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Diversifying sub-Mediterranean pinewoods with oak species in a context of assisted migration: responses to local climate and light environment

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Abstract

Questions: How do thermal migration distance and extreme cold events affect seedling emergence and survival in assisted migration schemes in the sub-Mediterranean context? What role does plant provenance play? Can biotic interactions such as nurse effect of the overstorey and shrub layer buffer the negative responses to plant translocation? Are any of these effects species-specific?

Location: Three pinewoods in the Catalan Pre-Pyrenees, northeast Iberian Peninsula.

Methods: We used a replicated field trial to test the early years establishment of two contrasted provenances of four *Quercus* species (*Q. coccifera*, *Q. ilex*, *Q. faginea* and *Q. pubescens*) that were sown and planted along gradients of elevation and understorey microsite conditions in sub-Mediterranean pinewoods. Seedling responses to translocation were evaluated through seedling emergence, seedling survival and re-sprouting after dieback events according to seedling provenance, thermal migration distance, extreme cold events and microenvironment.

Results: The study reports high success of both the planting (with an overall 76.3% of initial 3-yr survival) and sowing (with an overall 50% of seedling emergence) experiments. The results show that: (1) the thermal migration distance and the occurrence of extreme cold events have strong effects on the responses of the translocated species (particularly the evergreen oaks); (2) the forest overstorey plays an important role in attenuating the negative effects of thermal migration distance on seedling survival; and (3) these responses are species-specific. The evergreen *Quercus* species showed more evidence of high ecotypic differentiation in terms of cold tolerance, enabling local provenances to respond better to translocation. In contrast, marcescent species, showed high phenotypic plasticity that led to a better overall establishment success.

Conclusion: The implementation of assisted migration is a feasible option to increase the diversity and resilience of the sub-Mediterranean pinewoods. Assisted migration programmes should manage risks by thoroughly considering thermal migration distances and the occurrence of extreme cold events when selecting species and seed sources, since Mediterranean tree species show different strategies regarding adaptation to cold. Programme managers should also consider the advantage of planting/sowing under relatively closed canopy to buffer some of the negative responses associated with translocation.

Introduction

Across the northern shore of the Mediterranean Basin, generalized depopulation in rural areas over the second half of the twentieth century has led to the abandonment

of once cultivated areas and pastures, and thus to a strong decrease in human interventions on forests (Vicente-Serrano et al. 2004; Lasanta-Martinez et al. 2005; Chauchard et al. 2007). These land-use changes, together with extensive reforestation programmes, have triggered extended

encroachment and densification processes in forests, mainly pinewoods (Améztegui et al. 2010; Navarro & Pereira 2012). More recently, the activity of seed dispersers like jays or mice (Gómez 2003), and the increasing cover of facilitating shrubs in the understorey of pine forests — favoured by the sharp decrease in livestock grazing pressure — are enabling a gradual entry of late successional broad-leaved species in their understorey (Gracia et al. 2007; Martín-Alcón et al. 2012), enhancing natural processes of tree species diversification (Gómez 2003; Gómez-Aparicio et al. 2005; Navarro-González et al. 2013; Martín-Alcón et al. 2015b). An increase in tree species diversity is generally thought to enhance the forest resilience to environmental changes, including variations in disturbance regimes (e.g. Campbell et al. 2009; Thompson et al. 2009; Puettmann 2011). In the particular case of the sub-Mediterranean pine forests, the presence of resprouting species such as oaks in the understorey of forests dominated by non-resprouting and non-serotinous pines such as black pine (*Pinus nigra* Arn. subsp. *salzmannii*) or Scots pine (*Pinus sylvestris* L.) is essential for rapid vegetation recovery after the occurrence of forest fires (Puerta-Piñero et al. 2011; Martín-Alcón et al. 2015a).

Natural tree species diversification processes are still far from widespread at landscape and regional scales, due to limiting factors such as seed dispersal constraints (Zamora et al. 2010; González-Moreno et al. 2011), unfavourable stand structures — i.e. over-stocked pine plantations (Navarro-González et al. 2013; Martín-Alcón et al. 2015b) — or harsh microsite conditions (Gomez-Aparicio et al. 2009). To cope with such limitations and accelerate the natural process, forest managers are increasingly looking at assisted diversification measures based on planting or sowing late successional species (Gomez-Aparicio et al. 2009; Palacios et al. 2009; González-Rodríguez et al. 2011; Prévosto et al. 2011).

The climatic conditions to which Mediterranean tree populations have been locally adapted are expected to change dramatically in response to rapid on-going global warming (Benito-Garzón et al. 2008; Keenan et al. 2011). In this context, assisted migration practices can be considered as a way to help implement diversification actions in particularly vulnerable areas (Kreyling et al. 2011; Frascaria-Lacoste & Fernández-Manjarrés 2012; Pedlar et al. 2012; Benito-Garzón et al. 2013; Leverkus et al. 2015). Assisted migration — also known as assisted colonization, or population translocation — is the intentional movement of focal units (i.e. ecotypes, species, taxa, functional types or life forms) to recipient localities where these focal units are currently absent and cannot be expected to colonize by natural means within a short time frame (i.e. years or decades; Kreyling et al. 2011). In forestry, assisted migration is generally focused on keystone tree species

moved within, or modestly beyond, a species' current range (Kreyling et al. 2011; Frascaria-Lacoste & Fernández-Manjarrés 2012; Pedlar et al. 2012). The assertion that populations growing under warmer conditions can be safely translocated to colder regions still needs to be further explored, since they may mal-adapt to extreme cold events in those localities, which would result in significant economic loss (Benito-Garzón et al. 2013). Common garden and field experiments are the most powerful tools for testing population translocations (Matyas 1996), but these types of field experiments remain scarce, at least in the Mediterranean context.

