

Introducing resprouters to enhance Mediterranean forest resilience: importance of functional traits to select species according to a gradient of pine density

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Summary

1. Resprouter species are important for Mediterranean ecosystem resilience, but they are scarce in landscapes dominated by pioneer pines. Sound knowledge of resprouter seedling functional responses and establishment success across different pine habitats would help guide forest restoration efforts.

2. Four broadleaved resprouter species, that is two shrubs – *Arbutus unedo* and *Pistacia terebinthus* – and two trees – *Fraxinus ornus* and *Sorbus domestica* – were planted under an experimentally created gradient of pine cover from totally open conditions to dense pine cover.

3. Seedling survival and growth were monitored for 5 years. Phenological, physiological and morphological traits were measured to gain insight into the mechanisms of pine–seedling interaction.

4. Interaction outcomes varied according to species identity, pine cover treatment and time. Light-to-moderate pine cover induced greater height growth and little or no effects on diameter and survival of the two trees. Competition was always detected for shrubs, whereas competition and facilitation were noted for trees. Within pine stands, negative interactions increased with tree cover, making dense stands the most limiting. Interactions were only detectable after 2–3 years, but increased in intensity with time.

5. Functional responses to increasing pine cover indicated a seedling strategy of carbon gain optimization in the shade (increased specific leaf area and leaf area, decreased leaf dry matter content), particularly in tree species seedlings. Increasing pine cover induced higher water stress, but lower photochemical stress. The deciduous species had a longer vegetation season under pine canopies, whereas the evergreen shrub *Arbutus unedo* showed a lower polycyclism rate and flower production.

6. *Synthesis and applications.* Moderate pine cover facilitates the establishment of deciduous trees at the expense of shrubs. This pattern can be attributed to a higher shade tolerance of the trees than the shrubs combined with a low tolerance of trees to photoinhibition. We therefore recommend using evergreen shrubs for the restoration of open land and high-specific-leaf-area deciduous trees for pine stand diversification. However, in dense forests, thinning is needed to increase light availability prior to seedling introduction.

Key-words: forest dynamics, forest resilience, functional strategy, leaf traits, phenology, pine habitat, plant–plant interactions, resprouters, restoration, seedling establishment

Introduction

Restoration of Mediterranean forest cover is a major factor in meeting global change challenges (Vallejo *et al.*

2006, 2012; Lindner *et al.* 2010). In particular, the expected increase in wildfire frequency and intensity (Moriondo *et al.* 2006) may have dramatic consequences for the maintenance of vegetation cover and soil protection (Lindner *et al.* 2010). In this context, broadleaved resprouters are particularly interesting candidates for

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restoration projects as their resprouting ability reduces both time needed for vegetation recovery and vulnerability to fire intervals (Pausas *et al.* 2004; Vallejo *et al.* 2006; Puerta-Piñero *et al.* 2012). Broadleaves are considered keystone species for protection against desertification and fire impacts (Pausas *et al.* 2004; Puerta-Piñero *et al.* 2012) as they promote ecological resilience, that is the ecosystem's capacity to absorb changes without losing fundamental functional and structural integrity (e.g. see Mori 2016). These species are, nevertheless, poorly represented in Mediterranean landscapes where recent land abandonment and reforestation patterns have favoured pioneer species such as Aleppo pine (*Pinus halepensis* Mill.) (Barbero *et al.* 1990). Broadleaved population dynamics are severely limited by both seed arrival and seedling establishment in ecosystems where summer drought is a strong constraint for seedlings (e.g. Mendoza *et al.* 2009). Seed limitations can be overcome by artificial introduction, but the question of which safe site favours seedling establishment remains. The presence of an already settled plant has a huge influence on the ability of seedlings to establish (Lortie *et al.* 2004), as vegetation cover modifies the resource availability, abiotic stress and the hazards seedlings have to deal with, resulting in either facilitative or competitive interactions (Callaway & Walker 1997). The influence of pioneer vegetation on the establishment of later-successional species is a long-standing debate in ecology (Connell & Slatyer 1977) – a debate that is still not resolved, but has direct relevance for ecosystem management and restoration actions (Walker, Walker & del Moral 2007). The use of Aleppo pine in reforestation has largely been based on the expectation that it will facilitate the establishment of other late-successional, broadleaved species like oaks (Pausas *et al.* 2004; Cortina *et al.* 2011). Although supported by observational studies (Lookingbill & Zavala 2000), this pattern may be attributable to preferential dispersal within the habitat (Gómez 2003) rather than any facilitation of seedling establishment. Indeed, experiments tend to find negative effects of pine cover on broadleaved seedling establishment (Maestre *et al.* 2003; Bellot *et al.* 2004; Maestre & Cortina 2004). However, pine–seedling interaction outcomes can vary with pine density (Gómez-Aparicio *et al.* 2009; Prévosto *et al.* 2011; Sheffer *et al.* 2013), target species identity (Callaway 1998) and response variables, as conflicts between survival and growth have often been evidenced (e.g. Benavides *et al.* 2015).

