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# Twelve-year oak seedling survival and growth in post-coal mining pastures of northern Spain: Combined effects of nurse shrubs and grazing exclusion

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A B S T R A C T

Facilitative interactions among plants can support vegetation recovery in degraded environments, yet their medium-term effectiveness in restoration remains insufficiently understood. We conducted a 12-year field experiment in reclaimed open-cast coal mines in northern Spain to assess whether native colonizer legume shrubs enhance the survival and growth of seedlings of two *Quercus* species. A total of 800 seedlings were planted under four treatments combining the presence/absence of shrub and grazing, allowing us to disentangle biotic and abiotic facilitation mechanisms. Shrubs enhanced seedling survival, particularly for *Q. pyrenaica*, by buffering early mortality during summer droughts. Medium-term seedling survival under shrubs was markedly higher than in shrub-free areas (13–25 % vs. 1–4 %). Herbivory had a limited effect on survival, with fencing providing marginal benefits in specific years. Slow increments of *Quercus* seedling height and diameter over time were found, being more pronounced for *Q. petraea*, and varying as the combined effect of shrubs and grazing exclusion. Annual growth varied over time for both *Quercus* species, being greater under than outside shrubs for *Q. petraea*, while for *Q. pyrenaica,* the shrub effect depended on the year. *Q. pyrenaica* seedlings exhibited higher annual growth than *Q. petraea*. Differences in seedling annual growth with and without shrubs were smaller in the driest years. We conclude that native shrubs play a key facilitative role in the medium-term restoration of degraded oak ecosystems under sub-Mediterranean conditions. Their effectiveness varies by species and response variable (survival vs. growth), and the underlying facilitation mechanisms differ over time.

## 1. Introduction

Over the last decades, numerous studies have revealed the capacity of shrubs to modify their microenvironment in ways that facilitate the establishment of other plant species, including trees (Callaway, 1992; Pugnaire and Lázaro, 2000; Callaway et al., 2002; Muhamed et al., 2013; Alday et al., 2014; Guignabert et al., 2020; Maamary et al., 2025). Facilitation occurs through direct mechanisms such as microclimatic buffering (Moro et al., 1997a, b; Gómez-Aparicio et al., 2005, 2008; Prieto et al., 2011; Muhamed et al., 2013; Costa et al., 2017) and soil amelioration (Pugnaire et al., 1996a, 2004; Gómez-Aparicio et al., 2005; Prieto et al., 2011; Mihoč et al., 2016; Guignabert et al., 2020; Muñoz-Cerro et al., 2023), as well as indirect mechanisms including herbivore protection (Rebollo et al., 2002; García and Obeso, 2003;

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Gómez-Aparicio et al., 2008), pollinator attraction (Ghazoul, 2006), and changes in soil microbial community (Ezeokoli et al., 2020), edaphic fauna, and mycorrhizal associations (Moora and Zobel, 2010; Casanova-Katny et al., 2011).

According to the stress-gradient hypothesis (Bertness and Callaway, 1994), facilitative interactions are more prevalent under high environmental stress, such as drought or intense herbivory. Consequently, positive plant–plant interactions have been widely documented in harsh environments, including the Iberian Peninsula (e.g., Pugnaire et al., 1996a, b; Moro et al., 1997a, b; Callaway et al., 2002; Brooker et al., 2008), where forest regeneration is constrained by four main factors: (i) poorly developed soils, (ii) summer drought, (iii) high herbivore pressure, and (iv) interannual climatic variability (Martínez-Ruiz et al., 2021a). However, the direction and strength of these interactions can vary over time, influenced by factors such as the type and intensity of stress (Michalet et al., 2006; Maestre et al., 2009; Guignabert et al., 2020), the identity and functional traits of both nurse and target species (Maestre et al., 2009; Rolo et al., 2013; Madrigal-González et al., 2014; Costa et al., 2017; Maamary et al., 2025), their developmental stage (Bertness and Callaway, 1994), and the performance metrics used to assess facilitation (Maestre et al., 2005; Costa et al., 2017).

In Mediterranean ecosystems, the role of shrubs in promoting oak establishment and growth is well documented (Castro et al., 2004; Padilla and Pugnaire, 2006; Cuesta et al., 2010; Muhamed et al., 2013; Perea and Gil, 2014; Costa et al., 2017; Cruz-Alonso et al., 2020), and their use has been widely proposed in reforestation efforts (Castro et al., 2002, 2006, 2021; Benayas and Camacho Cruz, 2004; Gómez-Aparicio et al., 2004; Muhamed et al., 2013; Navarro-Cano et al., 2019). However, few studies have explored the facilitative role of nurse shrubs in the reforestation of severely degraded environments such as post-coal mining landscapes, particularly over long temporal scales (but see Torroba-Balmori et al., 2015; Alday et al., 2014, 2016; Martínez-Ruiz et al., 2021a).

Our previous research in post-coal mining areas of NW Spain has shown that facilitation is key to the natural colonization of these sites by oaks (Milder et al., 2013; Martínez-Ruiz et al., 2021b). Shrubs act as ecosystem engineers, rapidly colonizing degraded substrates and creating favourable microsites for the establishment of late-successional species such as *Quercus petraea* (Matt.) Liebl. and *Q. pyrenaica* Willd. (Torroba-Balmori et al., 2015; Alday et al., 2016). Soil limitations (López-Marcos et al., 2020) and herbivory (Sigcha et al., 2018) are major constraints on vegetation dynamics in these areas, while shrubs can mitigate both through soil improvement (Muñoz Cerro et al., 2023) and herbivore protection (Torroba-Balmori et al., 2015; Alday et al., 2016).

Despite growing evidence of the benefits of nurse plants in forest restoration (Gómez-Aparicio, 2009; Rey et al., 2009; Castro et al., 2021), further research is needed to identify the specific microsites and facilitation mechanisms involved —such as microclimatic buffering, soil enhancement, and physical protection— and how these vary over time. It is also essential to assess the performance of different oak species with contrasting ecological strategies under varying climatic conditions, using multiple indicators such as survival and growth (Costa et al., 2017). Such knowledge is critical for advancing precision restoration approaches that maximize tree establishment success while minimizing costs and disturbance (Castro et al., 2021).

Moreover, understanding facilitation is particularly relevant for the conservation of temperate Eurosiberian species like *Q. petraea*, which reach their southern distribution limit in the sub-Mediterranean mountains of the Iberian Peninsula (Gazol et al., 2022), and the sub-Mediterranean mountain species *Q. pyrenaica*, in the transition between Atlantic and Mediterranean climates of Southern France, Spain, Portugal, and northern Morocco (Hernández-Santana et al., 2008; Lorite et al., 2008; Nieto-Quintano et al., 2016). These rear-edge populations are especially vulnerable to climate change (Martínez-Ruiz et al., 2021a), and it remains unclear whether increasing drought in these transitional environments will shift plant–plant interactions from facilitation to competition (Maestre et al., 2005, 2009; Cuesta et al., 2010; Soliveres et al., 2015).

This facilitation mediated by shrubs can be critical in reclaimed open-cast coal mines of sub-Mediterranean areas, often characterized by shallow, poorly structured soils with low water-holding capacity (López-Marcos et al., 2020), which exacerbate summer drought effects and limit oak development. Additionally, shrubs may help to mitigate herbivory (Gómez et al., 2001), another major constraint on seedling establishment (Gómez et al., 2003; Rodríguez-Doce, 2010); however, their effectiveness against both herbivory and drought is subject to the interannual climate variability (Gómez et al., 2001).