Here, we present the findings of the initial 3-yr monitoring period on a long-term field experiment in which we sowed acorns and planted seedlings from two contrasted provenances along gradients of elevation and microsite conditions (canopy openness and herbaceous and shrub cover). The study included the four most widespread *Quercus* species in the calcareous mountains of the eastern Iberian Peninsula (*Q. coccifera* L., *Q. ilex* L., *Q. faginea* Lam. and *Q. pubescens* Wild.), which were planted and sown in the understorey of sub-Mediterranean pinewoods. Our general objectives were to gain deeper insight into the main factors driving the success of assisted migration practices, and to assess how some of the species most suitable for diversifying sub-Mediterranean pinewoods will respond to translocation-induced changes in climate conditions. Previous studies on the ecophysiological responses of these species to extreme climatic events have observed broad inter- and intraspecific differences in phenotypic plasticity and local adaptation capacity (Martínez-Ferri et al. 2001; Gimeno et al. 2008; Andivia et al. 2011; Arend et al. 2011; Wellstein & Cianfaglione 2014). We expected to find that: (1) climate, and particularly minimum temperatures, would play a determinant role in seedling emergence and mortality in the first few years, especially at high elevations; (2) extreme cold events (if any) would accentuate seedling mortality; (3) plant provenance would strongly affect emergence and survival, with warmer provenances performing worse, especially at high elevations; (4) biotic interactions, through the protection provided by the overstorey and/or shrub cover, could partially buffer the signs of mal-adaptation to local conditions, especially those species and provenances established further from their current climatic range; and (5) responses to translocation distance and extreme cold events, as well as the effects of plant provenance and biotic interactions, would be species-specific.

Methods

Study area

The experiment was conducted at three pinewoods of natural origin located in the Catalan Pre-Pyrenees (NE Iberian

Peninsula), a mountain range extending from east to west, south of the main Pyrenean range (Fig. 1). The three forests are located on northern slopes of the same valley but set 10–15 km apart from each other, in mountains dominated by limestone and calcareous soils, covering an altitudinal gradient from around 900 to 1700 m a.s.l. In the area, this gradient includes the transition from sub-Mediterranean to upper montane bioclimatic territories, and involves the *Pinus nigra*–*P. sylvestris* transition zone, with *P. nigra* clearly dominating the overstorey up to 1100 m and *P. sylvestris* dominating from 1400 m upwards. Although forests in the area are clearly dominated by pines, some individuals or small groups of broad-leaved tree species (*Quercus*, *Acer*, *Sorbus* or *Prunus*) can be found sparsely distributed along the slopes, more frequently at low elevations. The main understorey species is common box (*Buxus sempervirens* L.), but other species of genera *Juniperus*, *Cotoneaster*, *Crataegus* or *Arctostaphylos* are also frequent (Burriel et al. 2004).

Species characteristics

We selected four resprouting *Quercus* species, each of which is widely distributed in the western Mediterranean Basin and part of the on-going process of tree species diversification in Mediterranean pine forests (Navarro-González et al. 2013; Vayreda et al. 2013; Martín-Alcón et al. 2015b). *Q. coccifera* L. and *Q. ilex* L. are common evergreen sclerophyllous oaks in Mediterranean areas of the Iberian Peninsula, whereas *Q. faginea* Lam. and *Q. pubescens* Willd. are semi-deciduous (marcescent) oaks commonly growing in sub-Mediterranean locations. All four species can be found growing naturally in the study sites, with the exception of *Q. coccifera*, which is nevertheless common in the southern slopes of the same mountains. The four species can be ranked on drought tolerance as $Qc > Qi > Qf > Qp$ (see ranges of Thornthwaite precipitation effectiveness index in their distribution areas in Table 1), and in the

opposite order for cold tolerance (Table 1). All the species are considered intolerant to intermediate-tolerant to shade (Niinemets & Valladares 2006), although they are favoured by moderate to high shading during the seedling establishment phase (Broncano et al. 1998; Retana et al. 1999; Lookingbill & Zavala 2000; Quero et al. 2006; Gómez-Aparicio et al. 2008; Caldeira et al. 2014).

For three of the four species studied (*Q. ilex*, *Q. faginea* and *Q. pubescens*) we selected vegetative material (seeds and plants) from two provenance regions (i.e. genetically different; Alía et al. 2005): (1) a local provenance, which corresponds to the study area (central Catalan Pre-Pyrenees); and (2) a provenance, which corresponds to warmer sites, located in the mountainous area extending from the south Iberian range to the Mediterranean coast in the case of *Q. ilex* and *Q. faginea* and in the Catalan Pre-Coastal range in the case of *Q. pubescens* (Fig. 1; see a more accurate delimitation of each provenance region in Appendix S1). In the case of *Q. coccifera*, for which our study sites were in all cases located beyond its ecological range, only the local provenance was tested. In order to obtain a better idea of the suitability of the study locations for each of the species and provenances, we compared the main climatic characteristics of the experimental sites to the mean climatic characteristics of their current range (Table 1; see further explanation about the climatic characterization in Appendix S2). All the experimental sites satisfy the water requirements of the study species, but their thermal conditions are at the coldest limit of their requirements for all the provenances tested, or even below these ranges in some cases (Table 1).