Attempts to introduce resprouters in the Mediterranean Basin have mostly focused on the dominant species of mature forests, most often oaks (*Quercus* sp.), yet very little is known about the regeneration ecology of a number of other species that might, nevertheless, prove good candidates for restoration (Padilla *et al.* 2009). It has been proposed that species-specific interaction outcomes are linked to species strategies in terms of stress tolerance and competitive ability (Liancourt, Callaway & Michalet 2005; Maestre *et al.* 2009). Incorporating functional traits (*sensu*

Violle *et al.* 2007) into plant–plant interaction studies is suggested as a promising approach to emerge such plant strategies (Reich *et al.* 2003; Pérez-Harguindeguy *et al.* 2013) and interaction mechanisms (Butterfield & Callaway 2013). This approach can help understand the principles guiding species-specific responses to neighbours and thus to select which species would be best adapted to the local habitat conditions (Clark *et al.* 2012; Butterfield & Callaway 2013). Among functional traits, the role of phenology in mediating plant–plant interactions has received little attention despite being a major axis of plant strategy along with species-specific environmental drivers (Kikuzawa 1995; Caffarra & Donnelly 2010). Mediterranean plants show various phenological strategies in response to the summer drought constraint (Lillis & Fontanella 1992), so the changes in phenology across habitats can largely influence seedling establishment success (Monnier *et al.* 2012).

This study examined the interactions between Aleppo pine and seedlings of four resprouter species over a 5-year period using an experimental *in situ* approach in which we manipulated pine density to create a canopy cover gradient from totally open to closed pine stands. Seedling development patterns and functional trait variations across this gradient were monitored. The target species were two shrubs – *Arbutus unedo* L. and *Pistacia terebinthus* L. – and two trees – *Sorbus domestica* L. and *Fraxinus ornus* L. These species are all naturally present in the region, but scattered within forest and shrubland habitats without forming dense stands. As they established recently and at low densities, their ecology is still poorly known – particularly in the regeneration phase.

The aim of this study was to assess the Mediterranean forests' restoration potential of the four target resprouter species based on their functional responses to habitat conditions created by pine cover. We hypothesized that i) increasing pine density would improve seedling survival, but reduce seedling growth, ii) pine–seedling interaction outcomes would be more competitive for shrubs and facilitative for trees. In addition, we expected to find that functional traits would reflect adaptation to environmental factors and thus help select the most suitable species for each pine cover condition.

Materials and methods

SITE AND EXPERIMENTAL DESIGN

The experiment was conducted in southern France, at Saint-Mitre-les-Remparts (80 km west of Marseille city), in a flat area on the Mediterranean coast at a mean altitude of 130 masl (43°4'N; 5°0'W). The site was former terraced agricultural land that was abandoned in the middle of the XXth century, but recently partly reused by cattle. The landscape today is a mosaic of areas kept open by grazing activities or covered by 50- to 60-year-old stands of Aleppo pine that naturally colonized the abandoned lands. Soils are calcareous with a sandy-loam texture (55% sand, 30% silts and 15% clay), low stoniness and a mean

depth of 40 cm (25–48 cm). The climate is typically Mediterranean with a summer drought period from June to August and rainy springs and autumns. Mean temperature is 14.5 °C and mean precipitation is 550 mm based on historical records (1961–2010, Istres weather station). During the experiment (2009–2014), mean annual precipitation was 563 mm (minimum 327, maximum 705) with high seasonal variability and mean annual temperature was 15.6 °C (minimum 14.6, maximum 16.2).

We selected neighbouring areas of natural pine stands and open lands. Vegetation in open lands was manually cut each year to prevent closure of the system. In 2007, natural pine stands were thinned to produce four pine cover treatments: (i) no pine cover (open), (ii) light pine cover, (iii) moderate pine cover and (iv) dense pine cover. Each treatment was replicated in four 25 × 25 m plots surrounded by a 5-m-wide buffer zone. In each plot, 18 seedlings per species were planted systematically every 2 m, alternating species (i.e. 72 seedlings per plot, 1152 plants in total) in hand-dug holes (30 × 30 × 30 cm). Plots were fenced to prevent herbivorous damage by wild (forest) or domestic (open areas) animals. In 2013, light (photosynthetically active radiation; PAR) transmittance, mean summer soil moisture and air temperature were measured by placing probes under each pine cover treatment, as described in Gavinet *et al.* (2015). The treatment characteristics are listed in Table 1.

Our four target species are described in data bases as intermediate shade and drought tolerant (Gachet, Vêla & Taton 2005; Niinemets & Valladares 2006; Rameau *et al.* 2008), although their relative tolerance varies among data bases. All four target species possess the desired trait of being resprouters. The two trees also produce valuable wood and *A. unedo* and *S. domestica* produce edible fleshy fruits with useful properties for managers. Seeds were collected at different sites sharing similar ecological conditions, using different trees for each species to allow for intraspecific variability. The seeds were germinated and cultivated in a nursery for 1 year, transplanted in the field in November 2009 using containers of volume 560 cm³ and then immediately cut at 10 cm to limit the transplant shock.

SEEDLING MONITORING

Seedlings were individually tagged and seedling survival, stem basal diameter and height were recorded yearly for 5 years (2010–2014). Phenological, morphological and physiological traits were followed on a subset of 15 randomly selected seedlings per species per treatment (3–4 seedlings per species per plot, i.e. 240 seedlings in total).

Phenology was followed from April to November during the two last years (2013 and 2014). Apical bud stage at the first sampling date was recorded using a method adapted from the scale of Meier (2001): bud stage was rated 0 for dormancy, 1 for beginning of bud swelling, 2 for beginning of budburst, 3 for beginning of leaf-out and 4 for first fully expanded leaf. The previous year's

growth unit was identified on each seedling. Current growth unit length was recorded twice monthly in spring and autumn and monthly in summer and used to compute a height increment per day since the last census date. The number of leaves on the growth unit was recorded at each census date and used to calculate the percentage of fallen leaves at the last sampling date.

