RESEARCH ARTICLE

Restoring for the present or restoring for the future: enhanced performance of two sympatric oaks (*Quercus ilex* and *Quercus pyrenaica*) above the current forest limit

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Reforestation is common to restore degraded ecosystems, but tree-species choice often neglects ongoing environmental changes. We evaluated the performance of planted seedlings of two oak species at two sites in a Mediterranean mountain (Sierra Nevada, SE Spain): one located within the current altitudinal forest range (1,600–1,760 m), and one above the upper forest limit (1,970–2,120 m). The forest service planted 1,350 seedlings of the deciduous Pyrenean oak and the evergreen Holm oak in a postfire successional shrubland. After 2 years, seedlings were monitored for survival, and a subset of 110 Pyrenean oaks and 185 Holm oaks were harvested for analyses of biomass and foliar nutrient status, δ^{13}C, and δ^{18}O. Both species showed the highest survival and leaf N status above the upper forest limit, and survival increased with altitude within each plot. The deciduous oak benefited most from planting at higher altitude, and it also had greater biomass at the higher site. Correlations between foliar N, δ^{18}O, and δ^{13}C across elevations indicate tighter stomatal control of water loss and greater water-use efficiency with increasing plant N status at higher altitude, which may represent a so-far overlooked positive feedback mechanism that could foster uphill range shifts in water-limited mountain regions. Given ongoing trends and future projections of increasing temperature and aridity throughout the Mediterranean region, tree-species selection for forest restoration should target forecasted climatic conditions rather than those prevailing in the past. This study highlights that ecosystem restoration provides an opportunity to assist species range shifts under rapidly changing climate.

Key words: assisted colonization, climate change, isotopic analysis, reforestation, stable isotopes, uphill shifts

Implications for Practice

- Due to ongoing climate warming and aridification in large areas of the planet, optimum conditions for reforestation may now include sites that were previously beyond species distribution ranges, especially for more drought-sensitive tree species.
- In mountain areas with increasing aridification due to climate change, proper conditions for forest restoration may now be found at higher elevation than in the past, as species climatic niches are shifting uphill.
- Restoring with consideration of future climatic conditions will assist species uphill range shifts under rapidly changing climate, as natural shifts are often limited by biotic and abiotic constraints.
- Assisted colonization of degraded ecosystems may aid the persistence of target species while enhancing ecosystem adaptation to climate change.

Introduction

Restoration activities are widespread to recover the integrity and sustainability of ecosystems, enhance biodiversity, and recover ecosystem services (SER 2004; MA 2005). Given the importance of past vegetation as an indicator of the current potential vegetation in degraded areas, a traditional paradigm is to take the ecosystems of the past as reference models to be re-established (Hobbs & Harris 2001; Harris et al. 2006; Choi et al. 2008).

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Consequently, reforestation—among the most frequent restoration activities in terrestrial ecosystems—often aims at regaining the cover of native plant species whose presence in the area was recorded in the past. However, these efforts are doomed to fail in cases in which the environmental conditions required by the planted species are no longer present or are predicted to change in the near future, for example, due to climate change (Hobbs & Harris 2001; Harris et al. 2006; Choi et al. 2008; Woodworth 2013). In fact, the potential distribution ranges of many tree species are shifting latitudinally toward the poles and altitudinally up the mountains as a consequence of increasing temperatures and drought frequency and intensity (Kelly & Goulden 2008; Jump et al. 2009; Matías & Jump 2014). These range shifts are particularly evident in mountains due to the much smaller distances over which the changes occur as compared with latitudinal shifts (Jump et al. 2009). Mountains thus provide ideal study systems to evaluate the success of forest restoration under rapidly changing climatic conditions.

Oak forests are among the most widespread vegetation types in the Northern Hemisphere, and they provide numerous ecological, societal, and economic services. In many places, these ecosystems have been degraded or encounter difficulties in their regeneration (Dey et al. 2008; MacDougall et al. 2010), so reforestation with species of *Quercus* is frequently considered in restoration policy (e.g. EEC regulation no. 2080/92). Deciduous and evergreen oak species coexist in large areas of their distribution ranges. When they coexist, evergreen oaks typically dominate drier positions of the landscape, whereas deciduous oaks are often restricted to higher elevations and/or wetter areas (Blanca et al. 2001; Blondel et al. 2010). Evergreen trees exhibit a more conservative water-use behavior than deciduous ones due to a tighter control of stomatal conductance and a greater sensitivity to leaf-to-air water vapor pressure differences (Mediavilla & Escudero 2003; López-Iglesias et al. 2014). Under the expected scenario of rising temperatures and increasing aridity in the Mediterranean Basin (Easterling et al. 2000; IPCC 2012), environmental conditions should become less favorable for oak forest regeneration within their current range, especially for deciduous oak species with lower drought tolerance (Gea-Izquierdo et al. 2013).

In this study, we seek to investigate the success of reforestation with two sympatric oak species in a Mediterranean mountain area (Sierra Nevada, SE Spain). We planted seedlings of an evergreen (*Quercus ilex*) and a deciduous (*Q. pyrenaica*) oak species, both of which form native forests and woodlands in the Mediterranean region. The study considered two altitudes within distinct vegetation belts: (1) approximately 1,700 m a.s.l. (above sea level), where both oak species currently form mature forests, and (2) approximately 2,050 m a.s.l., an area above the current distribution range of forests in Sierra Nevada. Seedlings were monitored during 2 years for demographic parameters (survival and growth), and leaf nutrient concentrations (N, P) and isotopic composition ($\delta^{13}C$ and $\delta^{18}O$) were measured at the end of the second growing season. This allows evaluating the ecophysiological response of the oak seedlings to the environmental conditions prevailing at these sites of contrasting elevation.