Although the role of positive plant–plant interactions in ecosystem functioning and restoration is well established (Whisenant, 1999; Pickett et al., 2001; Maestre et al., 2003), few long-term field studies have assessed their practical potential under real-world conditions of environmental degradation. To address this issue, we conducted a twelve-year field experiment in a reclaimed open-cast coal mine in northern Spain, evaluating the influence of two native nurse shrubs (*Genista florida* (L.) Link and *Cytisus scoparius* L.) on the medium-term survival and growth of planted seedlings of *Q. petraea* and *Q. pyrenaica*. Specifically, we tested three novel hypotheses that address underexplored dynamics in long-term restoration ecology: (1) that nurse shrubs enhance early and medium-term oak performance by mitigating herbivore pressure —a mechanism rarely quantified over extended timescales; (2) that the net outcome of shrub–oak interactions shifts toward competition or neutrality during meteorologically harsh years, highlighting the context-dependence of facilitation; and (3) that *Q. petraea* and *Q. pyrenaica* exhibit distinct responses due to their different tolerance to drought stress, emphasizing the importance of species-specific traits in restoration success. These hypotheses were tested through a twelve-year field experiment in a reclaimed coal mine, offering rare empirical insights into the temporal and ecological complexity of plant–plant interactions in degraded landscapes.

## 2. Materials and methods

### 2.1. Study site and temporal shifts in climatic conditions

The study was conducted from 2011 to 2022, in a 17-ha reclaimed open-cast coal mine near Guardo, Palencia, Northern Spain (latitude 42º 48’ N, longitude 4º 52’ W, ca. 1200 m a.s.l.). Nestled in the southern foothills of the central Cantabrian Range, the climate is sub-humid Mediterranean (MAPA, 1991), with an annual mean temperature of 9.7 ºC and average yearly precipitation of 941 mm (normal period: 1991–2022; data provided by the Spanish National Meteorological and Climatological Agency, AEMET, from the Meteorological Station 2234 at Cervera de Pisuerga). Precipitation is irregularly distributed throughout the year, with rainfall concentrated in autumn and spring, and a dry season in summer during which less than 4 % of the total annual precipitation occurs. The mean minimum temperature in the coldest month (January) is –1.9 ºC, and the mean maximum in the warmest month (July/August) is 25.5 ºC.

However, according to the dominant trend in Mediterranean areas (Moreno et al., 2005; Kelley et al., 2012; Masson-Delmotte et al., 2023), the climate in the study area has changed during the 12 years of monitoring (2011–2022) compared to the normal period, 1991–2022 (Armijos-Montaño, 2022). Particularly, there has been a reduction in water balance (Standardized Precipitation Evapotranspiration index, SPEI) and an increase in the potential evapotranspiration of Thornthwaite, PET (Armijos-Montaño, 2022), associated with the increase in the average annual temperature by 0.59 ºC (Fig. S1). These patterns reveal the occurrence of progressively longer and more severe drought episodes for the meteorological station of Cervera de Pisuerga during the monitoring period in comparison with the normal period (Armijos-Montaño, 2022). In addition, substantial interannual variability in precipitation and temperature was recorded during the monitoring period (Tables S1 and S2).

Close to the Montaña Palentina Natural Park, the ecosystem surrounding the mine consists of temperate broad-leaved deciduous forests dominated by *Quercus pyrenaica* and *Q. petraea*, established over the dominant limestones of the Paleozoic Era (Milder et al., 2013). Their soils are Typic Dystroudepts (Soil Survey Staff, 2022) with sandy clay loam texture and acid pH (4.3 −4.8) without evidence of carbonates, high organic matter content, and low content in available phosphorous (López-Marcos et al., 2020).

The opencast coal mine was reclaimed in October 2000, using a combination of topsoiling and hydroseeding after regrading the mine to the original contour by filling the open pit with coal wastes from nearby mines (Torroba-Balmori al., 2015). The fine-textured topsoiling material consisted of a mixture of topsoil and sediments from deeper parts of the neighbouring opencast pits, amended with cattle manure (Martínez-Ruiz et al., 2021b). This mixture contained a very poor seed bank (González-Alday et al., 2009) and had a clay-loam texture, with a pH of 6.5, electrical conductivity of 114.3 mS/cm, easily oxidizable carbon of 19.8 g/kg, available phosphorous of 9.7 mg/kg, and an effective depth of 10–15 cm (López-Marcos et al., 2020). These post-mine soils are classified as Lithic Udorthents (*sensu* Soil Survey Staff, 2022) and exhibit a very low water-holding capacity compared to the natural forest soil (1.0–3.4 vs.19.87 ± 1.52 g/cm$^2$; López-Marcos et al., 2020).

After topsoiling, the mine was hydroseeded with a grassland perennial species mixture (more details in Alday et al., 2011). The reclaimed area has been colonized by native legume shrub species from the surrounding forest, primarily *Cytisus scoparius* and *Genista florida* (Martínez-Ruiz et al., 2021a), and is subject to grazing by wild ungulates (deer, roe deer, and wild boar) and livestock (cattle and horses; Milder et al., 2013).

### 2.2. Experimental design and data collection

The experimental set-up used in this work, with grazed and non-grazed plots, was previously used to investigate the soil amelioration that shrubs can induce in grazed areas (Muñoz-Cerro et al., 2023) and the short-term effects (the first two growing seasons) of nurse shrubs and herbivory exclusion on *Quercus* spp. seedling survival and growth (Torroba-Balmori et al., 2015). We now assess the combined short and medium-term effects on seedling survival, annual growth, height, and diameter, as well as their relationship with the climate over the study period (2011–2022). We get deeper into the differentiation of the main facilitation vias: protection against herbivores and microclimate amelioration, and the impact of the local conditions on the strength of facilitation processes for two different *Quercus* species over time.

The experimental set-up established in February 2011 consisted of a split-plot design with two nearly flat sites, having two 30 m x 30 m plots each (one of them fenced to prevent grazing), and the four plots with grassland and shrubland vegetation (Fig. 1). Within each plot, ten 2 m x 2 m sub-plots (five without shrubs and five with 2–3 shrubs) were randomly allocated approximately 4 m apart; shrub presence or absence was not manipulated for the experiment. The experimental design thus included the following grazing (G) x shrub (S) combinations: (a) no grazing, no shrubs (G-S-); (b) no grazing, shrubs (G-S+); (c) grazing, no shrubs (G+S-); (d) grazing, shrubs (G+S+).

The fences preventing livestock and wild ungulate grazing consisted of wire mesh fencing (2 m high, mesh hole: 5 cm in width x 15 cm in length) stretched between anchor posts (Torroba-Balmori et al., 2015). The nurse shrub species used were the two main natural colonizers of the mine, *C. scoparius* and *G. florida*, with similar vertical structures in the mine (mean height 222 ± 6.6 cm). Both species are non-thorny leguminous shrubs capable of actively fixing the atmospheric nitrogen (Talavera et al., 1999). They share common traits, such as structural form and leaf phenology, and typically co-exist in mining areas, forming mixed stands. Due to their similar structure and ecological functioning, they were not differentiated during the experiment, following the methodology commonly used in facilitation studies involving species from the same functional group.