Experimental design

We selected three altitudinal levels at each of the three forests studied: low (around 1000 m a.s.l.), intermediate (around 1250 m a.s.l.) and high (around 1500 m a.s.l.). These levels represent a range of thermal migration dis-

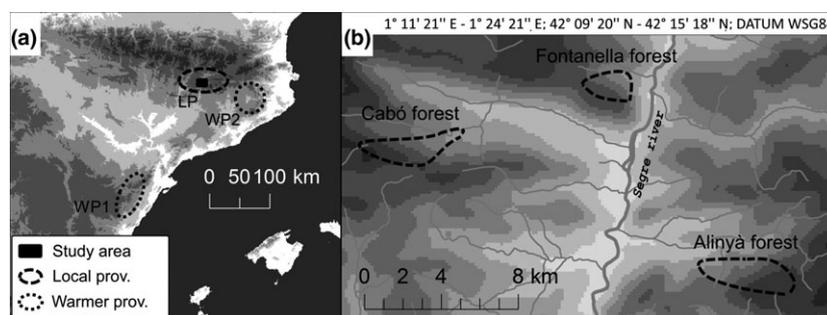


Fig. 1. Location of (a) the study area in northeast Iberian Peninsula and approximate zonation of local provenance (LP) of the vegetative material of all four species (*Q. coccifera*, *Q. ilex*, *Q. faginea* and *Q. pubescens*), warmer provenance of *Q. ilex* and *Q. faginea* (WP1) and of *Q. pubescens* (WP2); and (b) the study area spanning the three forests hosting the experiment.

Table 1. Descriptive statistics (mean \pm SD) for latitude, elevation and the main climatic attributes in the experimental sites and in the distribution area of each species in each of the provenance regions from which the vegetative material was collected (Appendix S1).

	Latitude (°)	Elevation (m)	Annual Precipitation (mm)	Mean Annual T (°C)	Mean Maximum T (°C)	Mean Minimum T (°C)	Thornthwaite PE Index	
Experimental sites (by elevation)								
High	42.2 \pm 0.1	1526.1 \pm 58.2	846.0 \pm 23.1	7.3 \pm 0.2	11.3 \pm 0.0	4.0 \pm 0.3	1.06 \pm 0.03	
Intermediate	42.2 \pm 0.1	1267.6 \pm 50.0	838.0 \pm 84.5	9.1 \pm 0.2	13.6 \pm 0.5	5.3 \pm 0.1	0.93 \pm 0.08	
Low	42.2 \pm 0.1	969.0 \pm 70.8	827.0 \pm 29.5	10.9 \pm 0.2	16.0 \pm 1.0	6.5 \pm 0.1	0.82 \pm 0.06	
Species	Provenance Region							
<i>Q. coccifera</i>	Local	41.6 \pm 0.4	610.5 \pm 119.9	643.9 \pm 92.5	13.1 \pm 1.3	18.1 \pm 0.9	5.9 \pm 1.0	0.58 \pm 0.13
<i>Q. ilex</i>	Local	42.1 \pm 0.2	699.2 \pm 114.7	697.6 \pm 117.2	11.1 \pm 1.1	16.9 \pm 1.1	4.5 \pm 1.3	0.69 \pm 0.13
<i>Q. ilex</i>	Warmer	40.5 \pm 0.2	615.3 \pm 121.0	615.3 \pm 121	12.1 \pm 0.9	17.6 \pm 1.1	6.6 \pm 0.9	0.60 \pm 0.12
<i>Q. faginea</i>	Local	42.1 \pm 0.1	719.1 \pm 110.8	719.1 \pm 110.8	10.9 \pm 1.3	17.2 \pm 1.3	4.4 \pm 1.4	0.70 \pm 0.13
<i>Q. faginea</i>	Warmer	40.6 \pm 0.1	640.0 \pm 97.9	640.0 \pm 97.9	11.9 \pm 0.9	17.1 \pm 1.0	6.6 \pm 0.9	0.64 \pm 0.09
<i>Q. pubescens</i>	Local	42.2 \pm 0.2	894.8 \pm 114.1	794.8 \pm 114.1	9.9 \pm 1.1	16.2 \pm 1.1	3.4 \pm 1.2	0.80 \pm 0.13
<i>Q. pubescens</i>	Warmer	42.0 \pm 0.2	848.1 \pm 115.0	848.1 \pm 115.0	11.5 \pm 1.5	18.1 \pm 1.3	6.9 \pm 1.7	0.84 \pm 0.13

tance for all the species, defined as the difference in thermal conditions between the current species' distribution area and the recipient locality. Accordingly, the species most displaced from its current distribution range was *Q. coccifera* (for which the difference in annual average mean daily temperature between its current range and the high altitudinal level of the experimental sites (ΔT_{mean}) reaches 5.8 °C). Conversely, the least displaced species was the local provenance of *Q. pubescens* (for which ΔT_{mean} in relation to the high altitudinal level of the experimental sites reaches 2.6 °C; Table 1).

At each elevation, two 12 m \times 12 m plots were established under contrasting conditions of canopy openness: one plot (canopy plot) was located under continuous pine overstorey, and the other (gap plot) was placed under a small canopy gap (mostly originating from old cutting and occasionally natural tree fall). The gap extent was equivalent to the area occupied by two to three adult trees (see further information about forest structural attributes in the experimental sites in Appendix S3).

Seven 2-yr-old seedlings of each combination of species \times provenance were planted in each plot in Oct–Nov 2011, for a total sample size of 882 seedlings (126 per species and provenance). Seedlings were randomly distributed across each plot and planted at least 1 m apart to avoid cross-interactions. The seedlings had been grown in nurseries located in the same region of provenance in which the seeds had been collected. Even though all plots were fenced off to prevent damage by wild or domestic animals, 29 seedlings (out of 882) had to be excluded from analyses due to damage by animals (probably small rodents).