Stable isotope ratios provide time-integrated information on plant physiological response to changing abiotic conditions (Dawson et al. 2002). In C3 plants, leaf carbon isotopic ratios—$\delta^{13}C$, the ratio of ^{13}C to ^{12}C—are related to the ratio of intercellular to atmospheric CO_2 concentrations (Farquhar et al. 1989), and can provide a time-integrated measure of intrinsic water-use efficiency (WUE_i). WUE_i is defined as the ratio between net photosynthetic rate (A) and stomatal conductance to water vapor (g_s) (Dawson et al. 2002). Water shortage and drought stress induce the progressive closure of stomata, which reduces both A and g_s, although A is reduced to a lesser extent than g_s, which thus increases WUE_i. At the same time, the lower diffusion of CO_2 into the leaf due to stomatal closure increases the intercellular concentration of ^{13}C, leading to more of the heavy isotope being assimilated and the photosynthate becoming more enriched in ^{13}C (Farquhar et al. 1989). Leaf oxygen isotopic composition ($\delta^{18}O$) is affected by the isotopic signature of the source water used by the plant, but also by changes in stomatal conductance and transpiration. As foliar $\delta^{18}O$ is affected by g_s (so that higher values of g_s lead to lower leaf $\delta^{18}O$ values) but not by A, leaf $\delta^{18}O$ data can greatly aid the interpretation of leaf $\delta^{13}C$ data (Barbour 2007). This is so because stomatal limitations to photosynthesis affect both $\delta^{13}C$ and $\delta^{18}O$, whereas biochemical limitations influence $\delta^{13}C$ but not $\delta^{18}O$ (Scheidegger et al. 2000). Measuring foliar nutrient concentrations and plant growth parameters can further aid in the interpretation of leaf $\delta^{13}C$ and $\delta^{18}O$ data (e.g. Querejeta et al. 2008).

Given the current trend of increasing aridification in the Mediterranean Basin (IPCC 2012) and in the study area in particular (Ruiz Sinoga et al. 2011), we hypothesize that the establishment and performance of the two oak species will be favored at higher elevation as a response of species range shifts. On the other hand, given the greater drought sensitivity of Mediterranean deciduous species compared with evergreen species (Mediavilla & Escudero 2003; Gea-Izquierdo et al. 2013; López-Iglesias et al. 2014), we hypothesize that the deciduous *Q. pyrenaica* will show a greater response to changes in elevation and climate between sites than the evergreen *Q. ilex*. The results of this study should help to elucidate whether the potential altitudinal distribution/regeneration niche of the target oak species might have expanded upslope in response to the prevailing warmer and drier conditions, and also reveal whether the success of ecosystem restoration in mountain areas may be enhanced by considering changes in climatic conditions.

Methods

Study Species

Quercus ilex L., the Holm oak, is a sclerophyllous evergreen tree widely distributed across the Western Mediterranean Basin. *Quercus pyrenaica* Willd., the Pyrenean oak, is a deciduous tree distributed from SW France through N Morocco. In the southern Iberian Peninsula, both species grow up to 1,800 m a.s.l., as part of the Supramediterranean vegetation belt (Costa-Tenorio et al. 1998; Valle 2003), whereas the vegetation above this altitude is

dominated by stunted and cushion shrubs characteristics of the Oromediterranean belt (Valle 2003). In S Spain, *Q. pyrenaica* forests are frequently mixed with *Q. ilex*, although the deciduous *Q. pyrenaica* often substitutes its evergreen counterpart at higher elevations and at more mesic sites (Costa-Tenorio et al. 1998). Despite the key importance of the conservation of both types of oak forests (Lorite et al. 2008; WWF 2011), they have been extensively degraded, and they currently occupy small, fragmented patches within their potential range (Costa-Tenorio et al. 1998; García & Jiménez Mejías 2009; WWF 2011). In particular, the Sierra Nevada populations of *Q. pyrenaica* are relict in Andalusia due to intensive human exploitation and land-use changes (Pérez Luque 2011).

Study Site and Experimental Design

The study was conducted between 2010 and 2011 in the Sierra Nevada National and Natural Park (SE Spain), in an area that was affected by a wildfire that burned 3,400 ha of shrublands and 40–60-year-old pine plantations in September 2005 (Leverkus et al. 2012). Pine species had been planted at different elevation according to their climatic requirements, and the fire was of high severity across the burnt area (Marañón-Jiménez et al. 2013). Two plots greater than 20 ha in surface and approximately 1.5 km apart were established in collaboration with the local Forest Service to test the success of native-forest restoration: one at 1,700 m a.s.l. (low plot, hereafter; altitude of the centroid of the plot), and the other one at 2,050 m a.s.l., with higher rainfall and lower temperatures in the latter (high plot; Table 1; Fig. 1). These altitudinal (and, consequently, climatic) differences led both plots to be categorized onto different bioclimatic belts or life zones (Blanca et al. 2001; Valle 2003). The low plot was in the Supramediterranean belt, where forests of both oak species are part of the historical vegetation. The high plot was located in the Oromediterranean belt, thus above the current altitudinal limit of native oak forests (Valle 2003). Both plots were dominated by early-successional shrubs and perennial grasses that regenerated abundantly after the fire (Table 1). Plant species composition differed among plots, with typical species from the Supramediterranean and lower-elevation vegetation belts at the low plot and species from the Oromediterranean belt at the high plot (Appendix S1, Table S1, Supporting Information). The plots had similar bedrock (micaschist) and soil type (Haplic phaeozems; Marañón-Jiménez et al. 2013). Soil texture, nutrient content, mineral composition, and other properties were similar between plots. Only soil pH, bulk density, and N differed slightly among plots (Table 1), in a way that could be expected due to the differences in elevation (Reich & Oleksyn 2004). The plots also had similar slope (circa 30%), although they were both terraced 40–60 years prior to the study to ease the plantation of pines, thus minimizing potential effects of slope on seedling development. Both plots had a dominant W/SW aspect (Table 1, Fig. S1).