Pre-dawn leaf water potential, indicating plant water stress, was measured at the end of the drought season during the last week of August. Before sunrise, a healthy leaf was cut, placed in a plastic bag and transported in an icebox for the immediate *in situ* measurement with a pressure chamber (PMS/1000, PMS Instrument, USA). Chlorophyll fluorescence was measured in the middle of the day (12:00–16:00) at the end of summer using a portable fluorimeter (Pocket Pea, Hansatech Instruments, UK). Leaf clips were installed to allow the sampled leaves to adapt to the dark for at least 30 min. Fluorescence was measured using a flash of 3500 µmol m⁻² s⁻¹ for 10 s. Maximal fluorescence and minimal fluorescence (F_m and F_0) were used to calculate the efficiency of photosynthetic energy conversion: $F_v / F_m = (F_m - F_0) / F_m$. F_v / F_m ratio gives an indication of the photosynthetic status of the plant, with values lower than 0.85 indicating that photosynthetic efficiency is reduced by stress (Maxwell & Johnson 2000). Specific leaf area (SLA), leaf dry matter content (LDMC) and mean leaf area (LA) were measured according to Pérez-Harguindeguy *et al.* (2013) on 15 leaves per species and cover condition. Leaves were cut in the field, wrapped in moist paper, placed in sealed plastic bags in an icebox, brought to the laboratory, placed in a refrigerator and processed within 24 h. Leaves including petiole were gently blotted dry with tissue paper to remove any surface water before measuring water-saturated fresh mass. The leaf samples were scanned flat to measure their area using WinFOLIA software (Regent Instruments, Canada) and then oven-dried at 70 °C for 3 days and weighed to determine their dry mass. SLA was calculated as the ratio of leaf area to dry mass, and LDMC was calculated as the ratio of water-saturated fresh mass to dry mass.

DATA ANALYSIS

Survival differences between species, pine cover treatments and their interaction were tested using Cox proportional hazards regression models that estimate seedling survival time according to the different factors and taking into account censored data (Cox 1972; R 'Survival' package). Changes in diameter and height over time were analysed for each species by fitting linear mixed models with cover density, year and their interaction as fixed factor and individuals nested in plots as random factors, with an autocorrelation structure of order 1 (R 'nlme' package, 'lme' procedure). Data were log-transformed to improve normality, and heteroscedasticity was assessed with diagnostic plots. The effects of species identity, pine treatment and their interactions on growth parameters and traits were analysed with linear mixed models ('nlme' package) for continuous variables and generalized linear mixed models for

Table 1. Characteristics of the different pine cover treatments, measured in 2013 ($n = 4$ plots per treatment)

	Open	Light pine cover	Moderate pine cover	Dense pine cover
Basal area (m ² ha ⁻¹)	0	10.2 ± 0.9	19.2 ± 0.7	32.0 ± 3.9
Transmitted PAR (%)	100	31.1 ± 1.4	15.5 ± 1.2	8.6 ± 0.5
Summer soil moisture (%)	20.4 ± 1.3	15.6 ± 0.6	16.5 ± 0.7	16.3 ± 0.6
Summer daily maximum temperature (°C)	35.2 ± 0.3	34.8 ± 0.4	33.0 ± 0.4	30.8 ± 0.2

non-continuous variables ('lme4' package, 'glmer' procedure). We used a Poisson distribution for leaf number and a binomial distribution for the percentage of fallen leaves. Bud stage was analysed with an ordered logistic regression ('MASS' package, 'polr' procedure). Multiple comparisons were then made with pre-defined linear contrasts ('multcomp' package, 'glht' procedure). To obtain an overview of pine interactions with seedlings, we calculated the relative interaction index (RII) according to Armas, Ordiales & Pugnaire (2004) for the final performance variables, that is final survival rate, diameter or height. This index is expressed as $(P_w - P_o)/(P_w + P_o)$, where P_w is the value of the plant performance variable with neighbours (i.e. with pines) and P_o is its value without neighbours (i.e. in open plots). This index ranges from -1 (competition) to 1 (facilitation) and was calculated for each pine cover treatment. The growth unit height increment was compared between cover conditions at each date using nonparametric tests. All analyses were performed using R software v. 3.1.0.

Results

SEEDLING SURVIVAL AND GROWTH

Survival was influenced by pine treatment \times species interaction (likelihood ratio $\chi^2=59.1$, d.f. = 9, $P < 0.001$, see

Table S1, Supporting Information). In open plots, survival rates were high and did not significantly differ between species, ranging from $79 \pm 20\%$ (*A. unedo*) to $98 \pm 3\%$ (*P. terebinthus*) after 5 years (Fig. 1). This high survival rate was maintained in all pine cover treatments for *F. ornus*, whereas *P. terebinthus* survival rates decreased progressively with increasing pine cover to $21 \pm 9\%$ under dense pine cover. Survival of *S. domestica* and *A. unedo* decreased under dense pine cover to $64 \pm 11\%$ and $21 \pm 6\%$, respectively. *F. ornus* and *S. domestica* thus showed better survival rates than the other two species under pine cover, and *F. ornus* was the best-surviving species under dense pine cover.