One year after plant establishment, we selected five sowing points in each of the 18 plots (3 forests \times 3 eleva-

tions \times 2 levels of canopy openness). Three acorns of each species \times provenance combination were sown at 4-cm depth in each sowing point in Nov 2012. Acorns were collected the same autumn from trees growing in the same region of provenance from which the seedlings had been acquired. Non-viable acorns were eliminated through floating and visual screening prior to sowing. Each sowing point was covered with a 80 cm \times 80 cm wire mesh (0.6 cm mesh size) to avoid predation. No signs of seed predation by small rodents (including voles) were observed throughout the study period, but one of the plots had to be discarded due to severe damage presumably caused by a mustelid.

Monitoring

For the plantation experiment, seedling mortality was regularly monitored throughout the duration of the experiment. With the aim of disentangling the main factors driving mortality for each species at each location, we divided the observed mortality into either winter mortality (registered after each winter season) or summer mortality (registered after each summer season). The plots were frequently visited, and we only assigned mortality to a given period (summer or winter) when plants were found to be dead at the beginning of a period but had been recorded as healthy (absence of any symptoms of disease) at the end of the previous one. All seedlings determined as dead during one of the field campaigns were re-visited during the next growing season. Those seedlings that were able to resprout after the dieback event were then reclassified as alive for the analysis of mortality, and thus coded as 'resprouted'.

Seedling emergence from the sowing experiment was inspected and registered at different dates: Jun 2013, Oct

2013, Jun 2014 and Oct 2014. Every new seedling recorded was identified and its health status monitored during the next visits. We stopped monitoring seedling emergence after Oct 2014 since only two new emergences had been registered in that visit. At that point, all the individuals were unearthed in order to check whether they were independent seedlings or different stems of the same individual. Seedlings that qualified as multi-stemmed were then re-considered as a single individual. Seedling emergence was determined as the number of emerged seedlings per plot (i.e. the sum of the five sowing points in each plot) during two growing seasons after the date of sowing.

Characterization of the environment and micro-site explanatory variables

We examined meteorological data in the area over the 3-yr study period and compared it to the mean climatic data (see Appendix S2 for detailed explanation). This revealed the occurrence of some extreme climatic events over the 3 yr of the study, and in particular an extraordinarily dry and cold period in the first winter after planting (from Dec 2011 to Feb 2012; Appendix S2), which exposed the vegetation to significant risk of frost damage (aggravated by the low water content in the soil). During the first summer there was another rather dry period that extended over 3 mo (from Jun to Aug 2012), accompanied by slightly above average maximum temperatures. To characterize the microsite conditions of the planted seedlings, light availability and percentage herbaceous and shrub cover were measured for each seedling (Table 2). Light ratio was calculated as the percentage transmitted photosynthetic photon flux density (%PPFD) using two Li-190SA quantum sensors (Li-Cor, Lincoln, NE, US) in paired mode (see Appendix S3). Percentage herbaceous and shrub cover surrounding the seedlings was visually estimated to the nearest 5% using a 80 cm × 80 cm square centered on the plant.

Data analyses

Seedling emergence was analysed using a log-linear mixed effects Poisson model, with counts of emerged seedlings

per plot (from 0 to 15) as the response variable. GLMM parameters were estimated using maximum likelihood (ML) with Gauss-Hermite quadrature approximation (Pinheiro & Chao 2006). We fitted one model for each of the four species, and elevation (at three levels), canopy openness (two levels) and provenance (two levels) were included as fixed effects in the model, whereas forest was considered a random factor. Selection of variables for inclusion in the final models was based on Akaike's information criterion (AIC), with lower AIC values indicating stronger empirical support for a model (Bolker et al. 2009). Once the best model was obtained, it was compared against the null model (containing only random intercept and fixed intercept) using the likelihood ratio (LR) test.

The effect of elevation, canopy openness and region of provenance on survival of planted seedlings was assessed with survival function curves based on Kaplan–Meier estimates, and the Mantel-Cox log-rank test was used to determine the significance of the differences between factor levels. To test the effect of both categorical and continuous covariates on seedling survival, we used a mixed effects Cox model (Therneau & Grambsch 2000), which is a modification of the commonly used Cox's Proportional Hazards (coxPH) model (Cox 1972) that allows for inclusion of random effects. Summer and winter mortality were segregated as response variables, so we fitted a mixed effects Cox model for each response variable and species. Elevation and provenance were introduced as fixed factors, and the three variables measured at microsite level (herbaceous cover, shrub cover and light availability) and initial seedling size were introduced as fixed covariates. Plot and forest were considered random factors. For the Cox model, the variables for inclusion in the final models were selected by comparing the full model against reduced models in terms of the log-likelihood (Loglik) value, with higher Loglik values indicating a better fitting model (Huelsenbeck & Crandall 1997). The hazard ratio (HR) was computed for each significant predictor variable. For categorical variables, HR represents the quotient of the hazard functions for each of the factor levels compared to a reference level. For continuous variables, HR indicates the expected change in the risk of mortality with a one unit increase in the explanatory variable.

Table 2. Descriptive statistics (mean ± SD) of the microsite attributes measured at the seedling level, grouped by altitudinal level and type of canopy openness ($n = 147$).