Climate in the area is typical Mediterranean, with mild, wet winters and hot, dry summers. Mean precipitation recorded at a nearby meteorological station at 1,652 m a.s.l. averages 511.1 ± 239.1 mm (period 1989–2011; values for climatic variables are mean ± SD). Rainfall during the summer months (June–September) was 60.9 mm in 2010, 12.9 mm in 2011, and 52.8 ± 35.0 in the period 1989–2009. Mean minimum and maximum daily temperatures of the coldest month (January) were −1.1 and 6.8°C in 2010, −0.7 and 5.5 in 2011, and 0.5 ± 2.6 and 8.6 ± 2.7°C in 1989–2009. Mean minimum and maximum daily temperatures of the hottest month (July) were 18.1 and 27.3°C in 2010, 16.6 and 25.5°C in 2011, and 17.9 ± 2.1 and 27.5 ± 2.2°C in 1989–2009. The differences in climatic conditions between the two plots were estimated from interpolated maps obtained from the Sierra Nevada Global Change Observatory for 1981–2010 (http://linaria.obsnev.es/). These rendered a mean rainfall of 550 ± 215 mm at the low plot and 630 ± 227 mm at the high plot, a mean minimum daily temperature of 5.6 ± 1.2°C at the low plot and 3.4 ± 1.2°C at the high plot, and a mean maximum daily temperature of 16.2 ± 1.1 at the low plot and 13.4 ± 1.1°C at the high plot.

In March–April 2010, the local Forest Service conducted an experimental oak plantation in the study plots. An excavator dug holes of approximately 60 × 60 × 60 cm in the terrace beds, in which forestry workers planted the seedlings at approximately 400 seedlings per hectare (Leverkus et al. 2012). The seedlings of the two species were intermingled across each experimental plot (Fig. 1; Appendix S2, Fig. S2).

Seedling Survival

A subsample of 642 and 540 *Q. ilex* (low and high plot, respectively) and 549 and 501 *Q. pyrenaica* seedlings (low and high plot) were tagged to monitor seedling survival, and their position was recorded with a Leica GPS SR20 with external antenna. These seedling numbers were obtained after a resampling procedure to eliminate small differences in sample size among different postfire management areas (Appendix S3, Table S2). Survival was monitored in June 2010 to discard seedlings that died due to transplanting shock, and thereafter at the end of the first summer (September 2010), first winter (June 2011), and second summer (September 2011). We also intended to monitor damage due to ungulate herbivores, but it was negligible and not further considered. We acknowledge that there is no spatial replication of each elevation (greatly due to the complex logistics of collaborating with different stakeholders). However, given that the seedlings were planted in a large area (>20 ha) at each altitude, that the plots had similar topographic and soil characteristics, and that seedlings of the two species were completely intermingled, we consider that the design allows to compare the performance of these two oak species at different elevations. In addition, it was possible to evaluate the effects of altitude gradients within each plot (150–170 m) on seedling survival given the existence of precise data on seedling position.

Seedling Biomass, Nutrient Content, and Isotopic Composition

In September 2011 (2 years after planting), a total of 87 and 90 *Q. ilex* (low and high plot, respectively) and 45 and 42 *Q. pyrenaica* seedlings (low and high plot) were harvested for biomass, leaf nutrient (N and P), and leaf isotopic (δ^{13}C, δ^{13}O)

Table 1. Key properties of the study plots. [a]Values are the range of elevation. [b]10th and 90th percentile of pixel values calculated in ArcGIS from digital elevation models. [c]Values indicate mean ± 1 SE of the mean hereafter. [d]Properties measured a few weeks after the fire. Pine density within each plot was sampled in 36 quadrats of 25×25 m, and tree height on 30 randomly-chosen trees within each quadrat. [e]See Appendix S1 for indicator species and percent cover of most abundant species; for detailed species composition and abundance, see Leverkus et al. (2014). [f]Sampled in 2008. Soil texture data are based on three samples per plot and were analyzed with Mann–Whitney U-tests. The rest of the soil properties are based on 20 samples per plot and were analyzed with Student's t-tests. Soil data were extracted from Marañón-Jiménez et al. (2013). Significance levels are as follows: ns, not significant; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Variable	Low Plot		High Plot
Elevation (m a.s.l.)[a]	1,600–1,760		1,970–2,120
Area (ha)	21		32
Aspect (degrees)[b]	222–283		225–264
Direct solar radiation at summer solstice (W h m^{-2})[b]	6,406–6,893		6,722–7,060
Bioclimatic belt	Supramediterranean		Oromediterranean
Dominant prefire afforested species	*Pinus nigra*		*Pinus sylvestris*
Pine density (individuals per hectare)[c,d]	1,064 $\pm$ 67		1,051 $\pm$ 42
Pine height (m)[d]	6.6 $\pm$ 0.1		6.2 $\pm$ 0.1
Average plant cover in 2007[e]			
Perennials (%)	42.9		61.8
Annuals (%)	26.3		11.1
Bare soil (%)	30.9		27.1
Soil properties[f]			
Texture	Sandy loam		Sandy loam
Clay (%)	12.5 $\pm$ 1.5	ns	8.8 $\pm$ 0.3
Fine loam (%)	16.7 $\pm$ 1.3	ns	12.5 $\pm$ 0.4
Coarse loam (%)	11.9 $\pm$ 0.7	ns	9.7 $\pm$ 0.4
Sand (%)	58.9 $\pm$ 3.2	ns	69.0 $\pm$ 0.1
Stoniness (% vol.)	41.8 $\pm$ 1.3	ns	45.2 $\pm$ 1.7
Bulk density (g/cm^3)	1.3 $\pm$ 0.1	*	1.2 $\pm$ 0.1
Cation exchange capacity (cmol$^+$/kg soil)	5.3 $\pm$ 0.3	ns	4.6 $\pm$ 0.3
pH	7.3 $\pm$ 0.1	***	6.7 $\pm$ 0.1
Nutrient content			
Soil organic matter (%)	3.32 $\pm$ 0.18	ns	3.57 $\pm$ 0.18
C_{tot} (%)	1.17 $\pm$ 0.10	ns	1.30 $\pm$ 0.13
N_{tot} (%)	0.07 $\pm$ 0.01	**	0.09 $\pm$ 0.01
NH_4^+ (ppm)	3.10 $\pm$ 0.82	ns	3.66 $\pm$ 0.85
NO_3^- (ppm)	1.17 $\pm$ 0.35	ns	1.47 $\pm$ 0.28
P_{inorg} (ppm)	1.87 $\pm$ 0.15	ns	2.64 $\pm$ 0.38