Within each sub-plot, ten 1-year-old seedlings of *Q. petraea* and ten of *Q. pyrenaica* were planted in March 2011 and tagged, resulting in a total of 400 seedlings per *Quercus* species. The seedlings, provided by the central nursery of Junta de Castilla y León (Cantabrian Mountains provenance), were grown in cylindrical forestry pots (type: S.L 35, 235 cm$^3$, 16 cm deep) with peat-based substrate. They were measured (main stem length and root collar diameter) prior to planting. *Q. pyrenaica* seedlings were smaller than *Q. petraea* seedlings in height (Qpy: 14.6 ± 0.73 vs. Qpt: 23.0 ± 1.15; $F=201.66$, $p < 0.0001$) and diameter (Qpy: 3.7 ± 0.18 vs. Qpt: 4.2 ± 0.21; $F=67.82$, $p < 0.0001$).

Seedlings were spaced 30 cm apart. When planted outside shrubs, they were arranged in two rows; when planted under shrubs, they were arranged in a single row around the shrub stem, at a distance of 20 cm from it (see Torroba-Balmori et al., 2015). When the lowest branches of the shrub prevented the seedlings from being placed at that distance, the seedlings were planted as near to the stem as possible (ca. 30 cm). The

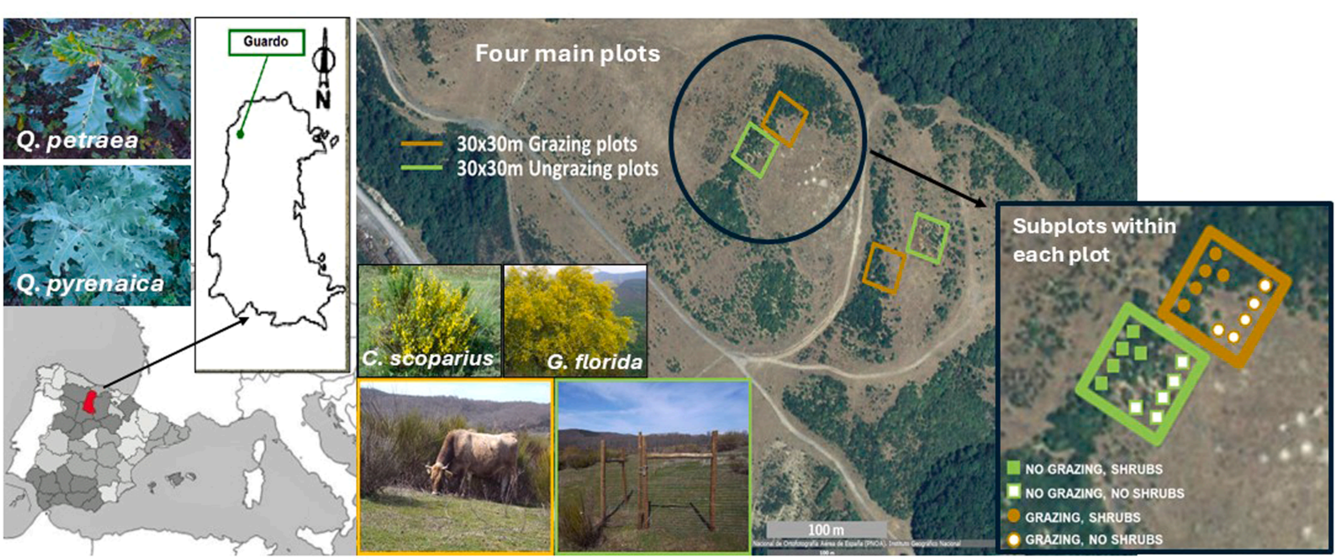


**Fig. 1.** Location and scheme of experimental design in the study area.

plantation was carried out using a small auger (20 cm×6 cm) to minimize damage to shrub roots and avoid disturbing soil structure. The soil extracted with the auger was returned to the planting holes and firmly pressed down around the seedlings, ensuring that the root collar remained at ground level.

One month later, seedling survival was recorded, classifying as dead those individuals lacking evident chlorophyll and dry stems (99.8 % of seedlings survived; Torroba-Balmori et al., 2015). Seedlings were monitored every autumn for twelve consecutive years (2011–2022) to record survival, height, annual main stem growth (cm), and root collar diameter (mm). Survival data were corrected in subsequent surveys to account for individuals initially recorded as dead but later resprouted.

### 2.3. Statistical analysis

The role that shrubs, grazing, planted species, and time played in seedling survival was analysed using generalized linear mixed models (GLMM). In model construction, we used the full factorial design, including as fixed effects the simple effects of the presence/absence of shrubs and grazing, *Quercus* species, and time, and their interactions. In these models, random effects accounting for spatial and temporal dependence were included (site, plot, sub-plot, individual, and year; Pinheiro and Bates, 2000). The survival data, having a binary response (live or not), were analyzed by logit-link binomial models, with the *glmer* function. We also compared the number of plants alive/that survived at 12 years by pairwise comparisons, with the Bonferroni correction applied after the partial GLMM (only for survival data of 2022).

Plant height, basal stem diameter, and annual growth were analyzed over time using linear mixed models (LMMs) fitted with the *lmer* function, employing the same fixed and random effects structure as used in the survival analysis; data were square-root-transformed to satisfy the assumption of normality. For the analysis of annual growth, individuals that experienced herbivory during a given sampling year and the subsequent year were excluded, which explains the absence of data for some treatment combinations in specific years. Additionally, some diameter measurements were excluded during data cleaning due to inconsistencies caused by caliper positioning. Accurate placement of the caliper at root collar height and maintaining a consistent horizontal angle from a fixed reference direction is critical for measurement precision and dataset consistency. These issues also contributed to data gaps in some treatment combinations across years.

In all analyses, alternative autocorrelation structures and heteroscedasticity specifications (e.g., Pinheiro and Bates, 2000) were also evaluated to improve model fit, and since no sufficient evidence of heteroscedasticity or autocorrelation was detected, they were estimated under the assumptions of homoscedasticity and no autocorrelation.

All statistical analyses were implemented in the R software environment (version 4.1.2; R-Core Team, 2025). Seedling survival analyses were conducted using the *lme4* package for GLMM (version 1.1–35.5; Bates et al., 2015), while height, diameter, and annual growth were analysed using the *nlme* package for LMMs (version 3.1–162; Pinheiro et al., 2023).