Plot-Level Attributes	Low Elevation		Intermediate Elev.		High Elev.	
	Canopy	Gap	Canopy	Gap	Canopy	Gap
Herbaceous cover (%)	37.9 ± 26	38.8 ± 22.1	39.9 ± 25.6	52.6 ± 27.3	36.9 ± 23.3	43.1 ± 22.7
Shrub cover (%)	11.6 ± 7.7	20.8 ± 15.9	31.5 ± 25.6	16.6 ± 12.9	22.1 ± 18.1	20.9 ± 14.9
Light ratio (%PPFD)	17.9 ± 2.4	36.4 ± 7.2	19.6 ± 5.5	36.8 ± 10.3	13.3 ± 2.2	28.8 ± 6.9

Finally, to assess seedling resprouting after dieback, logistic mixed effects models were fitted for each species using the ML method with Laplace approximation in the same model structure (i.e. candidate predictors and random factors) as in the mixed effects Cox models. We created a response variable named 'resprouted' that takes value of '1' for seedlings that were able to resprout and survived and '0' otherwise. The inclusion of variables in the logistic mixed effects models was based on the AIC, and comparison of nested null and best models was assessed using the LR test. All analyses were performed using R 3.1.1 software (R Foundation for Statistical Computing, Vienna, AT) and the 'lme4' v. 1.1-7, 'survival' v. 2.38-1 and 'coxme' v.2.2-4 packages for R.

Results

Seedling emergence

The emergence of oak seedlings occurred during the first two growing seasons. A total of 69 *Q. coccifera*, 249 *Q. ilex*, 267 *Q. faginea* and 305 *Q. pubescens* seedlings emerged during this period, representing 27%, 49%, 52% and 60% of the sown acorns, respectively. *Q. coccifera* presented the most delayed emergence, with 43.5% occurring during the second growing season compared to around 23% for the other species. For all species, lag to emergence was related to altitudinal level, with plots at high elevations showing the most delayed emergence (40.8% during the second growing period) compared to intermediate (25.6%) and low elevation plots (16.6%). We found no significant differences in emergence date between the two levels of canopy openness or between seed provenances. For all species except *Q. pubescens*, emergence was significantly lower at plots located at highest elevation but did not differ between low and intermediate plots (Table 3). Seed provenance only affected seedling emergence for *Q. ilex*, with the warmer provenance presenting lower emergence rates across altitudinal

levels. No significant differences in emergence were found between canopy and gap plots.

Seedling survival

Seasonal patterns and altitudinal effects

Overall survival rate of planted seedlings after three growing seasons was significantly higher ($P < 0.001$) for marcescent species (*Q. faginea* and *Q. pubescens*, both showing 82.7% survival) than for evergreen oaks (*Q. coccifera* and *Q. ilex*, with 63.2% and 69.9% survival, respectively). Furthermore, these two groups showed different seasonal patterns of mortality: mortality for evergreen oaks occurred mostly during winter (93% and 90%, respectively), especially the first winter (80% and 73%), and mortality was significantly higher at the highest plots ($P < 0.001$ for both species). On the other hand, mortality for marcescent oaks concentrated on the first 2 yr after planting, but was evenly distributed over seasons, and with much lower effect of elevation on survival.

When splitting the data into winter and summer mortality, mixed effects Cox models showed that winter mortality rates were significantly higher at the highest altitudinal level compared to the lowest level for all four species (Table 4). This effect was stronger in the case of *Q. pubescens* (HR = 9.328) and *Q. coccifera* (HR = 8.070), followed by *Q. ilex* (HR = 5.75), and was weaker, but still significant, for *Q. faginea* (HR = 3.806). The high HR value in *Q. pubescens* was due to the almost null winter mortality in the lowest altitudinal level (Fig. 2). For *Q. ilex*, significantly higher winter mortality rates were also found in the intermediate altitudinal level (HR = 2.273) compared to the lower level. Both local and warmer provenances of *Q. ilex* were negatively affected by elevation, although the effect was more pronounced for the warmer provenance seedlings (see Kaplan–Meier curves for the interaction between elevation and provenance in Fig. 2). In fact, the significantly higher mortality rates of the warmer prove-

Table 3. Results of the log-linear mixed effects Poisson models of seedling emergence. Significant fixed terms in the best model for each of the sown species are shown, along with the AIC of both the best model (AIC_{Best}, containing all the fixed terms that produced a significant effect) and the null model (AIC_{Null}, containing only the intercept), and the significance of the LR test realized for model comparison. Elevation level is: H = High. Provenance level is: W = Warmer.

Species	Best Model Terms (Fixed)	Estimate	SE	Sig.	AIC _{Best}	AIC _{Null}	P (>Chisq)
<i>Q. coccifera</i>	Intercept	1.598	0.231	0.002	29.207	42.978	<0.001
	Elevation = H	-1.420	0.448	0.007			
<i>Q. ilex</i>	Intercept	1.877	0.144	<0.001	57.713	71.118	<0.001
	Elevation = H	-0.466	0.173	0.007			
	Provenance = W	-0.402	0.130	0.002			
<i>Q. faginea</i>	Intercept	2.480	0.127	<0.001	35.626	39.271	0.022
	Elevation = H	-0.405	0.146	0.07			
<i>Q. pubescens</i>	Intercept	2.101	0.060	<0.001	–	41.100	–

Table 4. Mixed effects Cox proportional hazards model of 3-yr winter and summer mortality of the planted seedlings of the four *Quercus* species. Significant fixed factors and covariates in the best model for each of the species are shown with their hazard ratio (HR) values, along with the log-likelihood (Loglik) values of both the best model (Loglik_{BM}, containing all the fixed terms that produced a significant effect) and the null model (Loglik_{NM}, containing only the intercept), and the significance of the LR test realized for model comparison. Elevation levels are: H (High) and IM (Intermediate). Provenance level is: W = Warmer.