Pine cover treatment also affected the seedling diameter and height, but this effect was time-dependent (Fig. 2). Pine cover treatment effects on seedling dimensions increased with time and were only detectable after the first 2–3 years except for *P. terebinthus* height. Final diameter and height were affected by pine treatment \times species interaction (Table 2). Diameter was always highest in open conditions and lowest under dense pine cover, but the magnitude of diameter reduction differed strongly

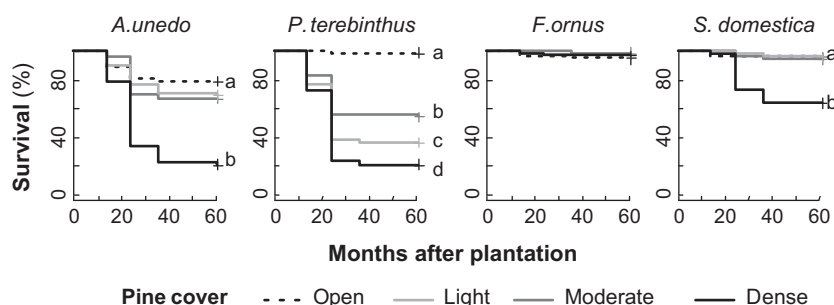


Fig. 1. Probability of seedling survival for the first 5 years. Letters indicate significant differences between pine cover treatments at 5 years ($P < 0.05$).

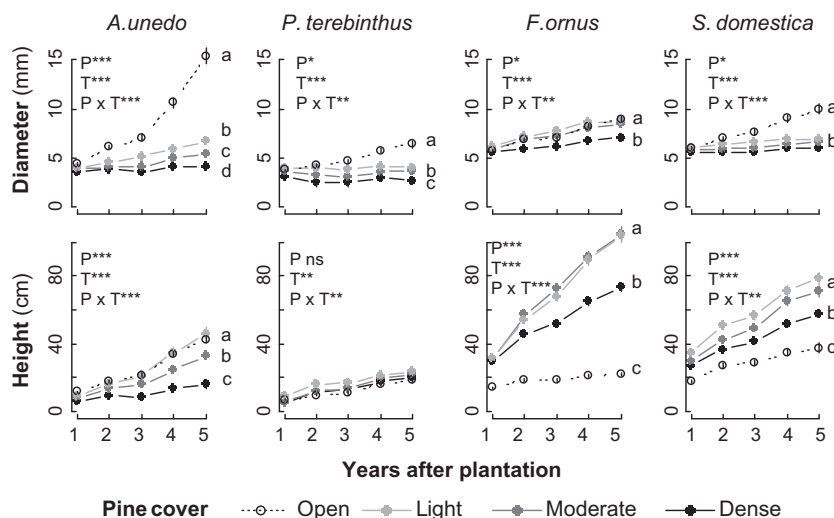


Fig. 2. Species diameter and height growth as a function of time and pine cover treatments. P and T indicate the results of linear mixed models testing for influence of pine cover treatment and time, respectively, with $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, ns: not significant. Letters indicate the differences between pine cover treatments at 5 years ($P < 0.05$).

Table 2. Results of linear mixed models testing the effects of pine cover conditions, species identity and their interaction on growth parameters in 2014 after 5 years of growth ($n = 15\text{--}72$ seedlings per species \times pine cover interaction). Plots were included as random factors. Significant P values are indicated in boldface

	d.f.	Diameter		Height	
		F	P	F	P
Species (S)	3	213.2	<0.001	303	<0.001
Pine cover (P)	3	15.9	<0.001	10.2	<0.001
S \times P	9	26.9	<0.001	54.8	<0.001
Residuals	850				

between species (Figs 2 and 3). Diameter was reduced by about 70% for *A. unedo* and 40% for *S. domestica* under all pine covers, by 40% (light pine cover) to 70% (dense pine cover) for *P. terebinthus* and by 20% under dense pine cover only for *F. ornus*. Species ranking thus changed along the pine cover gradient: in open plots, *A. unedo* had the greatest diameter, followed by *S. domestica*, *F. ornus* and *P. terebinthus*. Under all pine cover treatments, *F. ornus* had the greatest diameter, followed by *S. domestica*, *A. unedo* and *P. terebinthus*. Unlike diameter, height showed contrasting responses to the pine cover gradient according to species. Height was not affected by pine cover for *P. terebinthus*, was reduced under moderate and dense pine cover for *A. unedo*, but was strongly stimulated for *F. ornus* and *S. domestica* under pine (Fig. 2). Height of *F. ornus* and *S. domestica* was significantly increased under light pine cover (fivefold and twofold higher than in open plots, respectively). As a result of this species-specific effect of pine cover on height growth, no species outperformed the others in all treatments. In the open, *A. unedo* was the tallest species, followed by *S. domestica*. Under pine cover, *F. ornus* was tallest, followed by *S. domestica*. *P. terebinthus* was the shortest species under all conditions.

The calculated RII values showed that outcomes of pine-seedling interactions depend on response variables, species identity and pine cover (Fig. 3). Under light and moderate stands, neutral interactions to competition with

pine prevailed for the two shrub species for both survival and growth. Neutral interactions for the survival and facilitation of height growth were observed for the two trees, while competition for diameter growth occurred for *S. domestica* only. Nevertheless, negative effects increased with pine density for all species and response variables except for *F. ornus* survival. Denser pine cover increased the competition survival and growth for the two shrubs and decreased the facilitation for height of the two trees. Under the densest stands, the sign of interaction outcomes (RII values) shifted from neutral to competitive interactions for *S. domestica*, *A. unedo* height growth and, to a lesser extent, *F. ornus* diameter growth.