## 3. Results

### 3.1. Seedling survival

The GLMM revealed significant simple effects of Shrub and Time on seedling survival, along with three key three-way interactions (Table 1; Fig. 2). Seedling survival declined significantly over time for both *Quercus* species, with consistently higher survival under shrub cover and for *Q. pyrenaica*, except during the first year post-planting under shrubs (Fig. 2 A). Survival outside shrubs dropped during the first dry season (Qpy: 17.0 %, Qpt: 5.5 %), while under shrubs it decreased more gradually, with the steepest decline occurring after the second dry season (Qpy: 54.5 %, Qpt: 45.7 %). Over the following years, survival

**Table 1**
Model parameters estimates derived from GLMM for seedling survival. (S- G- Qpt): *Q. petraea* outside shrubs and without grazing. Qpy: *Q. pyrenaica.*

| Fixed effects | Estimates ± SE | *Z*-value | *p* |
|---|---|---|---|
| Intercept (S- G- Qpt) | 23.47 ± 15.18 | 1.55 | 0.122 |
| Grazing | −8.95 ± 10.75 | −0.83 | 0.405 |
| Shrub | 33.64 ± 7.52 | 4.47 | < 0.001 |
| Qpy | 4.01 ± 5.05 | 0.79 | 0.427 |
| Time | −5.68 ± 1.78 | −3.19 | 0.001 |
| Grazing x Shrub | 10.08 ± 1.75 | 0.94 | 0.348 |
| Grazing x Qpy | 6.53 ± 8.03 | 0.81 | 0.416 |
| Shrub x Qpy | 3.62 ± 5.76 | 0.63 | 0.530 |
| Grazing x Time | −3.90 ± 1.30 | −3.01 | 0.003 |
| Shrub x Time | −2.86 ± 0.28 | −10.12 | < 0.001 |
| Qpy x Time | −1.72 ± 0.41 | −4.19 | < 0.001 |
| Grazing x Shrub x Qpy | −13.15 ± 8.93 | −1.47 | 0.141 |
| Grazing x Shrub x Time | 3.35 ± 1.35 | 2.48 | 0.013 |
| Grazing x Qpy x Time | 2.94 ± 1.41 | 2.08 | 0.034 |
| Shrub x Qpy x Time | 1.30 ± 0.54 | 2.42 | 0.016 |
| Grazing x Shrub x Qpy x Time | 1.42 ± 1.50 | −0.95 | 0.343 |

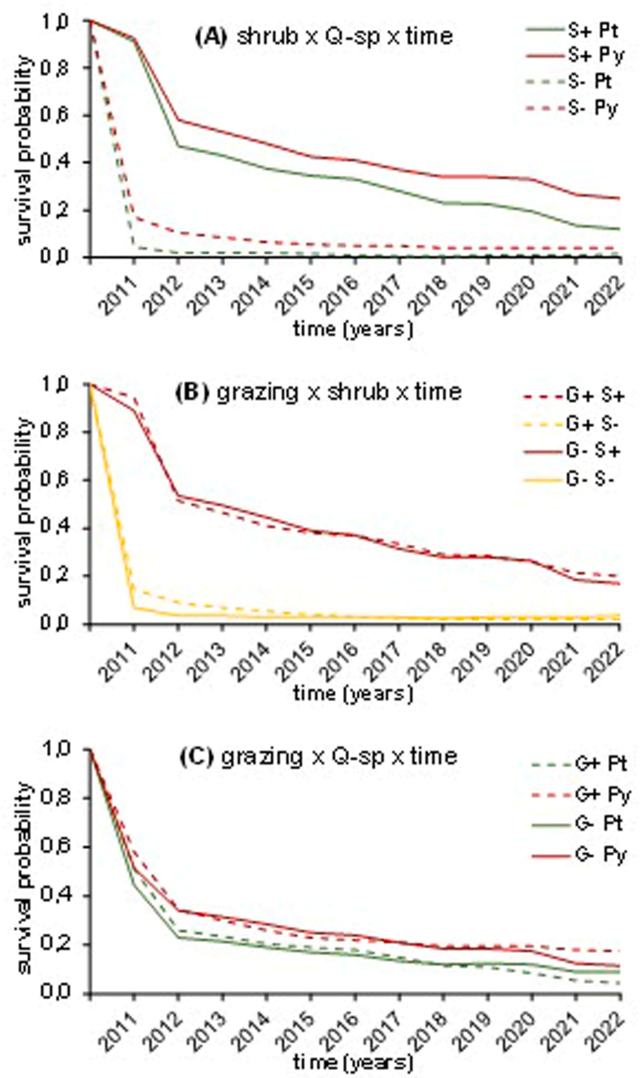


**Fig. 2.** (A) Seedling survival for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) in areas with shrubs (S+) or without shrubs (S-) through the study period (2011–2022). (B) Seedling survival in grazed (G+) and ungrazed (G-) areas with shrubs (S+) or without shrubs (S-) through the study period (2011–2022). (C) Seedling survival for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) in grazed (G+) and ungrazed (G-) areas through the study period (2011–2022). The fitted lines represent the minimal adequate GLMM.

continued to decrease under shrubs, while outside shrubs it stabilized at low levels. By autumn 2022 (12 years post-planting), survival differences between shrub and open areas narrowed considerably (under shrubs: Qpy: 25 %, Qpt: 13 %; outside: Qpy: 4 %, Qpt: <1 %; p = 0.02).

Grazing effects were time-dependent, significantly reducing survival during 2012–2014 and 2020–2021. Grazing exclusion improved survival under shrubs in some years (2012–2014), likely due to the combined protective effects of shrub cover and fencing (Fig. 2B). Initially, shrub presence had a stronger influence than grazing exclusion. Outside shrub areas, grazing exclusion did not enhance survival and was associated with lower survival during the first five years. By 2022, grazing exclusion showed no significant benefit, even under shrubs (G−: 13 % vs. G+: 20 %; p = 0.18).

Species-specific responses to grazing varied over time (Fig. 2 C). For *Q. petraea*, survival was higher under grazing until 2019, after which the trend reversed. For *Q. pyrenaica*, survival was higher under grazing in the initial (2011) and final (2021–2022) years, but greater without grazing between 2013 and 2016. In 2022, grazing exclusion significantly improved *Q. petraea* survival (G−: 8.5 % vs. G+: 4.5 %; p = 0.02), whereas *Q. pyrenaica* survival remained higher under grazing (G−: 11.5 % vs. G+: 17.5 %; p = 0.12).

By autumn 2022, survival was below 35 % across all combinations of grazing, shrub cover, and species, and dropped below 5 % in treatments without shrubs. GLMM and pairwise comparisons based on 2022 data confirmed a significant effect of shrub presence (p = 0.012), enhancing survival in both species. Additionally, a significant Grazing × Q-sp interaction was detected (p = 0.005), with slightly higher survival of *Q. pyrenaica* in ungrazed plots, and higher survival of *Q. petraea* under grazing.

### 3.2. Seedling height

The LMM revealed significant simple effects of Grazing, Shrub, and Time on seedling height, along with several significant two- and three-way interactions, including those involving *Quercus* species (Table 2). Seedling height patterns varied by *Quercus* species and treatment combinations (Fig. 3 A). *Q. petraea* seedlings were consistently taller under shrubs, regardless of grazing. In contrast, *Q. pyrenaica* showed opposing trends depending on grazing: seedlings were taller under shrubs in grazed areas, but taller outside shrubs in ungrazed areas. Grazing exclusion also amplified interspecific height differences: under shrubs, *Q. petraea* was taller than *Q. pyrenaica*, while the reverse was observed outside shrubs.

Shrub cover and grazing jointly influenced height trajectories over time (Fig. 3B). In ungrazed plots, seedling height increased steadily, being greater under shrubs until 2018 and outside shrubs from 2020 onward. By 2022, seedling height had increased by a factor of four under shrubs (92 ± 12 cm) and eleven outside shrubs (104 ± 9 cm). In contrast, grazing strongly limited height growth: by 2022, seedlings reached only 43 ± 0 cm under shrubs and 13 ± 4 cm outside, representing a 1.5-fold increase and a 0.8-fold decrease, respectively. Consequently, the height gap between seedlings in ungrazed shrub-covered plots (G−S+) and grazed open plots (G+S−) widened over time. Notably, grazing exclusion did not produce immediate height benefits during the first two years (2011–2012).