measurements. As for seedling survival, these numbers were obtained after a resampling procedure (Appendix S3, Table S2). Harvested seedlings differed from those tagged for survival monitoring, but they were within the same area and randomly selected among live individuals at the time of sampling. The exact position of these seedlings was not recorded. After harvesting, seedlings were oven dried at 40°C for 48 hours, and leaves and stems were separately weighed. Leaves from the 2011 growing-season cohort (i.e. all *Q. pyrenaica* leaves, but only current-year *Q. ilex* leaves) were finely ground prior to analyses. Nitrogen concentration was measured with the combustion furnace technique at 850°C (Leco TruSpec auto-analyser, St. Joseph, MI, U.S.A.), and phosphorus with the molybdovanadate method (AOAC 1975) with a PerkinElmer 2400 spectrophotometer (Waltham, MA, U.S.A.). The samples were dried at 105°C by a thermogravimetric analyzer (Leco TGA 701), and nutrient concentrations referred to dry weight.

For the analysis of foliar δ^{13}C, we used two replicate samples of 0.5–0.6 mg weighed in tin capsules. Samples were then placed in the autosampler of a Carlo Elba 1500 NC elemental analyzer connected to an Isotope Ratio Mass Spectrometer (Thermo Finnigan Delta plus XL; Thermo Fisher Scientific, MA, USA). For foliar δ^{18}O analysis, three replicate subsamples of 0.3 mg were weighed in silver capsules and mixed with 0.6 mg of graphite. The samples were then placed in the autosampler of a High Temperature Conversion elemental analyzer connected to an Isotope Ratio Mass Spectrometer. The ISODAT NT software provided the δ^{18}O and δ^{13}C (‰) values, and the average value of the subsamples was calculated for each seedling. We expressed the isotopic composition of the samples in delta notation as follows:

$$\delta^{xx}\text{E} \ (‰) = 1,000 \times \left(R_{samp}/R_{stand} - 1 \right)$$

where ^{xx}E is the heavy isotope which is compared to the lighter one; R refers to the molar ratio of the heavy to the light isotope (i.e. ^{13}C:^{12}C or ^{18}O:^{16}O); samp refers to the sample; and stand refers to an international standard (V-PDB for C and V-SMOW for O). We used international and internal standards for analyses. Isotopic composition was measured at the Stable Isotope Laboratory of the Instituto Andaluz de Ciencias de la Tierra (Granada, Spain).
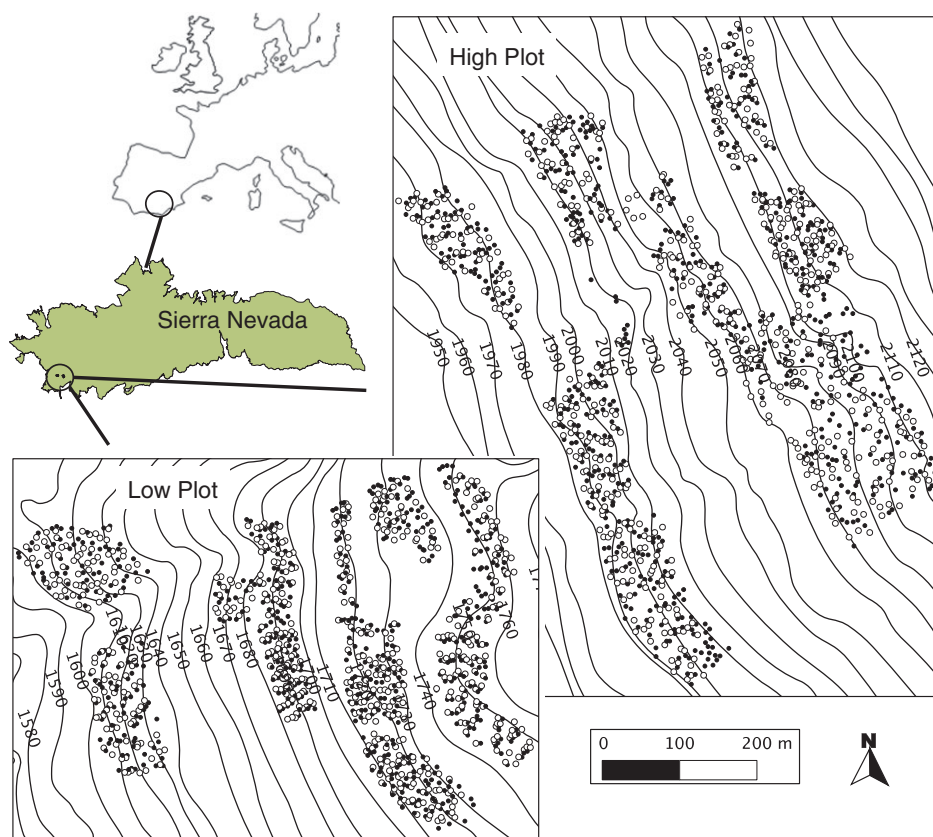
Figure 1. Map of the study plots showing the position of the monitored seedlings of *Quercus ilex* (black points) and *Quercus pyrenaica* (white points). Lines are 10-m topographic contour lines and values are in meters above sea level. Note that the seedlings of both species were intermingled within each plot; for spatial analysis, see Appendix S2.