LEAF PHYSIOLOGY AND MORPHOLOGY

Pre-dawn water potential gradually decreased with increasing pine cover, indicating a higher water stress under dense pines for all species (Table 3). Leaf photochemical efficiency (F_v / F_m) tended to decrease with decreasing pine cover, although this was significant only for *F. ornus* and *P. terebinthus*, and showed little difference between species: only *A. unedo* had a higher F_v / F_m value than *F. ornus* in the open.

Leaf dry matter content and leaf number were affected by pine cover and species identity; SLA and LA were affected by pine treatment \times species interaction (Table 3). SLA was similar between all species in the open and increased in response to increasing pine cover, but with different magnitudes (2.3-fold for *A. unedo* to 3.8-fold for *F. ornus* and *S. domestica*), leading to the differences between species. LDMC decreased from open to dense pine conditions. LA was lower in open conditions for *F. ornus* and *S. domestica*, but decreased under pines for *P. terebinthus* and did not change across cover conditions for *A. unedo*. LA was higher for the two tree species than for the shrubs under dense and moderate pine cover. Leaf number decreased sharply under pine cover for *A. unedo*, was lower in the open than under all pine treatments for *F. ornus*, peaked under moderate pine cover for *S. domestica* and did not change across cover conditions for *P. terebinthus*. Thus, *A. unedo* had the highest leaf

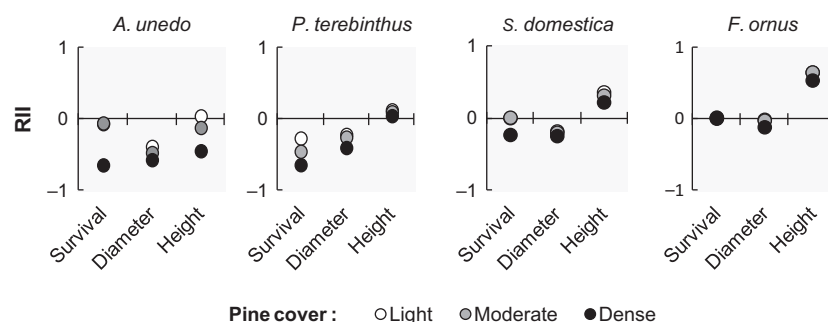


Fig. 3. Relative interaction index (RII) for 5-year-old seedlings according to pine density, target species and response variable. RII was calculated according to Armas, Ordiales & Pugnaire (2004) by comparing species performance under pine and in the open, and ranged between -1 (only competition) and $+1$ (only facilitation).

Table 3. Leaf physiological and morphological traits under different pine cover treatments. Data are means \pm standard errors of 12–15 individuals per species and treatment. F -values (χ^2 for leaf number) and significance levels are given for species (S, d.f. = 3), pine cover (P, d.f. = 3) and species \times pine cover interaction (d.f. = 9) for each trait (residuals d.f. = 213). Lowercase letters indicate the differences between treatments and uppercase letters indicate the differences between species detected by multiple comparison tests

	<i>A. unedo</i>	<i>P. terebinthus</i>	<i>F. ornus</i>	<i>S. domestica</i>
Physiological traits				
Pre-dawn water potential (MPa)				
S: 47.2***				
P: 27.8***				
S \times P: 1.4				
Open	-2.5 ± 0.3 a B	-0.8 ± 0.1 a A	-3.0 ± 0.4 a B	-2.7 ± 0.2 a B
Light cover	-3.3 ± 0.2 b B	-1.4 ± 0.1 b A	-3.8 ± 0.2 b B	-3.9 ± 0.3 b B
Moderate cover	-4.1 ± 0.2 b B	-1.1 ± 0.1 b A	-4.3 ± 0.2 b B	-3.9 ± 0.2 b B
Dense cover	-4.8 ± 0.2 c B	-2.3 ± 0.6 c A	-4.6 ± 0.1 c B	-5.1 ± 0.2 c B
F_v/F_m				
S: 5.1*				
P: 10.1***				
S \times P: 0.9				
Open	0.77 ± 0.02 b A	0.74 ± 0.01 b A	0.63 ± 0.06 b B	0.73 ± 0.02 b A
Light cover	0.75 ± 0.02 ab A	0.75 ± 0.01 ab A	0.68 ± 0.02 ab B	0.74 ± 0.02 ab A
Moderate cover	0.76 ± 0.01 ab A	0.78 ± 0.01 ab A	0.71 ± 0.03 ab B	0.77 ± 0.01 ab A
Dense cover	0.78 ± 0.01 a A	0.8 ± 0.01 a A	0.75 ± 0.01 a B	0.78 ± 0.01 a A
Morphological traits				
Specific leaf area ($\text{cm}^2 \text{g}^{-1}$)				
S: 126.1***				
P: 30.4***				
S \times P: 14***				
Open	57 ± 1 a	53 ± 10 a	57 ± 11 a	64 ± 13 a
Light cover	86 ± 5 ab B	154 ± 6 b A	158 ± 5 b A	179 ± 7 b A
Moderate cover	101 ± 2 ab C	156 ± 5 b B	201 ± 14 bc A	196 ± 6 b A
Dense cover	130 ± 6 b C	193 ± 7 b B	220 ± 7 c A	240 ± 9 c A
Leaf dry matter content (mg g^{-1})				
S: 59.9***				
P: 20.9***				
S \times P: 1.9				
Open	467 ± 4 a C	508 ± 5 a A	438 ± 9 a D	508 ± 13 a B
Light cover	473 ± 14 a C	506 ± 14 a A	428 ± 12 a D	470 ± 5 a B
Moderate cover	423 ± 7 b C	503 ± 12 b A	389 ± 8 b D	475 ± 10 b B
Dense cover	404 ± 15 c C	480 ± 11 c A	370 ± 11 D c	434 ± 6 c B
Mean leaf area (cm^2)				
S: 116.2***				
P: 14.1***				
S \times P: 9.7***				
Open	11.7 ± 1.1 B	25.1 ± 3.1 a A	22.2 ± 2.5 b A	21 ± 3.5 b AB
Light cover	14.4 ± 1.7	23.9 ± 3.4 ab	71.3 ± 7.2 a	44.5 ± 3.8 a
Moderate cover	13.9 ± 0.6 B	19.9 ± 2.5 ab B	106.2 ± 21.1 a A	45.4 ± 3.3 a A
Dense cover	10.3 ± 1.2 B	13.4 ± 1.9 b B	53.9 ± 5.3 a A	34.9 ± 2.1 a A
Mean leaf number				
S: 164.2***				
P: 25.6***				
S \times P: 99.1***				
Open	16.7 ± 1.1 a A	5.2 ± 0.4 B	5.1 ± 0.4 b B	3.9 ± 0.4 b B
Light cover	12.1 ± 1.3 b A	5.3 ± 0.3 C	8.7 ± 0.5 a AB	6.9 ± 0.6 a BC
Moderate cover	8.7 ± 0.8 b A	5.2 ± 0.5 B	8.5 ± 0.3 a A	6 ± 0.4 a AB
Dense cover	4.9 ± 0.4 c B	4.3 ± 0.3 B	8.2 ± 0.4 a A	4.7 ± 0.4 b B