From 2013 onward, grazing exclusion positively affected seedling height in both species, although initial differences were not significant. In contrast, height increases were more limited under grazing conditions (Fig. 3 C). Height divergence between grazed and ungrazed plots became more pronounced from 2014, especially for *Q. pyrenaica*. In ungrazed plots, both species showed substantial growth—approximately six times for *Q. pyrenaica* and five times for *Q. petraea*—reaching final

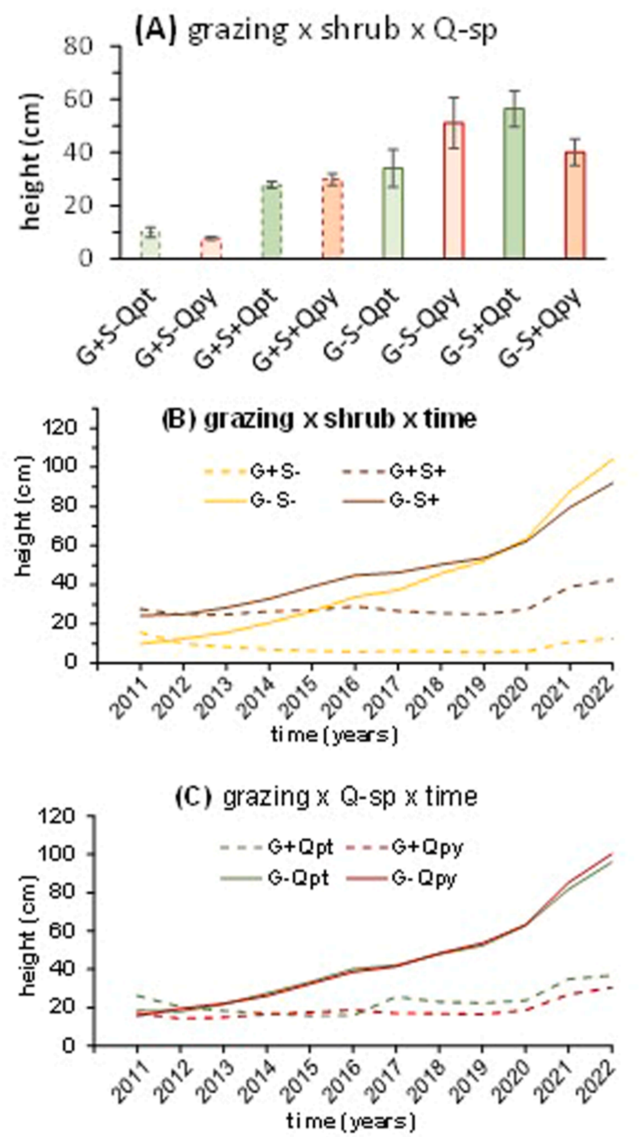


**Fig. 3.** (A) Seedling height for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) in grazed (G+) and ungrazed (G-) areas with shrubs (S+) or without shrubs (S-). (B) Seedling height in grazed (G+) and ungrazed (G-) areas with shrubs (S+) or without shrubs (S-) through the study period (2011–2022). (C) Seedling height for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) in grazed (G+) and ungrazed (G-) areas through the study period (2011–2022). The fitted lines represent the minimal adequate LMM.

**Table 2**
Model parameters estimates derived from LMM models for seedling height. (S- G- Qpt): *Q. petraea* outside shrubs and without grazing. Qpy: *Q. pyrenaica.*

| Fixed effects | Estimates ± SE | *t*-value | *p* |
|---|---|---|---|
| Intercept (S- G- Qpt) | 1.78 ± 0.70 | 2,55 | 0.012 |
| Grazing | 2.8 ± 0.88 | 3,19 | 0.002 |
| Shrub | 2.55 ± 0.67 | 3,81 | < 0.001 |
| Qpy | 0.25 ± 0.65 | 0,39 | 0.699 |
| Time | 0.58 ± 0.08 | 7,24 | < 0.001 |
| Grazing x Shrub | −2.11 ± 0.91 | −2,32 | 0.021 |
| Grazing x Qpy | −2.45 ± 0.89 | −2,76 | 0.006 |
| Shrub x Qpy | −1.02 ± 0.68 | −1,50 | 0.135 |
| Grazing x Time | −1.08 ± 0.16 | −6,79 | < 0.001 |
| Shrub x Time | −0.15 ± 0.07 | −1,97 | 0.049 |
| Qpy x Time | 0.042 ± 0.08 | 0,52 | 0.606 |
| Grazing x Shrub x Qpy | 2.53 ± 0.92 | 2,74 | 0.006 |
| Grazing x Shrub x Time | 0.65 ± 0.16 | 4,04 | < 0.001 |
| Grazing x Qpy x Time | 0.47 ± 0.17 | 2,83 | 0.005 |
| Shrub x Qpy x Time | −0.13 ± 0.08 | −1,52 | 0.129 |
| Grazing x Shrub x Qpy x Time | −0.24 ± 0.17 | −1,39 | 0.164 |

heights of 100 ± 21 cm and 96 ± 9 cm, respectively. Under grazing, *Q. petraea* surpassed *Q. pyrenaica* in height from 2017 onward. By the end of the study, the heights for seedlings with grazing were 37 ± 0 cm for *Q. petraea* and 31 ± 22 cm for *Q. pyrenaica*, representing increases of 1.4 times for *Q. petraea* and 1.8 times for Q. pyrenaica compared to the initial planting heights, with *Q. petraea* starting from a higher baseline.

### *3.3. Seedling diameter*

The LMM showed significant simple effects of Grazing, Shrub, and Time on seedling basal diameter, along with strong two- and three-way interactions involving *Quercus* species (Table 3). *Q. petraea* seedlings consistently exhibited greater diameter values under shrub cover, regardless of grazing. In contrast, *Q. pyrenaica* showed opposite trends depending on grazing: diameter was greater under shrubs in grazed plots, but greater outside shrubs in ungrazed plots (Fig. 4 A). Grazing exclusion amplified interspecific differences in both microsites, while grazing reduced them.

Basal diameter growth was jointly affected by shrub cover and grazing over time (Fig. 4B). In ungrazed plots, diameter increased progressively, reaching fourfold under shrubs and ninefold outside shrubs by 2022. Under grazing, growth was slower —2.4 times under shrubs and 1.5 times outside shrubs— with consistently higher values under shrub cover. Differences between ungrazed and grazed open plots widened over time, although grazing exclusion had no immediate effect during the first two years.

Grazing exclusion promoted greater diameter growth in both species (Fig. 4 C), with divergence between grazed and ungrazed plots emerging earlier and more strongly in *Q. pyrenaica*. By 2022, *Q. pyrenaica* had a larger diameter than *Q. petraea* in ungrazed plots (19.5 ± 0.6 mm vs. 17.8 ± 0.6 mm), while the reverse was observed under grazing (8.1 ± 0.3 mm vs. 9.5 ± 0.0 mm). Diameter increased 6 times in ungrazed plots for both species, compared to only 2.3 times under grazing.

