 2009	<i>F</i>	3.86	1.37	12.49	4.88	1.62	3.86	8.43	0.25
		<i>P</i>	<i>0.051</i>	0.243	<i>0.001</i>	<i>0.028</i>	0.205	<i>0.051</i>	<i>0.004</i>	0.618
	Total	<i>F</i>	1.07	0.16	3.85	6.78	4.71	0.68	0.69	2.66
		<i>P</i>	0.302	0.685	<i>0.051</i>	<i>0.010</i>	<i>0.031</i>	0.412	0.407	0.105
F_v/F_m	15 May 2008	<i>F</i>	16.13	8.26	63.81	0.23				
		<i>P</i>	<i><0.001</i>	<i>0.004</i>	<i><0.001</i>	0.629				
	1 July 2008	<i>F</i>	8.24	5.2	46.22	2.96				
		<i>P</i>	<i><0.001</i>	<i>0.024</i>	<i><0.001</i>	0.087				
	9 August 2008	<i>F</i>	28.85	1.04	50.87	0.42				
		<i>P</i>	<i><0.001</i>	0.31	<i><0.001</i>	0.516				
	10 September 2008	<i>F</i>	32.07	10.35	30.95	4.55				
		<i>P</i>	<i><0.001</i>	<i>0.002</i>	<i><0.001</i>	<i>0.035</i>				
	5 May 2009	<i>F</i>	<i><0.01</i>	8.46	12.17	0.01	0.98	2.76	1.18	0.98
		<i>P</i>	1	<i>0.004</i>	<i>0.001</i>	0.934	0.324	0.099	0.279	0.325
	23 June 2009	<i>F</i>	12.39	10.81	26.13	0.19	0.4	0.18	0.82	0.89
		<i>P</i>	<i>0.001</i>	<i>0.001</i>	<i><0.001</i>	0.6674	0.53	0.676	0.366	0.348
	25 August 2009	<i>F</i>	28.77	11.69	47.19	4.72	2.64	0.3	3.66	0.53
		<i>P</i>	<i><0.001</i>	<i>0.001</i>	<i><0.001</i>	<i>0.032</i>	0.107	0.588	<i>0.058</i>	0.466
	5 October 2009	<i>F</i>	28.76	12.93	18.14	1.53	8.91	2.23	1.4	2.02
		<i>P</i>	<i><0.001</i>	<i><0.001</i>	<i><0.001</i>	0.218	<i>0.003</i>	0.138	0.239	0.157

Significant effects ($P < 0.05$) are highlighted in italics

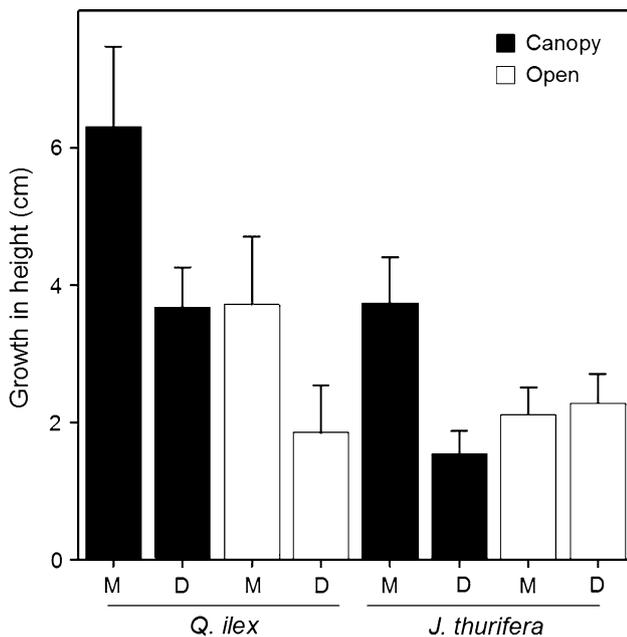
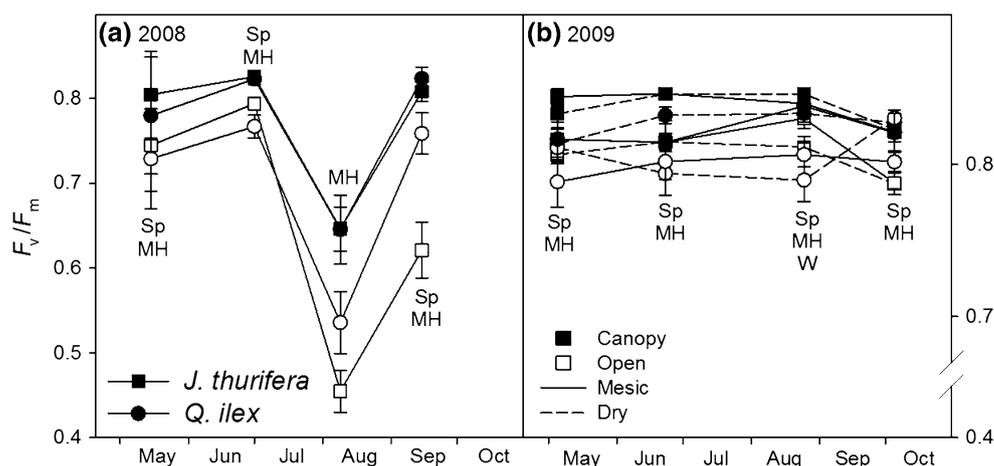