number in the open, while *F. ornus* had the highest leaf number under dense pine stands.

PHENOLOGY

Bud stage at first sampling date in 2013 was lower in the open than under all pine covers for the two trees, although

only significantly lower for *F. ornus* and *S. domestica*, indicating an earlier budburst under pines (Table 4). Comparing across species, we found that *A. unedo* in the open and *F. ornus* under light or moderate pine cover had the earliest budburst. Leaf fall at last sampling date was higher in the open, although not significant for *P. terebinthus*. The percentage of fallen leaves was lower for

Table 4. Phenological responses to pine cover treatments. Data are means \pm standard errors of 15 individuals per species and treatment. Likelihood ratio χ^2 values are given for species (S), pine cover (P) and species \times pine cover interaction. Lowercase letters indicate the differences between treatments for one species and uppercase letters indicate the differences between species detected by multiple comparison tests

	<i>A. unedo</i>	<i>P. terebinthus</i>	<i>F. ornus</i>	<i>S. domestica</i>
Bud stage at first sampling date (5 April 2013)				
S: 16.4***				
P: 24.5**				
S \times P: 46.3***				
Open	2 \pm 0.1 A	1.3 \pm 0.3 AB	0.7 \pm 0.2 b B	1.5 \pm 0.1 AB
Light cover	2.1 \pm 0.2 AB	1.5 \pm 0.2 B	2.5 \pm 0.2 a A	2 \pm 0.2 AB
Moderate cover	1.7 \pm 0.2 AB	1.6 \pm 0.1 B	2.4 \pm 0.2 a A	2.2 \pm 0.1 AB
Dense cover	2 \pm 0.1	1.5 \pm 0.2	2.1 \pm 0.2 a	2.1 \pm 0.2
Percentage of fallen leaves at last sampling date (29 October 2013) for deciduous species				
S: 19.3***				
P: 68.4***				
S \times P: 21.4**				
Open	—	26.9 \pm 8.7 B	35.6 \pm 9.2 a AB	57.4 \pm 9 a A
Light cover	—	19.5 \pm 4.6 AB	8.5 \pm 1.5 b B	19.7 \pm 4 b A
Moderate cover	—	16.7 \pm 5.9	4 \pm 2.9 b	18.4 \pm 7.5 b
Dense cover	—	16 \pm 5.3 A	2.8 \pm 1.5 b B	4.3 \pm 3 b AB

P. terebinthus in the open and for *F. ornus* under all pine covers.

Shoot elongation occurred mainly in early spring for all species and much earlier in 2014 than in 2013 (Fig. 4).

The growth unit increment tended to peak later in the open than under pine cover for *A. unedo* and *F. ornus*, and to decrease earlier under dense pine cover for *A. unedo* and *S. domestica*. In 2014, about half the