There was also a significant effect of shrubs on seedling diameter over time, whose sign depended on the *Quercus* species (Fig. 4D). For *Q. petraea*, shrub presence generally enhanced diameter growth, except in the final two years, when seedlings outside shrubs were thicker. *Q. pyrenaica* showed a brief early benefit (2011–2013), but no clear advantage later (2019–2022). By 2022, basal diameter had increased 3.3 times under shrubs (Qpy: 11.7 mm; Qpt: 13.4 mm) and 5.3 times outside shrubs (Qpy: 15.8 mm; Qpt: 18.2 mm).

### *3.4. Seedling annual growth*

The LMM revealed a significant interaction between shrub presence, *Quercus* species, and time on seedling annual growth (Table 4). Overall,

**Table 3**
Model parameters estimates derived from LMM models for seedling diameter. (S- G- Qpt): *Q. petraea* outside shrubs and without grazing. Qpy: *Q. pyrenaica.*

| Fixed effects | Estimates ± SE | *t*-value | *p* |
|---|---|---|---|
| Intercept (S- G- Qpt) | 1.11 ± 0.21 | 5.39 | < 0.001 |
| Grazing | 1.13 ± 0.28 | 4.03 | < 0.001 |
| Shrub | 0.66 ± 0.21 | 3.11 | 0.002 |
| Qpy | 0.21 ± 0.22 | 0.95 | 0.344 |
| Time | 0.27 ± 0.03 | 9.02 | < 0.001 |
| Grazing x Shrub | −0.92 ± 0.29 | −3.16 | 0.002 |
| Grazing x Qpy | −0.82 ± 0.29 | −2.78 | 0.005 |
| Shrub x Qpy | −0.26 ± 0.22 | −1.15 | 0.252 |
| Grazing x Time | −0.39 ± 0.06 | −6.49 | < 0.001 |
| Shrub x Time | −0.068 ± 0.03 | −2.28 | 0.023 |
| Qpy x Time | 0.03 ± 0.03 | 1.07 | 0.287 |
| Grazing x Shrub x Qpy | 0.72 ± 0.31 | 2.33 | 0.019 |
| Grazing x Shrub x Time | 0.28 ± 0.06 | 4.56 | < 0.001 |
| Grazing x Qpy x Time | 0.14 ± 0.06 | 2.22 | 0.026 |
| Shrub x Qpy x Time | −0.08 ± 0.03 | −2.43 | 0.015 |
| Grazing x Shrub x Qpy x Time | −0.069 ± 0.06 | −1.06 | 0.289 |

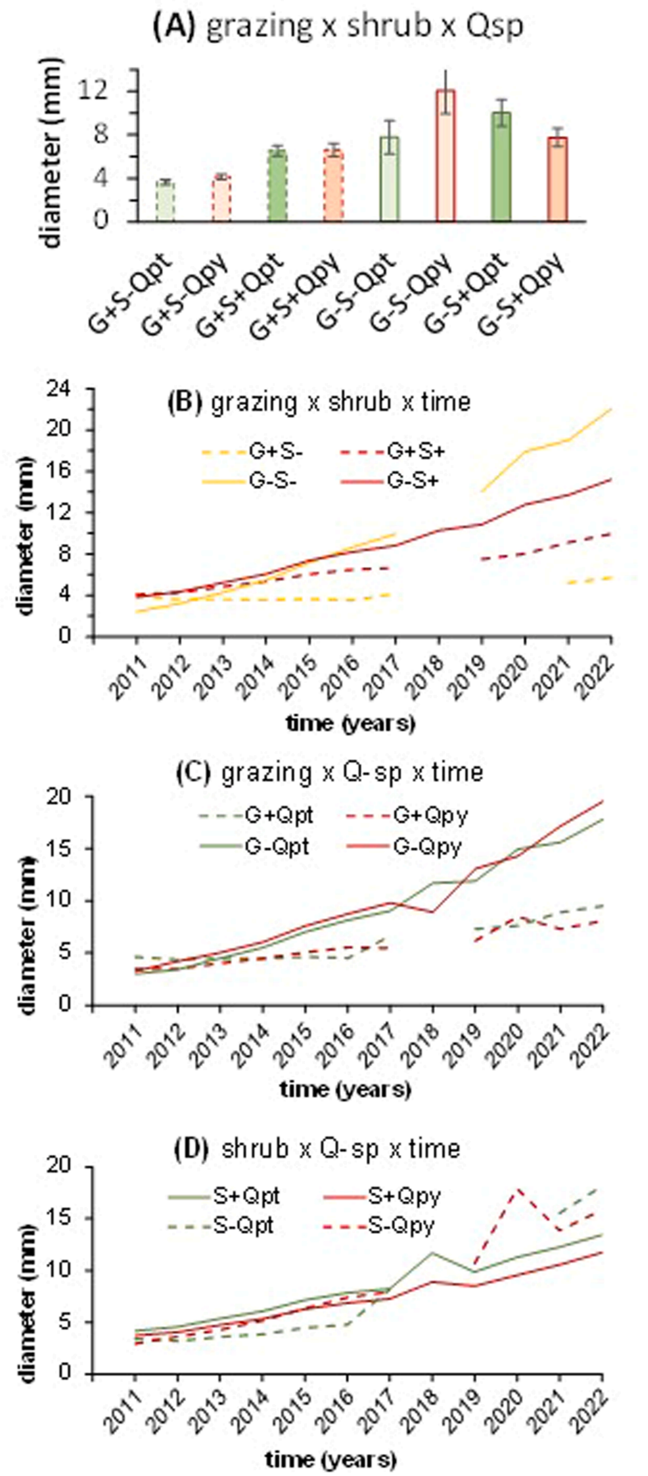


**Fig. 4.** (A) Seedling diameter for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) in grazed (G+) and non-grazed (G-) areas with shrubs (S+) or without shrubs (S-). (B) Seedling diameter in grazed (G+) and ungrazed (G-) areas with shrubs (S+) or without shrubs (S-) through the study period (2011–2022). (C) Seedling diameter for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) in grazed (G+) and ungrazed (G-) areas through the study period (2011–2022). (D) Seedling diameter for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) in areas with shrubs (S+) or without shrubs (S-) through the study period (2011–2022). The fitted lines represent the minimal adequate LMM.

**Table 4**
Model parameters estimates derived from LMM models for seedling annual growth. (S- G- Qpt): *Q. petraea* outside shrubs and without grazing. Qpy: *Q. pyrenaica.*

| | Estimates ±SE | t-value | *p* |
|---|---|---|---|
| **Intercept (S- G- Qpt)** | 1.8 ± 0.53 | 3.41 | < 0.001 |
| Grazing | −1.57 ± 1.52 | −1.04 | 0.299 |
| Shrub | 0.056 ± 0.47 | 0.12 | 0.906 |
| Qpy | −0.29 ± 0.46 | −0.62 | 0.533 |
| Time | 0.05 ± 0.10 | 0.52 | 0.605 |
| Grazing x Shrub | 1.62 ± 1.52 | 1.06 | 0.289 |
| Grazing x Qpy | 1.89 ± 1.55 | 1.21 | 0.225 |
| Shrub x Qpy | 0.37 ± 0.47 | 0.78 | 0.436 |
| Grazing x Time | 0.37 ± 0.65 | 0.57 | 0.572 |
| Shrub x Time | 0.06 ± 0.10 | 0.65 | 0.517 |
| Qpy x Time | 0.15 ± 0.10 | 1.45 | 0.146 |
| Grazing x Shrub x Qpy | −1.83 ± 1.56 | −1.17 | 0.241 |
| Grazing x Shrub x Time | −0.46 ± 0.65 | −0.71 | 0.481 |
| Grazing x Qpy x Time | −0.64 ± 0.65 | −0.98 | 0.327 |
| **Shrub x Qpy x Time** | −0.21 ± 0.10 | **−2.07** | **0.039** |
| Grazing x Shrub x Qpy x Time | 0.76 ± 0.65 | 1.17 | 0.243 |

*Q. pyrenaica* grew more than *Q. petraea*, though differences varied by year (Fig. 5). *Q. petraea* consistently grew better under shrubs (mean: 6.23 cm vs. 3.7 cm), especially in 2011 and 2018–2019. In contrast, *Q. pyrenaica* showed higher growth under shrubs from 2011 to 2014, but from 2015 onward, growth was greater outside shrubs, with minimal microsite differences between 2019 and 2021.