Statistical Analyses

We analyzed the effect of elevation on 2-year seedling survival at two spatial scales. First, across plots we used a two-way factorial analysis of deviance with quasibinomial errors, with *Elevation* (a categorical factor defined by plot), *Species*, and the interaction between them as explanatory factors. Second, within each plot we used logistic regression models to test the effect of *Elevation* (a continuous variable with measurements for each individual seedling) on seedling survival, also including *Species* and the *Species × Elevation* interaction in the model. The models were simplified to test for the significance of these terms (Crawley 2013).

Plant biomass, foliar nutrient concentrations, and isotopic ratios were analyzed with two-way analysis of variance (ANOVA), considering *Elevation*, *Species*, and the interaction between them as explanatory variables. Previous to analysis, data were transformed to improve homogeneity of variance. To test for correlations between foliar isotopic ratios, nutrient concentrations, and seedling aerial biomass, we calculated Pearson's product–moment correlation coefficients for the seedlings of each *Species × Elevation* combination separately. For correlations with $\delta^{18}O$, we first removed outliers (as defined in Crawley 2013). For analyses we used R version 2.15.0 (R Development Core Team 2012).

All analyses were carried out after resampling procedures with 10,000 permutations to homogenize the number of seedlings from each postfire management area in each plot (Appendix S3). In each permutation, we ran the models and extracted the appropriate test statistics (*F*-values in all cases). The reported *p* values were later calculated from the average *F*-values and degrees of freedom from the permutations. All the means and correlation coefficients presented here are averages of the values obtained in the permutations.

Results

Of all the planted oak seedlings, 61% were recorded alive after the first summer, 63% after the first winter (because some seedlings resprouted), and 54% after the second summer. Two-year survival was significantly greater at the high plot (67%) than at the low plot (43%), and greater for *Quercus ilex* (59%) than for *Quercus pyrenaica* (48%; Table 2; Fig. 2). Seedling survival significantly increased with seedling elevation within each of the plots (low plot: $F = 13.08$, $p < 0.001$; high plot: $F = 18.96$, $p < 0.01$), and this effect was consistent among species (i.e. no *Species × Elevation* interactions). The model coefficients for the slope of the *Elevation*
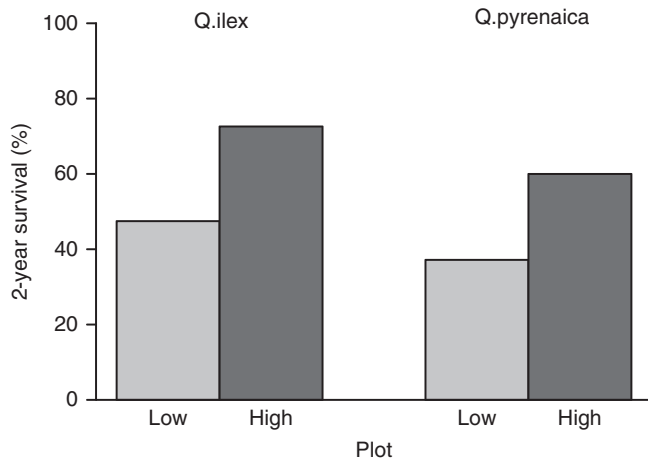
Figure 2. Seedling survival for *Quercus ilex* and *Quercus pyrenaica* after the second growing season (in September 2011).
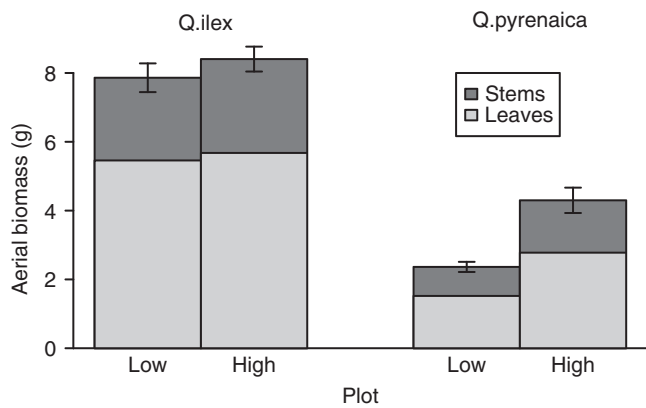

Figure 3. Mean (±1 SE) biomass of aerial tissues (stems + leaves) for each species and plot/elevation.

effect were consistently positive within each plot (low plot: 0.0079; high plot: 0.0044).

Seedling aerial biomass (stems, leaves, or total) was greater for *Q. ilex* than for *Q. pyrenaica* at both elevations, and greater at the high plot than at the low plot for both species. Differences in biomass between elevations were largest for *Q. pyrenaica*, leading to significant *Species × Elevation* interactions (Table 2; Fig. 3).

There were no significant differences in foliar δ^{13}C between species, but *Q. ilex* showed significantly higher foliar δ^{18}O than *Q. pyrenaica* at both elevations. Seedlings showed higher (i.e. less negative) foliar δ^{13}C values at the high plot than at the low plot, although this effect was significant only for *Q. ilex* when analyzing the two species separately (Table 2; Fig. 4). Both species showed higher foliar δ^{18}O values at the high plot than at the low plot (Table 2; Fig. 4).