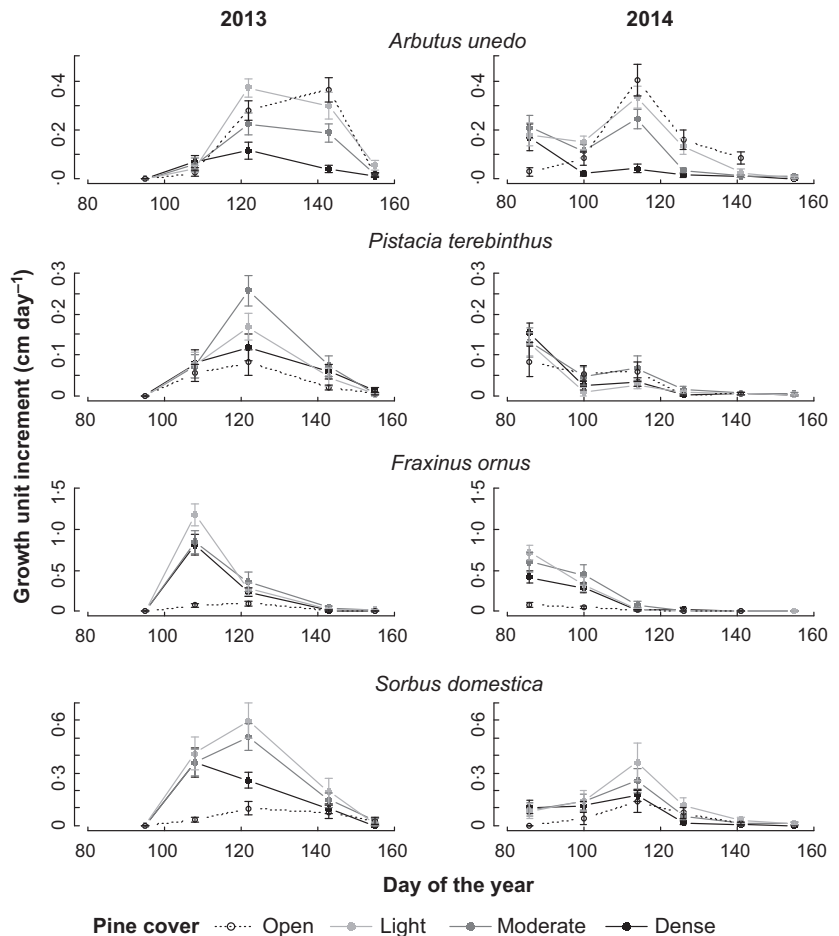


Fig. 4. Intra-annual dynamics of shoot elongation according to pine cover treatment for years 2013 and 2014.

A. unedo seedlings in the open and 20% under light pine cover produced a new growth unit in autumn, but this growth unit was very short (0.69 ± 0.09 cm). Flowering was also observed for 25% of *A. unedo* seedlings in open plots.

Discussion

Pine cover gradient influenced the survival, growth and functional traits in a species-specific way. As a result, no species outperformed the others across all habitats. In open conditions, the survival of all species was high, but growth response was contrasted and the evergreen shrub *A. unedo* showed the better growth. Increasing pine cover reduced shrub survival and growth, but enhanced tree height through increased vegetation season length and leaf development. Finally, dense pine cover was the most detrimental to survival and diameter growth for all species except *F. ornus*, which was the only species able to survive well in these conditions.

SEEDLING SURVIVAL AND GROWTH DEPEND ON PINE COVER, SPECIES AND TIME

Contrary to what was expected, increasing pine density did not improve the survival. This result could be explained by a stronger resource limitation (light and soil moisture) in forest compared to open conditions (Table 1). Pine effect was neutral-to-negative for diameter growth and positive for tree height: the presence of pine cover triggered a twofold height increase for *S. domestica* and a fivefold increase for *F. ornus* compared to open plots. This height increase occurred without changes in diameter for *F. ornus*, reflecting an overall better aerial growth. However, for *S. domestica*, height increase was paralleled by a reduction, although less important (factor 1.4) in diameter, which may reflect the elongation in response to shade rather than any real improved growth. Pine–seedling interaction outcomes thus varied according to life-form, as hypothesized, that is neutral effects to competition for shrubs but facilitative outcomes for tree height. Interactions also varied with pine density: pine effects were more negative with increasing density, causing an increase in competition, a decrease in facilitation and some shifts from neutral to competitive interactions. Comparing shrub species survival in open plots and under two pine densities, Bellot *et al.* (2004) also found that competition increased with pine cover. Over a broader gradient of pine cover ($0\text{--}77\text{ m}^2\text{ ha}^{-1}$), Gómez-Aparicio *et al.* (2009) observed that oak recruitment peaked under intermediate pine densities. Here, we also found that shrub seedling survival and growth were enhanced in open plots, but trees showed better height growth under moderate pine cover. Overall, these results confirm that neighbour density must be taken into account, as it can shift the balance between competition and facilitation (Callaway & Walker 1997). Here, dense pine stands were the

most limiting conditions for most seedling survival and growth factors, so a reduction in pine density should be considered to improve resprouter establishment.

Interestingly, pine cover effects on seedling performance increased with time and only became distinct after 2–3 years: this result may reflect the fact that the seedlings needed this time period in order to overcome the initial transplant, which means that further studies need to address at least this time interval. It has often been suggested that negative interactions increase with plant ontogenetic stage (e.g. Callaway & Walker 1997; Schiffers & Tielbörger 2006). Here, we did not find this pattern: competition increased with time for shrubs, whereas the facilitation increased with time for tree height. Through years, differences in growth response increased between the habitats, especially between the most favourable habitats (open for shrubs and light pine cover for trees) and other conditions. However, a longer study period would be needed to determine whether the beneficial effect of light-to-moderate pine cover on tree height is lasting or whether there is a shift to competition due to a progressive increase in light requirements of the seedlings in parallel with a reduction in light availability due to pine canopy closure. In this case, further reduction in pine cover may be needed later on to ensure the growth of established saplings and diversification of pine stands.