## 4. Discussion

In the studied coal mine reclaimed for livestock use under a sub-Mediterranean climate —characterized by recurrent summer drought exacerbated by the poor soil conditions— the performance of seedlings of two ecologically contrasted *Quercus* species (*Q. pyrenaica* and *Q. petraea*) increased under the cover of native colonizer shrubs (*Genista florida* and *Cytisus scoparius*). The facilitative effect was found for both *Quercus* species, but to a different degree depending on the species considered and the variable measured (e.g., survival or growth). The strength of facilitative effects on seedling survival and growth differed among treatments and exhibited temporal variation.

### *4.1. Seedling survival*

Twelve years of monitoring demonstrated that native shrubs (*G. florida* and *C. scoparius*) significantly improved the survival of planted *Quercus* species on post-mining soils compared to shrub-free microsites. This facilitative effect aligns with previous findings on positive neighbour interactions among woody species, particularly when shrubs act as nurse plants for tree seedlings (Gómez-Aparicio, 2009).

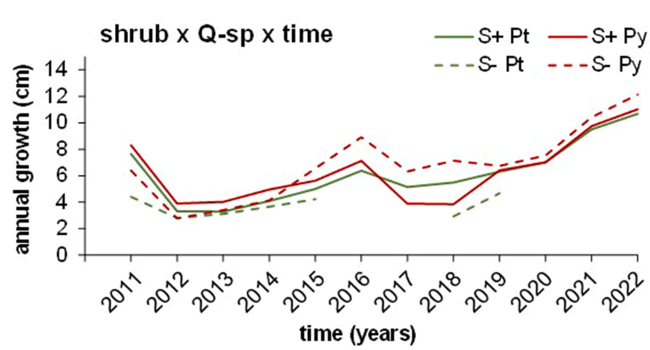


**Fig. 5.** Seedling annual growth for *Q. petraea* (Pt) and *Q. pyrenaica* (Py) species in areas with shrubs (S+) or without shrubs (S-) through the study period (2011–2022). The fitted lines represent the minimal adequate LMM.

Similar benefits have been reported for other leguminous shrubs such as *Retama sphaerocarpa* (L.) Bois. (Rolo et al., 2013), *Genista hirsuta* Vahl (Smit et al., 2007, 2008), and *Cytisus multiflorus* (L'Hér.) Sweet (Costa et al., 2017), supporting the use of shrubs as ecosystem engineers to promote the establishment of late-successional species in degraded environments (Bradshaw, 1997; Alday et al., 2014). In arid systems, however, nurse-based ecological restoration must be tailored to the species and environmental conditions involved (Noumi et al., 2015).

Shrubs likely improve seedling survival by ameliorating microclimatic conditions (Gómez-Aparicio et al., 2005, 2008; Smit et al., 2008; Muhamed et al., 2013) and enhancing soil properties such as fertility and water retention (Pugnaire et al., 2004; Costa et al., 2017; López-Marcos et al., 2020; Muñoz-Cerro et al., 2023).

As expected in Mediterranean systems (Navarro-Cerrillo et al., 2005; Castro et al., 2006; Costa et al., 2017), the first summer after planting was critical, with survival dropping to 11 % in shrub-free areas compared to 91 % under shrubs. In the second year, survival decreased under shrubs (50 %) but remained lower in shrubs-free areas (7 %), likely due to reduced rainfall. The low water-holding capacity of mine soils (López-Marcos et al., 2020) exacerbated drought stress, limiting the effectiveness of shrub facilitation during extreme conditions. Nonetheless, medium-term survival remained higher under shrubs: after 12 years, survival was 13 % for *Q. petraea* and 25 % for *Q. pyrenaica* under shrubs, compared to 1 % and 4 %, respectively, in areas without shrubs. These findings are consistent with studies showing that facilitation may decline under extreme stress (Maestre and Cortina, 2004; Michalet et al., 2006; Holmgren and Scheffer, 2010; Guignabert et al., 2020; Chaieb et al., 2021).

Although *Quercus* species can be unpalatable to herbivores due to high tannin content (Rodríguez-Doce, 2010), trampling and uprooting by ungulates can impact seedling survival (Torroba-Balmori et al., 2015). Shrubs may act as physical barriers, reducing herbivore damage even in the absence of spines (Gómez et al., 2001). However, in contrast to other Spanish sites (Gómez et al., 2003), fencing did not significantly improve seedling survival under shrubs, suggesting herbivory is not a major constraint in this area. This aligns with findings from Costa et al. (2017) in open oak woodlands.

The contrasting survival patterns between species likely reflects their different tolerance to drought stress, since *Q. petraea* is a non-Mediterranean species in contrast to *Q. pyrenaica* (Rodríguez-Calcerrada et al., 2008, 2010), which greater self-shading capacity (Rodríguez-Calcerrada et al., 2008) reduces radiation exposure and transpiration, enhancing water balance and minimizing photoinhibition and overheating (Bragg and Westoby, 2002).

Therefore, selecting species with traits suited to site-specific constraints is essential for successful reforestation. The use of shrubs as nurse plants should be guided by the ecological requirements of target species, which will also influence long-term soil development and ecosystem recovery (Mukhopadhyay et al., 2013).

### *4.2. Seedling height and stem diameter growth*

Over the 12-year period, *Quercus* seedlings exhibited slow but significant increases in height and diameter, with *Q. petraea* showing more pronounced growth than *Q. pyrenaica*. Specifically, *Q. petraea* tripled its height and increased its diameter by 2.8 times, while *Q. pyrenaica* grew only 2.4 times in both dimensions. These differences reflect initial size disparities (*Q. petraea* height and diameter were higher than those of *Q. pyrenaica* seedlings at the beginning of the experiment) and are consistent with the inherently slow growth of *Quercus* seedlings in Mediterranean environments, particularly under early-season drought stress (Costa et al., 2017; Navarro-Cerrillo et al., 2005). The greater growth of *Q. petraea* aligns with its higher responsiveness to light, as previously reported (Rodríguez-Calcerrada et al., 2008).

Seedling growth was influenced by the combined effects of shrub presence and grazing exclusion. The positive impact of shrubs on height and diameter was more evident in grazed areas, particularly for *Q. pyrenaica* and, to a lesser extent, *Q. petraea*. In ungrazed areas, *Q. petraea* maintained a consistent growth advantage under shrubs, while *Q. pyrenaica* showed diminishing shrub-related benefits over time. In ungrazed, shrub-free areas, growth was minimal or absent for both species.