Fig. 3 Mean (+SE; n varied according to survival and treatment combination) total growth in height of *J. thurifera* and *Q. ilex* saplings in the open (open bars) and under the canopy (closed bars) and for different watering treatments [mesic (M) and dry (D)]

Physiological measurements

The microhabitat had a significant effect on predawn F_v/F_m . Plants under the canopy had higher F_v/F_m than plants in the open, on all dates (Table 1; Fig. 4). Species differed significantly in mean F_v/F_m (except in August 2008): *J. thurifera* had higher F_v/F_m than *Q. ilex* subsp. *ballota* at the beginning and end of spring and at mid-summer (only in 2009), whereas the opposite occurred at the end of the summer (Table 2; Fig. 4). At the end of the summer, the difference between saplings under the canopy and in the open was higher in *J. thurifera* than in *Q. ilex* subsp. *ballota* saplings, i.e. there was a significant species × microhabitat interaction on F_v/F_m at the end of the summer, in both years (Table 1). Non-watered plants had higher F_v/F_m in mid-summer than watered plants (Table 2; Fig. 4). Finally, we found that there was a marginally significant (Table 2) microhabitat × watering interaction: differences between watered and non-watered plants were higher in the open than under the canopy. We found significant differences in predawn F_v/F_m among study sites for all measurement campaigns, except in May 2009 (Table 2).

Fig. 4 Mean (\pm SE; n varied upon treatment combination and year) maximum photochemical efficiency of photosystem II (F_v/F_m) during the measurement campaigns of **a** 2008 and **b** 2009 in *J. thurifera* (squares) and *Q. ilex* (circles), in the open (open symbols) and under the canopy (closed symbols) and subjected to different watering treatments [mesic (continuous lines), and dry (dashed lines; **b**)]. Letters indicate significant differences between ($P < 0.05$) Sp Species, MH microhabitats and W watering treatments



Discussion

Species-specific differences in the underlying facilitative mechanisms

In agreement with our prediction, adult *J. thurifera* trees facilitated the establishment of both conspecific and hetero-specific saplings. Saplings of *J. thurifera* and *Q. ilex* subsp. *ballota* survived more (higher final survival plus lower mortality rate), had higher photochemical efficiency (F_v/F_m) and grew more under the canopy of adult trees than in the open. These results concur with previous findings evidencing the facilitative effect of nurse plants on *Q. ilex* (Gomez-Aparicio et al. 2005; Puerta-Pinero et al. 2006; Smit et al. 2008; Cuesta et al. 2010) and on *J. thurifera* (Montesinos et al. 2007; Gimeno et al. 2012b).

As expected, mechanisms underlying facilitation differed between species. The more palatable saplings of holm oak benefited from the browsing protection provided by adult trees, whereas *J. thurifera* saplings did not. These results agree with previous studies showing the relevance of the protection from herbivores on holm oak recruitment (Gomez-Aparicio et al. 2008; Gomez and Hodar 2008). It has been argued that abandonment of traditional practices decreases the importance of facilitation by means of protection from browsing (DeSoto et al. 2010). However, in Iberian woodlands, abandonment of traditional practises also leads to the proliferation of wild herbivores, such as roe deer (*Capreolus capreolus*) or wild boar (*Sus scrofa*) (Mangas and Rodriguez-Estival 2010), which partially compensates for decreased domestic herbivore disturbance. Hence, we suggest that in our system, differential facilitation provided by protection against browsing could still play a role as a potential driver of community composition changes (Smit et al. 2007).

Both tree species benefited from alleviated abiotic stress during summer, but during winter, nurse trees

only improved the survival of *J. thurifera*. Underneath the canopy of adult trees, saplings experienced a more benign microenvironment: buffered temperatures; better quality soils, which were more porous and nutrient richer; lower irradiance and therefore lower evaporative demand (Breshears et al. 1997; Muhamed et al. 2013). In the shade, plants preserved greater photochemical efficiency, which reverted positively with greater growth and survival (Aragon et al. 2008; Valladares et al. 2008; ESM Appendix 1). In Mediterranean environments, summer drought is the main bottleneck to seedling and sapling performance and survival, which can be alleviated under the canopy of adult trees (Gomez-Aparicio et al. 2008). Our results were not an exception since mortality peaked during the first summer after transplanting and was greater in the open than under the canopy. Besides summer drought, in Mediterranean continental environments, evergreen saplings have to overcome the winter, when chilling temperatures co-occur with high solar irradiance (Martinez-Ferri et al. 2003). These constraints are also alleviated under the canopy of adult trees (Valladares et al. 2008; Gazol and Camarero 2012). In our experiment, saplings of *J. thurifera* in the open experienced a second mortality wave during the first winter, which was not mimicked by saplings under the canopy. In contrast, holm oak survival did not decrease during winter, suggesting greater sapling multi-tolerance to chilling temperatures and high irradiance (Martinez-Ferri et al. 2003; Baquedano and Castillo 2007; Gimeno et al. 2009; Ogaya et al. 2011), which is surprising, given that *J. thurifera* tends to establish in harsher climates than *Q. ilex*. However, healthy adult individuals of *J. thurifera* that inhabit the cold Mediterranean steppes have very efficient photoprotective mechanisms (Esteban et al. 2014), which suggests that resistance to high irradiance and chilling would develop further during ontogeny in this species.