Quercus pyrenaica had higher foliar N and P concentrations than *Q. ilex* at both elevations, and foliar N concentrations were higher in the high plot than in the low plot in both species (Table 2; Fig. 4). However, this difference was greater in
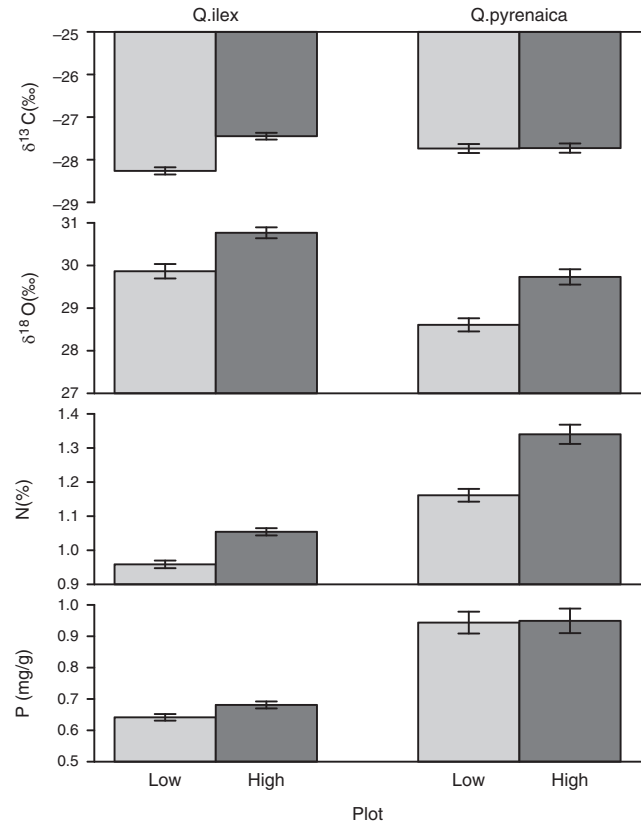

Figure 4. Mean (±1 SE) leaf isotope ratios and nutrient concentrations.

Q. pyrenaica (15% higher in the high plot) than in *Q. ilex* (10%), as indicated by a significant *Species × Elevation* interaction (Table 2, Fig. 4). Foliar P concentrations also tended to be higher at the high plot than at the low plot in *Q. ilex*, (Fig. 4), although not significantly.

Seedling aerial biomass was positively correlated with foliar N in both oak species at the high plot, negatively correlated with foliar δ^{13}C in *Q. ilex* at the low plot, and also negatively correlated with δ^{18}O in *Q. pyrenaica* at the high plot (Table 3). Foliar δ^{13}C and δ^{18}O values were positively correlated with each other in *Q. pyrenaica* at both elevations, and in *Q. ilex* at the higher elevation (Table 3). Foliar δ^{13}C was positively correlated with foliar nutrient status (N and/or P concentrations) in both oak species, except for N in *Q. ilex* and P in *Q. pyrenaica* at the lower elevation. Foliar δ^{18}O was also positively associated with foliar N concentration in *Q. pyrenaica* at both elevations. When pooling data across elevations, both foliar δ^{13}C and δ^{18}O were positively correlated with foliar N concentrations in each oak species separately (Fig. 5).

Discussion

The seedlings of both oak species showed higher two-year survival when planted above the upper forest limit than at a lower elevation where native oak forests are currently present. In addition, biomass growth and leaf nutrient status and isotopic

Table 2. Results of ANOVA for plant biomass and leaf nutrient and isotopic composition. [a]Weight and nitrogen data were square root-transformed prior to analysis. [b]Phosphorus data were log-transformed prior to analysis. [c]Average residual degrees of freedom of the models across simulations (for phosphorus there were fewer than the rest because some of the harvested seedlings had no P measurement).

| Response	df[c]	*Elevation* F	*Elevation* p	*Species* F	*Species* p	*Elevation × Species* F	*Elevation × Species* p
Two-year survival	2,229	132.4	<0.001	30.8	<0.001	0.8	0.38
W_{leaf}[a]	260	11.9	<0.001	190.7	<0.001	7.0	<0.01
W_{stem}[a]	260	14.8	<0.001	113.4	<0.001	3.5	0.06
W_{tot}[a]	260	14.2	<0.001	177.3	<0.001	6.3	<0.05
$\delta^{13}C$	260	35.3	<0.001	1.9	0.17	17.1	<0.001
$\delta^{18}O$	260	38.5	<0.001	44.7	<0.001	0.5	0.48
N (%)[a]	260	61.2	<0.001	226.3	<0.001	4.3	<0.05
P (mg/g)[b]	252.9	1.9	0.17	189.2	<0.001	1.5	0.22
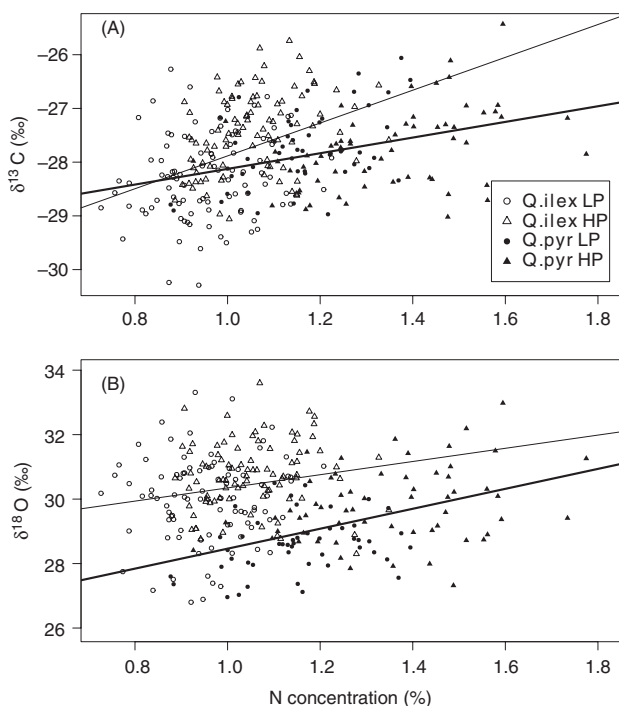
Figure 5. Correlations between leaf N concentration and isotopic composition across plots/elevations. Thin lines are lines of best fit for *Quercus ilex*, and thick lines for *Q. pyrenaica*. Correlation coefficients are as follows: (A) for $\delta^{13}C$: *Q. ilex* ($r = 0.40$, $p < 0.001$), *Q. pyrenaica* ($r = 0.37$, $p < 0.001$); (B) for $\delta^{18}O$: *Q. ilex* ($r = 0.23$, $p < 0.01$), *Q. pyrenaica* ($r = 0.47$, $p < 0.001$). LP, low plot; HP, high plot. For correlation coefficients separated by plot/elevation, see Table 3. The figure shows the data for all seedlings, while analyses were made after a resampling procedure (Appendix S3).

composition further support that seedlings performed better at the higher-elevation site, primarily due to an improved leaf N status and a reduction in drought stress, especially for the deciduous *Quercus pyrenaica*. Interestingly, seedling survival followed a clear positive trend with increasing elevation across and within plots (even within the plot located above the current forest range), further supporting an uphill shift in the climatic niche for regeneration of these oak species.