These findings confirm that shrubs facilitate *Quercus* growth through two primary mechanisms: (a) microclimatic amelioration and (b) protection from herbivory. While abiotic stress buffering appears to be the dominant driver of early growth, the role of herbivore exclusion became more relevant over time, particularly in shrub-free areas. This temporal shift may explain the lack of significant fencing effects during the initial years (Torroba-Balmori et al., 2015), a pattern also observed in other studies where fencing benefits become more apparent as saplings mature (Zamora et al., 2001; Baraza, 2004; Gómez-Aparicio et al., 2008).

The synergistic effect of shrubs and grazing exclusion was more pronounced for *Q. petraea*, suggesting greater sensitivity to environmental stress compared to *Q. pyrenaica* (Torroba-Balmori et al., 2015). Grazing exclusion amplified interspecific differences, especially in shrub-free areas where shrub facilitation was absent.

Enhanced growth under shrub canopies likely results from moderated light conditions, improved soil properties, and better water availability (López-Marcos et al., 2020). While some studies report reduced growth under nurse plants despite higher survival (Gómez-Aparicio et al., 2005; Marañón et al., 2004), our results indicate that facilitation in this context supports both survival and growth. This contrasts with the commonly observed trade-off between these two outcomes (Gómez-Aparicio, 2009), although stem elongation under shade has been documented (Pérez-Ramos et al., 2010). Ultimately, the balance between light availability and water stress determines growth responses (Baraza et al., 2004; Marañón et al., 2004). In our study, nurse shrubs promoted both survival and growth, supporting their use as a restoration tool for *Quercus* reintroduction in post-mining landscapes, as also observed in central-western Spain (Costa et al., 2017).

### *4.3. Seedling annual growth*

It was hypothesized that there is a beneficial effect of shrubs and grazing exclusion on *Quercus* seedling growth. However, only shrubs had a positive effect on annual growth, while grazing exclusion did not affect it, either in the short term (Torroba-Balmori et al., 2015) or in the medium term.

Overall browsing pressure on oaks was also low in other studies (Kellner and Swihart, 2017). However, we expected to find a compensatory effect on annual growth in response to herbivory pressure, as reported in previous studies (Retuerto et al., 2003). Compensatory growth in oak seedlings has been observed under moderate herbivory, especially in light-rich environments, although its occurrence is contingent upon damage severity and ecological conditions (Retuerto et al., 2003).

The higher seedling annual growth found beneath shrub canopies in comparison with shrub-free areas is probably caused by less stressful light conditions, and better soil properties and water status under shrubs (Muñoz-Cerro et al., 2023). These results contrast with other studies (Gómez-Aparicio et al., 2005; Marañón et al., 2004), where despite finding higher seedling survival in shady habitats, under neighbour plants the seedling growth decreased or did not improve compared with areas without shrubs. Neutral or negative interactions among nurse species and target species are usually found in facilitation studies when growth is considered, in contrast to the general positive effects upon survival (Liancourt et al., 2005; Gómez-Aparicio, 2009) but sometimes stem elongation can be higher in shaded microsites than in open areas (Pérez-Ramos et al., 2010). In addition, although *Quercus* seedlings under shade conditions may grow less than those under full light, the shortage of water may also reduce their growth, so the equilibrium between both factors determines the final response (Baraza et al., 2004; Marañón et al., 2004). In our study conditions, restoration with nurse shrubs does not confront survival against growth, but favours both, resulting in a promising technique for *Quercus* reintroduction in mine sites, as in other stressful environments (Costa et al., 2017).

However, the strength of shrub facilitation on annual growth also varied by *Quercus* species and year (*Shrub x Q-sp x Time* interaction). In particularly dry years (e.g., 2012, 2017, 2019), differences in growth between microsites with and without shrubs diminished, indicating that shrub-mediated amelioration was insufficient to fully buffer extreme drought.

During the second year after plantation seedling growth beneath shrub canopies decreased in comparison with the first year, and this was followed by differences in growth between species. Previous studies on seedling growth (Rodríguez-Calcerrada et al., 2008) found that when there was no water shortage, *Q. petraea* seedlings grew more than those of *Q. pyrenaica* in greater light conditions, those differences being minimal when both species were in shade. In contrast, our study showed that *Q. pyrenaica* growth was greater than *Q. petraea* in all conditions (i.e., under and outside shrubs), pointing out the higher stress undergone by *Q. petraea* compared with *Q. pyrenaica* on this reclaimed site. The limiting conditions of the summer drought probably affected more *Q. petraea*, with more drought-sensitive features, than *Q. pyrenaica*, better adapted to water stress (Rodríguez-Calcerrada et al., 2008), reducing its growth and the effectiveness of its reintroduction in post-mining sites compared with *Q. pyrenaica*.

While growth was similar for both *Quercus* species in some years (2011, 2016, 2017), *Q. pyrenaica* outperformed *Q. petraea* between 2012–2014, with the trend reversing from 2018 onward. This shift reflects species-specific stress responses: *Q. petraea* is more sensitive to drought, while *Q. pyrenaica* exhibits greater tolerance (Rodríguez-Calcerrada et al., 2008). Thus, *Q. petraea* initially lagged in growth (see Torroba-Balmori et al., 2015) but later surpassed *Q. pyrenaica* once established.

These results have important implications within the context of climate change, increasing aridity in sub-Mediterranean areas (García-Valdecasas Ojeda et al., 2021; Trullenque-Blanco et al., 2024) is expected to further constrain natural oak recruitment, alter species composition, and enhance the role of shrubs as key facilitators (Pérez-Ramos, 2014).

## 5. Conclusion

Our 12-year field experiment, conducted in a reclaimed coal mine under sub-Mediterranean climate conditions, demonstrates that the survival and growth of *Quercus pyrenaica* and *Q. petraea* seedlings were significantly higher in proximity to native nurse shrubs (*Genista florida* and *Cytisus scoparius*). Facilitation effects varied by oak species and the performance metrics used to assess facilitation, with *Q. pyrenaica* showing higher survival and *Q. petraea* showing greater growth responses. Native leguminous shrubs primarily mitigated abiotic stress, especially during early establishment, while grazing exclusion enhanced growth in later stages. No evidence of a shift from facilitation to competition was observed, even under increasingly harsh climatic conditions.

These findings highlight the potential of leguminous shrubs as effective tools for restoring degraded oak ecosystems, particularly for late-successional species at their bioclimatic limits. Restoration success depends on species-specific stress tolerance and future climate projections, which suggest increasing water stress. Although oak seedling performance was enhanced near shrubs, shrub cover may be insufficient under extreme drought conditions, especially for *Q. petraea*, underscoring the need for integrated restoration strategies.

### CRediT authorship contribution statement

**Elena Muñoz-Cerro:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Daphne López-Marcos:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Investigation, Data curation. **Armijos-Montaño Andrés R.:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Juan García-Duro:** Writing – review & editing, Visualization, Validation, Software, Investigation, Funding acquisition, Formal analysis, Data curation. **MARTINEZ-RUIZ CAROLINA:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123291.

### Data availability

Data will be made available on request.

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