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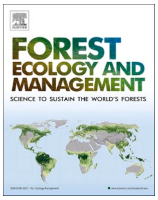

Drivers of seedling emergence and early growth of 12 European oak species: Results from a cross-continental experiment

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ABSTRACT

Seedling emergence constitutes a critical recruitment step, and early growth relates to plant competitive ability. Understanding their drivers has implications for forestry and forest ecosystem conservation, restoration, and adaptation to climate change. We seeded 6984 acorns in an experiment with 97 cases at 45 sites in 15 European countries, encompassing 12 oak species. We tested whether the quality of the acorn batch, site-level weather and soil characteristics, year of seeding, and species' mean specific leaf area (SLA) affected the emergence and early growth of seedlings after the first summer. Germination potential and acorn dry weight, measured under controlled conditions, were positively associated with emergence and early growth. Seedling emergence was negatively associated with the mean monthly temperature and cumulative winter precipitation, and it was higher in the seedling cohort that was spared from the 2021 drought. Additionally, seedling emergence was positively related to soil nutrient concentration and negatively to increasing soil pH, but not to water-holding capacity, and growth was unrelated to soils. Species-level SLA was not related to either response. The four main study species –*Quercus cerris*, *Q. ilex*, *Q. petraea,* and *Q. robur*– responded similarly to weather but not to soil conditions. We conclude that, at a continental scale, and assuming that species establish within their current distributions, (a) oak seedling emergence and early growth are associated with acorn quality rather than species identity or SLA, (b) they are highest at sites with low winter precipitation and temperature, (c) emergence is reduced in dry years, and d) soil properties play a secondary role at this early recruitment stage.

1. Introduction

Oaks (*Quercus* spp.) dominate forests and shrublands across the Northern Hemisphere and sustain high levels of biodiversity and provision of ecosystem services (da Silva et al., 2019). Oaks are also key components of wood-production forests (Johnson et al., 2019) and savannah-like agrosilvopastoral systems (Campos et al., 2013). Europe harbors some 30 native oak species (Kremer and Hipp, 2020), which are distributed from the Mediterranean to the southern limit of the Boreal region. Native oak populations have declined over the past decades due to deforestation, land-use changes, shifting climatic conditions, and pathogen outbreaks (Colangelo et al., 2017; Keča et al., 2016). However, their high adaptability to drought and other stressors (Kremer and Hipp, 2020; Leroy et al., 2020) may enable them to colonize new areas and replace more drought- and heat-sensitive species under climate change (Delzon et al., 2013). Promoting the abundance of oaks in drought-sensitive forests –such as beech forests and conifer monocultures– and gene flow among populations is thus an increasingly recommended approach to help forests adapt to climate change (Enderle et al., 2024; Gardner and Bullock, 2025). Additionally, enhancing oak recruitment in areas experiencing an increase in the mortality of older individuals is essential for sustaining their populations (Celma et al., 2024). Current policies such as the UN Decade of Ecosystem Restoration, the EU Biodiversity Strategy for 2030, the EU Nature Restoration Regulation, and the 3-Billion-Trees Pledge (European Commission, 2024) provide momentum to promote native oak species across Europe as key components of both natural and semi-natural habitats.

The maintenance and restoration of oak-dominated ecosystems hinge upon appropriate levels of recruitment. This refers to the process by which seedlings establish, survive, and grow to become part of the adult population. It requires individuals to cross critical transitions among multiple demographic stages, ranging from flowering to the establishment of a sexually mature individual (Crawley and Long, 1995; Pérez-Ramos and Marañón, 2008; Pulido and Díaz, 2005). Both natural regeneration and assisted regeneration through direct seeding of acorns represent viable nature-based solutions for the regeneration of ecosystems dominated by large-seeded species, including oaks (Ceccon et al., 2016; Löf et al., 2019), provided that herbivory and competition are low. These methods for regeneration are preferable to planting seedlings when the goal is to support tap root development (Grossnickle and Ivetić, 2017; Juan-Ovejero et al., 2025). However, the transition from a seed to an established seedling constitutes a potential demographic bottleneck, whereby losses can vary considerably across species, sites, and years (Grossnickle and Ivetić, 2017). Rapid early growth also increases competitiveness against neighboring vegetation, which is a critical aspect for the development of seedlings (Acácio et al., 2007; Kohler et al., 2020) and is therefore related to the capacity of oaks to dominate the vegetation. Understanding the drivers of seedling emergence and early growth is therefore highly relevant for the ecology, restoration, and management of oak-dominated ecosystems, and these drivers result from the interplay between early-life history traits and environmental factors.