These results suggest that the historical or present distribution range of tree species may no longer necessarily be a good predictor of seedling performance and establishment potential in this Mediterranean mountain ecosystem, which has been undergoing climate warming and aridification in recent decades.

Strong effects of drought stress on seedlings of both species were evidenced by demographic and physiological data. We observed high mortality rates, especially during the first but also during the second summer, while virtually no winter mortality occurred. We also found positive correlations between foliar $\delta^{13}C$ and $\delta^{18}O$ in surviving seedlings of both species (except for *Quercus ilex* at the lower site), indicating that seedling growth was limited by water stress and stomatal constraints on photosynthesis (Scheidegger et al. 2000). Summer drought is indeed one of the main demographic filters acting on seedlings in Mediterranean-type mountain ecosystems and a major cause of failure in ecosystem restoration activities (Castro et al. 2002, 2006; Gómez-Aparicio et al. 2004). The facts that mortality decreased with increasing altitude and that biomass growth was greater at the higher-elevation site, most likely due to the cooler and wetter summer conditions associated with higher altitude, further support that drought was a critically important stress factor for both oak species during the study period.

Biomass, leaf isotopic composition, and nutrient concentration data indicate that *Q. pyrenaica* seedlings derived a greater benefit from planting at the higher elevation than *Q. ilex* seedlings. *Quercus pyrenaica* seedlings showed massive mortality (over 60%), negligible biomass growth, and much lower N concentrations at the drier, lower-elevation site, which highlights the low drought tolerance of this species. Furthermore, *Q. pyrenaica* seedling biomass was positively correlated with leaf N concentration and negatively correlated with foliar $\delta^{18}O$ values across individuals at the higher-elevation area, indicating enhanced seedling growth with increasing foliar nutrient status and decreasing water stress (as suggested by lower $\delta^{18}O$ values; Barbour et al. 2000; Scheidegger et al. 2000; Barbour 2007).

Quercus ilex also showed 50% higher survival as well as 10% higher foliar N and P concentrations at the higher-elevation plot despite its greater drought tolerance. Plant nutrition might have been improved at higher elevation due to the slightly greater

Table 3. Pearson correlation coefficients between plant biomass and leaf nutrient and isotopic composition. N, nitrogen concentration; P, phosphorus concentration; W_{tot}, total weight of aerial biomass.

	Quercus ilex				Quercus pyrenaica			
	Low Plot		High Plot		Low Plot		High Plot	
Variables	r	p	r	p	r	p	r	p
W_{tot}–N	0.07	0.50	0.22	< 0.05	−0.06	0.70	0.28	0.07
W_{tot}–δ^{13}C	−0.21	0.05	−0.05	0.61	−0.13	0.39	−0.22	0.16
W_{tot}–δ^{18}O	0.11	0.31	−0.13	0.23	−0.13	0.39	−0.26	0.10
δ^{13}C–δ^{18}O	0.17	0.11	0.28	< 0.01	0.31	< 0.05	0.32	< 0.05
δ^{13}C–N	0.17	0.12	0.33	< 0.01	0.49	< 0.001	0.39	< 0.05
δ^{13}C–P	0.41	< 0.001	0.27	< 0.05	−0.10	0.52	0.38	< 0.05
δ^{18}O–N	0.15	0.17	0.07	0.51	0.29	0.06	0.29	0.07

soil N content and lower soil pH and bulk density. The negative association between seedling aerial biomass and foliar δ^{13}C across *Q. ilex* individuals at the lower elevation area also suggests decreasing seedling growth with increasing water stress (Farquhar et al. 1989; Dawson et al. 2002). Still, the enhanced biomass growth at higher altitude was not statistically significant for *Q. ilex* seedlings, and was small when compared with the increase shown by *Q. pyrenaica* seedlings. This result is in good agreement with previous knowledge on the contrasting water requirements of these sympatric oak species: whereas the evergreen *Q. ilex* can successfully cope with severe summer drought, *Q. pyrenaica* requires wetter conditions during the summer (Blanca et al. 2001; Gea-Izquierdo et al. 2013). More broadly, deciduous oak species show greater reductions in stomatal conductance in response to water stress than evergreen species (Acherar & Rambal 1992). The sclerophyllous leaves of *Q. ilex* confer it a greater ability to control transpiration by closing stomata during drought (Schiller et al. 2007). A tighter stomatal control of transpiration water losses in *Q. ilex* than in *Q. pyrenaica* (supported by higher leaf δ^{18}O values in *Q. ilex*; Barbour 2007) may thus explain the better performance of *Q. ilex* seedlings at the drier, lower-elevation area.