Species	Model	Terms	Estimate	SE	HR ¹	Sig.	Loglik _{BM}	Loglik _{NM}	P (>Chi ²)
<i>Q. coccifera</i>	Winter mortality	Elevation = H	2.088	0.511	8.070	<0.001	-179.21	-194.72	<0.001
		Light ratio	0.033	0.013	1.033	0.012			
		DO	-0.827	0.279	0.437	0.003			
<i>Q. ilex</i>	Summer mortality	Light ratio	0.153	0.071	1.165	0.032	-9.74	-13.25	0.008
		Light ratio	0.153	0.071	1.165	0.032			
	Winter mortality	Elevation = IM	0.821	0.417	2.273	0.049	-331.08	-316.44	<0.001
		Elevation = H	1.749	0.378	5.750	<0.001			
		Provenance = W	0.879	0.262	2.408	<0.001			
	Summer mortality	-	-	-	-	-	-	-	-
<i>Q. faginea</i>	Winter mortality	Elevation = H	1.337	0.567	3.806	0.018	-126.08	-129.46	0.034
	Summer mortality	Shrub cover	0.024	0.010	1.024	0.020	-86.65	-88.82	0.037
<i>Q. pubescens</i>	Winter mortality	Elevation = H	2.233	0.778	9.328	0.004	-143.72	-148.9	0.006
	Summer mortality	Light ratio	0.050	0.018	1.052	0.006	-77.57	-81.13	0.008

¹For categorical predictor variables, the hazard ratio (HR) represents the quotient of the hazard functions for each of the factor levels compared to a reference level (Low, for Elevation; Local, for Provenance). For continuous variables, HR indicates the expected change in risk of mortality with a one unit increase in the parameter in question.

nance *Q. ilex* compared to local provenance (HR = 2.408) were fundamentally linked to the winter mortality events (Table 4).

Canopy openness and biotic interactions

In the case of *Q. coccifera*, the negative effect of elevation on seedling survival was accentuated under gap conditions. The Cox models for this species revealed a significant effect of plant exposure (as light ratio at each seedling location, %PPFD) for both winter (HR = 1.033) and summer (HR = 1.165) mortality events. In the case of *Q. pubescens*, the Kaplan–Meier curves for factor interactions (Fig. 2) revealed that the negative effect of elevation was almost exclusively linked to warmer provenance seedlings planted under canopy gap conditions. Canopy openness was found to significantly affect seedling mortality for the two marcescent species, both of which showed significantly higher mortality rates under gap conditions ($P = 0.016$ for *Q. faginea* and $P = 0.013$ for *Q. pubescens*). Looking at the interaction between elevation and canopy openness, we found that the significant reduction of *Q. faginea* mortality rates under continuous canopy occurred only in the lower and intermediate altitudinal levels, but not in the higher level. A similar effect was found by the summer mortality Cox model for *Q. pubescens*, which showed a higher ratio of summer mortality of this species with increasing light ratio (HR = 1.052). Shrub cover negatively affected *Q. faginea* seedling survival during the summer periods but not the other oak species (Table 4). Similarly, size of the seedling at the time of planting

(represented by the seedling basal diameter, DO) had very little effect on seedling survival and only affected *Q. coccifera*, which showed a significantly lower ratio of winter mortality with increasing DO.

Seedling resprouting after dieback

The ability to recover by resprouting after a dieback event was higher for *Q. faginea* than for the other species (70.4% of the 142 seedlings of this species suffering a dieback event were able to re-sprout during the following seasons). The percentages of re-sprouted seedlings for the other species were 59.7% for *Q. coccifera* (from 77 dieback events), 59.0% for *Q. pubescens* (from 105 dieback events) and 54.5% for *Q. ilex* (from 156 dieback events). Surprisingly, none of the candidate explanatory variables showed a significant effect on resprouting in *Q. faginea* seedlings. For *Q. pubescens* and *Q. coccifera*, the models found an effect of seedling size, with individuals presenting higher stem diameter being more able to resprout (Table 5). Interestingly, the warmer provenances of *Q. pubescens* and *Q. ilex* showed significantly lower resprouting ability than the local provenances.

Discussion

Thermal distance and extreme cold events in assisted migration

The results of our study highlight that both the thermal distance between the current species' distribution range and the recipient locality and the occurrence of extreme cold events can have strong effects on the performance of