Facilitation under different levels of abiotic stress

Our experimental design allowed us to test whether the facilitation effect increases with both resource- (water availability) and non-resource-limiting (high irradiance and extreme temperatures) abiotic stresses, when two stress-tolerant species interact. We expected the difference in performance between plants under the canopy and in the open to be greatest under the dry treatment and during the summer (Bertness and Callaway 1994; Callaway et al. 2002). Our results showed that the facilitation effect reached a maximum during the first summer, when transplanted saplings were most vulnerable (Villar-Salvador et al. 2004; Jimenez et al. 2005) and heat, light and water stress peaked. In contrast, the results of the watering experiment did not fully agree with our predictions. We found that the facilitation effect was greater under drier conditions for *Q. ilex* subsp. *ballota* growth, but found the opposite for *J. thurifera*. Differences in F_v/F_m between treatments did not support our prediction either: at the end of the summer, the difference between plants in the open and under the canopy was greater for watered than non-watered plants. This later result has a twofold interpretation. First, it could be argued that over a certain threshold level of abiotic stress, the importance of facilitation starts to decrease (Michelet et al. 2006; Holmgren and Scheffer 2010). Second, this could be interpreted as a carryover effect from the previous season. Non-watered plants would have had the chance to acclimate to water scarcity during the previous dry spring, which would have led to higher stress tolerance during the summer (Villar-Salvador et al. 2004).

Our findings suggest that holm oak saplings, although more vulnerable to browsing, are more resistant to heat and water stress (greater photochemical efficiency at the end of both summers in both microhabitats), as well as to cold temperatures (lower mortality rates during the first winter after transplanting). Furthermore, holm oak saplings were capable of benefiting from stress alleviation provided by adult junipers under more severe water stress (greater facilitation effect under the dry treatment) than juniper saplings. All these factors together could provide holm oak saplings a competitive advantage over juniper saplings in a global change scenario, which combines decreased herbivore pressure and a drier and more extreme climate (IPCC 2014). Eventually, this could induce a shift in community composition from pure to mixed stands, in agreement with suggestions from previous studies (DeSoto et al. 2010). However, to fully anticipate eventual community changes, the entire plant cycle must be accounted for, and processes like the production of viable seeds, dispersal and germination are crucial in this regard. For instance, seed dispersal is very dependent on the properties of the surrounding propagule sources and on the dispersal agents (Kunstler et al.

2007; Aparicio et al. 2008). In our study area, bordering holm oak woodlands are very unproductive (Siscart et al. 1999) and their acorns are very small, in the limit of viability (Gimeno et al. 2009), while *J. thurifera* woodlands occupy an ample surface area and their dispersal relies on multiple agents (Escribano-Avila et al. 2012). Still, in a study performed in the same sites, Granda et al. (2012) reported the occurrence of holm oak saplings in *J. thurifera* woodlands, indicating its potential for successful dispersal and establishment in these woodlands.

Conclusion

Overall, our results partially support the classic idea that facilitation increases with abiotic stress (i.e. stress gradient hypothesis). Nevertheless, our conclusions are better framed under the broader conceptual framework proposed by Maestre et al. (2009), which suggested that the net effect of facilitation under different stress levels depends on the competitive ability of the interacting plants, i.e. tolerant vs. competitive, and the type of stress imposed, i.e. resource vs. non-resource. In our study, interaction occurs between a highly tolerant benefactor, adult *J. thurifera* trees, and two tolerant protégées. Besides this, tree saplings in our Mediterranean continental woodland were simultaneously exposed to resource- (water scarcity) and non-resource-limiting (high irradiance and extreme temperatures) stresses. Under this scenario, it is not possible to make straightforward predictions of the net outcome of plant–plant interactions and further complications arise when considering different response variables as estimators of plant performance (Maestre et al. 2005) and other stresses like herbivory (Smit et al. 2007). More recently, Holmgren et al. (2012) showed that drought alleviation by reduced irradiance, provided by the nurse tree, is maximised at intermediate irradiance levels. The observed patterns of both survival and photochemical efficiency along our irradiance gradient concurred with the predictions of Holmgren et al. (2012) (ESM Appendix 2). These patterns further suggest that the importance of facilitation does not necessarily follow a linear relationship with increasing abiotic stress, particularly when multiple biotic and abiotic stresses co-occur (Verwijmeren et al. 2013) and facilitation mechanisms vary upon species-specific traits such as palatability, drought, heat and cold tolerance. Our study challenges predictions from eco-physiological studies of individual species and calls for a more holistic view of species' responses to global change.

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Conflict of interest The authors declare that they have no conflict of interest and that the experiment complies with the current laws of Spain.

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