Quercus ilex (but not *Q. pyrenaica*) leaves were more enriched in ^{13}C at the higher-elevation site, which is in agreement with the well-known trend of increasing plant δ^{13}C values with increasing altitude due to decreased carbon isotope discrimination (Körner et al. 1988, 1991). However, contrary to expectation, foliar δ^{18}O values in both oak species were also greater at the high-elevation site. This result is striking, given that plants would be expected to become more depleted (rather than more enriched) in ^{18}O with increasing altitude due to the lower temperatures and vapor pressure deficits, more depleted meteoric water δ^{18}O values, and higher precipitation and water availability found at higher elevations in Mediterranean mountain areas (Dawson et al. 2002; Barbour 2007). This result may be explained by several nonmutually exclusive mechanisms. First, lower temperatures with increasing altitude also cause the viscosity of water to increase, which can slow the transport of water from the soil to the leaves (Roderick & Berry 2001), thereby decreasing stomatal conductance (Cernusak et al. 2013) and increasing leaf δ^{18}O values. Second, a delayed

leaf phenology at the colder, higher-elevation site (with greater physiological activity during the dry summer) may also have contributed to more enriched leaf δ^{18}O at higher elevation. And third, it is well established that photosynthetic capacity and water-use efficiency increase with increasing foliar N concentration (Field & Mooney 1986; Körner 1989; Sparks & Ehleringer 1997), which may allow improved stomatal control of water loss (thus leading to higher leaf δ^{18}O and δ^{13}C values). Given the global trends of increasing leaf nutrient status (N and P) with increasing altitude and colder temperatures (Körner 1989; Reich & Oleksyn 2004), we propose that improved stomatal control of water loss due to enhanced nutrient status could be a so-far overlooked but important positive feedback mechanism that could foster upward range shifts in water-limited mountain regions. Further studies in different geographical locations are warranted to test this intriguing hypothesis.

Implications for Management

The current distribution of native oak forests and woodlands in Sierra Nevada reaches 1,800 m a.s.l. (eventually 1,900 on south-facing slopes). The fact that seedlings of both oak species performed better above this upper limit when compared with a lower altitude considered more appropriate for oak forest establishment, and with seedling survival still increasing with altitude at the higher plot, may indicate an uphill shift of the climatic optimum for oak forest regeneration in Sierra Nevada. In fact, many studies show that upward shifts of species ranges are already happening under ongoing climate change and will be widespread in the near future (Kelly & Goulden 2008; Jump et al. 2009; Matías & Jump 2014). In Sierra Nevada, mean annual rainfall has shown decreasing trends during the last decades, including crucially important autumn rainfall after the long summer-drought period (Ruiz Sinoga et al. 2011). Furthermore, climate models predict an average temperature increase of 4.8°C by the end of the twenty-first century in these mountains (Benito et al. 2011), which would induce a yearly uphill shift of 14.8 and 13.4 m in the climatic niche of *Q. ilex* and *Q. pyrenaica*, respectively (Benito et al. 2011). Recent changes and future projections imply that areas currently occupied by subalpine shrublands are becoming suitable for the Pyrenean oak, and that areas currently occupied by the Pyrenean oak are becoming suitable

for the Holm oak (Benito et al. 2011), so the results reported here fall within the expected trend (cf. Gea-Izquierdo et al. 2013). Follow-up monitoring of the planted oaks in the coming decades are required to investigate whether the seedlings growing at high altitudes reach maturity and are able to reproduce naturally, and further experimental studies replicated under a wide range of environmental conditions—such as precipitation, land use, and temperature (Barbero et al. 1992; Pérez Luque 2011)—would provide invaluable insights into the extent of oak range shifts in water-limited Mediterranean mountain ecosystems.

Despite widespread uphill shifts in the climatic niches of plant species in Mediterranean mountain regions under climate change (e.g. Kelly & Goulden 2008), natural events of species upward migration may be constrained by the potential for seedling establishment, which may in turn rely on species interactions such as seed dispersal, competition, facilitation, parasitism, or herbivory (Jump et al. 2009; Benavides et al. 2013; Grassein et al. 2014). In our study area, successional vegetation of the Oromediterranean life zone (e.g. cushion shrubs) is abundantly regenerating at the higher-elevation site despite evidence indicating that the area may already be suitable for the growth of oak forests. Numerous processes may be slowing oak colonization at higher elevation, the first being acorn dispersal. European jays (*Garrulus glandarius* L.), the main long-distance acorn dispersers in the area, preferentially cache acorns in forest areas (Pons & Pausas 2008; Castro et al. 2012), which they do not encounter above the forest limit. Furthermore, seed predation by rodents and wild boars in the area has been shown to decimate the acorns available for germination and growth (Gómez et al. 2003; Leverkus et al. 2013). Current postfire vegetation regeneration patterns at the higher-elevation area are thus likely the result of the competitive dominance of resprouting shrubs and the presence of a well-established seed bank (Leverkus et al. 2014), and also of the time lag required for the migration of competing tree species from lower elevations.

The slow natural colonization rates of species with shifting potential ranges may partially be overcome through ecosystem restoration activities. As our results suggest, assisted colonization—taking species beyond their past or present distribution limits to sites projected to become more favorable in the future (Hoegh-Guldberg et al. 2008)—may improve transplant survival and performance in water-limited mountain areas and might also assist tree-species uphill range shifts under ongoing climate change. Although assisted colonization remains controversial (Hewitt et al. 2011), the debate overlooks the need of managers to define target ecosystems to be restored in degraded areas and the fact that species that were previously present in a place may often no longer thrive there. By ignoring climate change projections, reforestation efforts would be increasingly likely to fail or produce maladapted forests (Millar et al. 2007), including a wasteful use of limited resources for ecosystem restoration. Assisted colonization in degraded ecosystems could thus provide an effective means for aiding the persistence of target species while favoring forest adaptation to climate change (Millar et al. 2007; Seddon 2010; Lunt et al. 2013). Under "the premise of an uncertain but certainly variable future" (Millar et al. 2007), ecosystem restoration should be adaptive and have dynamic references and targets to enhance plant performance and ecosystem resilience under the environmental challenges expected during this century.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Within-plot variations in aspect.
Figure S2. Results of the $L(r)$ function from the spatial analysis described in Appendix S2.
Table S1. Cover of the most abundant plant species and results of indicator species analysis between the two plots.
Table S2. Number of seedlings available and used for analyses after resampling.
Appendix S1. Indicator species analysis.
Appendix S2. Spatial analysis of seedling distribution.
Appendix S3. Experimental area and resampling procedure.