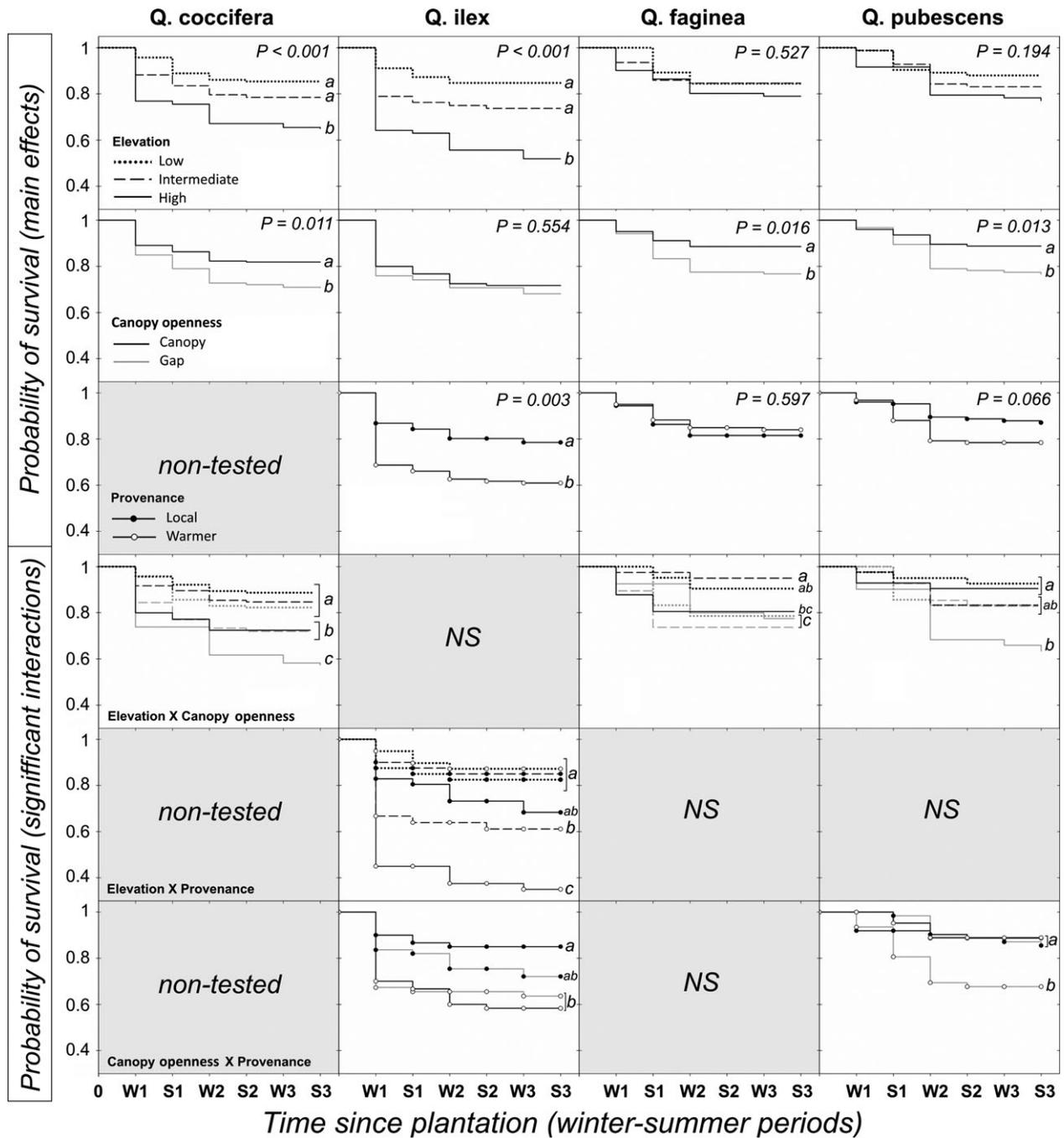


Fig. 2. Survival curves for the planted seedlings of the four tree species over the course of the 3-yr study period, based on Kaplan–Meier estimates. Rows represent the different main effects and interactions, and columns represent the different species. Legends for each row of the main effects are in the first plot of the row, and legends for each row of the interactions correspond to the union of the legends of the effects taking part in the interaction. *P*-values indicate significance of the log-rank test between factor levels for each species. W periods in the x-axis correspond to the 1st, 2nd and 3rd winter seasons after planting, and S periods to the summer seasons.

the translocated populations. Both factors therefore warrant careful consideration when selecting species and seed sources for assisted migration programmes (Vitt et al. 2010; Pedlar et al. 2013; Benito-Garzón & Fernández-

Manjarrés 2015). In our study, potential signs of species mal-adaptation to large thermal migration distances include: (1) the overall lower germination rate of *Q. coccifera*, which is the species most displaced from its ecologi-

Table 5. Results of the logistic mixed effects models of seedling resprout after dieback events. Significant fixed terms in the best model for each of the planted species are shown, along with the AIC of both the best model (AIC_{Best}, containing all the fixed terms that produced a significant effect) and the null model (AIC_{Null}, containing only the intercept), and the significance of the LR test realized for model comparison. Provenance level is: W = Warmer.

Species	Model Term (Fixed Effects)	Estimate	SE	AIC _{Best}	AIC _{Null}	P (>Chi ²)
<i>Q. coccifera</i>	Intercept	-4.035	1.289	101.07	109.80	0.001
	DO	1.284	0.447			
<i>Q. ilex</i>	Intercept	0.707	0.452	207.74	213.93	0.004
	Provenance = W	-0.999	0.362			
<i>Q. faginea</i>	Intercept	0.943	0.298	-	176.02	-
<i>Q. pubescens</i>	Intercept	4.873	2.086	134.13	145.11	<0.001
	Provenance = W	-2.377	1.091			
	DO	0.362	0.181			

cal range; (2) the lower germination rate at the highest altitudinal level (for all the species but *Q. pubescens*); (3) the mid-to-low survival of the evergreen *Q. coccifera* and *Q. ilex* seedlings planted at the highest elevation; and (4) the lower germination and survival of some of the warmer provenances (especially *Q. ilex*), for which the thermal migration distance was much higher than for the local provenances. In spite of this, a considerable proportion of seedlings of all species performed relatively well in all the altitudinal levels, and there were no significant differences in the performance of most of the species between the lowest and the intermediate levels. This would suggest these species are able to tolerate moderate displacements in elevation to colder sites.