FUNCTIONAL RESPONSES TO PINE COVER

The pine cover gradient strongly influenced most species functional trait values, indicating different plant functioning in response to environmental factors across habitats. Higher SLA and lower LDMC with increasing canopy cover reflect a strategy of carbon gain maximization under shade (Valladares & Niinemets 2008), which was particularly marked for the two trees with a parallel increase in leaf numbers and areas. However, these morphological adaptations to shade may have been partly responsible for a higher drought stress (decreasing pre-dawn leaf water potentials with pine cover) because drought tolerance conversely requires a low evaporative surface and a high below-ground biomass relative to above-ground parts (Kozłowski & Pallardy 2002; Valladares & Pearcy 2002; Lopez-Iglesias, Villar & Poorter 2014). A decrease in photochemical efficiency in open plots was observed despite a lower water stress, which suggests a photosynthetic stress in open plots (Valladares 2004; Sánchez-Gómez, Valladares & Zavala 2006) probably due to the strong increase in temperature extremes and irradiance levels in open plots (respectively, $+4.4\text{ }^{\circ}\text{C}$ and $+91\%$ compared with dense plots, Table 1).

Surprisingly, pine cover induced an earlier budburst and a later leaf fall for the two deciduous trees. Budburst usually requires a certain value of degree-days, occasional chilling periods and a certain photoperiod length (Lechowicz 1984), all of which are requirements that are expected to be met earlier in open conditions (von Arx,

Dobbertin & Rebetez 2012). However, budburst also requires carbohydrates (Kozlowski 1992) and so may be delayed by previous-year carbon shortage, for instance due to low light availability (Sanz-Pérez & Castro-Díez 2009) or excessive light (photoinhibition). The longer vegetation season may have partly compensated for the lower light availability under pines and explain why tree growth was maintained or improved. Polycyclism was observed only for *A. unedo* (Lillis & Fontanella 1992; Castro Díez & Montserrat-Marti 1998) and only in open or light pine cover conditions. This suggests that light availability is determining for polycyclism in *A. unedo* as also found in sessile oak (Nicolini, Barthélémy & Heuret 2000). The polycyclism of this species can be seen as an advantage in a Mediterranean climate where the favourable growing season is split into two parts (spring and autumn), whereas the absence of polycyclism in deciduous species makes them very dependent on favourable early-spring conditions.

SPECIES STRATEGIES EXPLAIN ADAPTATION TO DIFFERENT HABITATS

The two trees exhibited higher SLA and LA than the shrubs. These traits are linked with a high efficiency of light capture under shaded environments (Poorter *et al.* 2009). This could explain the higher shade tolerance of the two trees revealed by their high survival rates under dense stands (Kobe *et al.* 1995). Recent attempts to examine the interaction outcomes as a function of plant strategies have found that plants with acquisitive attributes such as high SLA and LA (Rolhauser & Pucheta 2016) or taller plants at maturity (Butterfield & Briggs 2011; Soliveres *et al.* 2014) are more liable to be involved in facilitative interactions. This relation was attributed to higher transpiration rates of tall plants with thin and large leaves due to their higher leaf area, leading to a higher benefit of microclimate amelioration by shading. In open plots, seedling survival was high for all species, probably linked to higher resource availability (light and water), but this occurred in the artificial absence of competition by ground vegetation. The height growth of the two trees was seriously hampered in open plots, probably due to a high sensitivity of the studied species to photoinhibition, as indicated by their lower chlorophyll fluorescence and earlier leaf fall. Other studies have also found that high SLA and LA are related to low tolerance to photoinhibition (e.g. Houter & Pons 2005). With a chronic photoinhibition blocking height growth, these two species may never reach their mature dimensions and are thus quickly out-competed by spontaneous vegetation in natural systems (Westoby *et al.* 2002). In contrast, the evergreen shrub *A. unedo* showed particularly strong development in open plots, reaching the maturity stage after just 5 years. These results are in line with the proposed higher tolerance of evergreens to high irradiances than deciduous species (Gómez-Aparicio, Valladares & Zamora 2006) and

highlight the fact that sensitivity to photoinhibition is a major trait for species adaptation to Mediterranean open habitats. Finally, in our study, *P. terebinthus* showed the poorest performance under all conditions, suggesting a low tolerance to both high irradiances and resource stress. This emphasizes the need to take into account species tolerance to prevailing stressful conditions both with and without neighbours in order to predict the interaction outcomes.

CONCLUSION: SPECIES SELECTION AND PINE STAND MANAGEMENT FOR RESTORATION

Seedling establishment is largely influenced by pine cover conditions and is also dependent on species' ecological tolerances to resource limitations. Pine cover induced competition mainly for light, leading to lower survival and growth of the two shrubs and a reduced polycyclism of the evergreen shrub. In contrast, the two deciduous trees, which are more shade-tolerant but photoinhibition-intolerant, drew benefits from light and moderate pine covers and showed greater height growth, higher leaf development and a longer vegetation season. However, their development is hampered, on the one hand, in very dense stands and, on the other hand, in totally open conditions due to photoinhibition stress. The pioneer Aleppo pine thus has a strong influence on vegetation dynamics by favouring shade-tolerant deciduous trees at the expense of light-demanding shrubs. Strategies for enhancing ecosystem resilience through the introduction of resprouters should take into account both the density of pine cover and species' ecological tolerance. The densest pine stands will need to be thinned before seedling introduction. Under moderate to low pine cover, introducing shade-tolerant trees with high SLA seems a good option to enhance the presence of resprouters, whereas in open habitats, photoinhibition-tolerant evergreen shrubs such as *A. unedo* are better adapted.

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Data accessibility

Plant and trait data are available from Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.k67j5> (Gavinet, Prévosto & Fernandez 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Cox proportional hazards model.