On the other hand, the fact that most of the winter mortality of the species showing higher sensitivity to cold (*Q. coccifera* and *Q. ilex*) occurred during the extreme cold event in the first winter confirmed the decisive role of such events as a driver of seedling responses to translocation (Ameztegui & Coll 2013; Benito-Garzón et al. 2013). However, the extraordinarily hot and dry summer periods did not lead to any substantial increase in mortality, which may be explained by the fact that all provenances came from drier sites, thus probably exhibiting a more conservative water-use behaviour (Leverkus et al. 2015).

The role of forest overstorey in buffering negative responses to translocation

The fact that forest overstorey plays an important role in maintaining a suitable microenvironment for the germination and early establishment of *Quercus* species has been widely reported and generally attributed to the fact that the canopy provides protection from direct exposure to light and high evaporative demand (Broncano et al. 1998; Lookingbill & Zavala 2000; Prévosto et al. 2011; Caldeira et al. 2014; Martín-Alcón et al. 2015b). In our study area, we found higher summer mortality in three of the four species (*Q. coccifera*, *Q. faginea* and *Q. pubescens*) when planted under gap conditions and at lower elevations, thus

confirming the facilitative role of canopy cover. In addition, the pine overstorey also played an important role in buffering the negative effects of thermal distance (represented by elevation) and extreme cold events on seedling survival, by reducing winter mortality at higher elevations. This result has important implications and suggests the advantage of planting/sowing under relatively closed canopy to buffer negative responses to cold in assisted migration programmes. Previous studies had also demonstrated a facilitative effect of shrubs in the establishment of *Quercus* seedlings, especially in the context of very open habitats (Rousset & Lepart 1999; Gómez-Aparicio et al. 2005; Kunstler et al. 2007; Smit et al. 2008), but we did not find any such effect here. The relatively low abundance of shrubs in the understorey of our study sites, together with the lack of important differences in shrub cover between the canopy and the gap plots might be the origin of this divergence.

Intra- and interspecific differences in responses to plant translocation

This experiment found important inter- and intraspecific differences in responses to translocation in terms of germination, survival and resprouting. We expected a high sensitivity to translocation for *Q. coccifera*, which is the species with the largest thermal migration distance to all the study sites. However, *Q. coccifera* showed more than 50% survival after the 3 yr, high resprouting rates after dieback and delayed seedling emergence, which indicates a non-negligible plasticity to cold temperatures. The plastic behaviour of this species was also observed by Baquedano et al. (2008), who found that phenotypic plasticity in response to water stress explained around 75% of the variability of different physiological and structural parameters among individual plants.

The other evergreen species (*Q. ilex*) was expected to respond to translocation in much the same way as *Q. faginea*, since both species co-exist in both provenance regions, where they occupy similar ecological niches with

regard to thermal conditions (Espelta et al. 2005). However, we found that *Q. ilex* was less able to cope with cold stress than *Q. faginea*, as shown by its higher mortality when growing at high elevations. This negative response was particularly important for *Q. ilex* plants from the warmer populations, which suggests the existence of high ecotypic specialization in this species (Gratani et al. 2003; Peguero-Pina et al. 2014). In contrast, provenance did not play a significant role in the survival of *Q. faginea* or *Q. pubescens* along the altitudinal gradient studied. Although previous studies have shown similar phenotypic plasticity to light and drought between evergreen and marcescent oaks (Espelta et al. 2005; Castro-Díez et al. 2006), our results would suggest higher plasticity of marcescent oaks in response to cold stress. This could be related to their higher capacity to adapt phenologically in response to low temperatures (Morin et al. 2007; Vitasse et al. 2014), in contrast to the reported higher phenological plasticity of evergreen oaks in response to summer drought (Montserrat-Martí et al. 2009).

Conclusions

This study serves as a first replicated field trial to evaluate the feasibility of management interventions based on planting or sowing late successional species for diversifying sub-Mediterranean pinewoods using an assisted migration approach. Initial establishment success was high in both the planting (with an overall 76.3% survival after the 3 yr, reaching 82.7% for the species showing better performance) and sowing (with an overall 50% of seedling initial emergence, reaching 60% for the species showing better performance) experiments, in line with previous diversification experiments carried out in Mediterranean pine forests (Palacios et al. 2009; González-Rodríguez et al. 2011; Prévosto et al. 2011). However, the performance of the translocated populations for some of the species was found to be highly dependent on the distance in thermal conditions from source locality to recipient locality, and on the occurrence of extreme cold events. Our results also showed the important role of forest overstorey in buffering the negative effects of thermal distance and extreme cold events on seedling survival. Finally, we found signs of high ecotypic differentiation in regard to cold tolerance among different oak species (in particular the evergreens). In contrast, the marcescent species, principally *Q. faginea*, showed signs of high phenotypic plasticity to cold. These key intra- and interspecific differences strongly underline the importance of managing risks in assisted migration programmes by employing multiple seed sources, establishing field trials to guide seed movements, and exercising caution when calculating migration distances.

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Supporting Information

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

Appendix S1. Delimitation of the provenance regions tested for the different species studied.

Appendix S2. Characterization of the main climatic attributes of the experimental sites and provenance regions.

Appendix S3. Characterization of other microsite attributes of the experimental sites.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.



Assisted migration is a feasible option to increase the diversity and resilience of the sub-Mediterranean pinewoods. In these interventions, the thermal migration distance and the occurrence of extreme cold events have strong effects on the responses of some species (particularly the evergreen oaks), and the forest overstory plays an important role in attenuating some negative effects of plant translocation.