The drivers of regeneration success may operate at various scales, including variations among source populations and species, as well as across broad geographic gradients. At the level of source populations, seed traits can be major determinants of oak seedling emergence and early growth. Using resources in the cotyledon, oak seedlings quickly develop a deep taproot after germination, and the shoots emerge later in the spring (Baskin and Baskin, 2014). A large amount of carbohydrates contained in the cotyledon is therefore an advantage for the seedling, leading to a positive functional relationship between seed size, germination rate, and seedling performance (Gómez, 2004; Matías et al., 2019). In addition, germination potential is the baseline for emergence and a key metric of acorn quality, which may also help to explain variations in early growth.

Across species, differences in early development can either be idiosyncratic or correlated with functional traits (Poorter et al., 2009). In particular, specific leaf area (SLA) —i.e., the ratio between leaf surface area and dry mass— serves as a major indicator of plant ecological strategies (Wright et al., 2004). Whereas high SLA is often associated with rapid resource acquisition, growth and photosynthetic capacity and is common in deciduous species, low SLA tends to indicate more conservative strategies of resource use, including drought tolerance, which are common in evergreen species and result in slower growth (Modrzyński et al., 2015). In addition, acquisitive species with high SLA tend to have greater morphological and physiological plasticity, suggesting a greater potential to cope with variable environmental conditions (Puchałka et al., 2023; Stotz et al., 2022). Whereas this trait can show variation within tree species, for instance in response to light (Reich et al., 1998) and water (Weithmann et al., 2022), interspecific variation in mean values of SLA is usually greater and may thus be regarded as an indication of different acquisition strategies resulting from macroevolutionary processes (Poorter et al., 2009). SLA may thus serve to explain differences among species in early development beyond the particular effect of species identity.

On the other hand, variation in seedling emergence and growth across broad geographical gradients is likely to respond to the main drivers of species' distributions relative to soil and climate. However, it is unclear whether soil characteristics and climate patterns may also explain variation in emergence and early growth across species, provided they are within their current range. Across large spatial gradients, weather conditions during winter time are likely key drivers of seedling emergence, as they would be related to the avoidance of seed desiccation and the triggering of germination (Xia et al., 2022). For early seedling growth, weather conditions in spring and summer can also be important, as they relate to the period of establishment and the beginning of primary production, and thus to the time when resources from the acorn become depleted (Quero et al., 2007; Villar-Salvador et al., 2009). In addition, variation in soil conditions can imply different access to resources, with implications for the resistance to abiotic stressors (Gessler et al., 2017). Although oaks represent a diverse genus with species adapted to a wide range of soils and climates (Kremer and Hipp, 2020), it is unclear whether general patterns exist in the responses of seedling emergence and early growth to large-scale variation in weather and soil gradients.

Whereas local studies have helped to understand the drivers of recruitment success at small scales, assessing the drivers that operate at larger scales requires replication across broad environmental gradients. A recent study with four European oak species revealed species-specific responses to latitude and microclimate across five sites spanning from Italy to Sweden (Meeussen et al., 2022). However, we are not aware of previous multi-site studies that have tested the combined effects of acorn quality, species traits, and large-scale environmental gradients on the early regeneration of different oak species. Through a coordinated, distributed experiment (Borer et al., 2014), we established a collaborative network of 45 sites across Europe to assess some of the drivers of regeneration of 12 oak species. Following a common study protocol (Leverkus et al., 2021), we seeded acorns of locally growing oak species and assessed their first-year emergence and growth. To reduce unexplained variation, we minimized differences in light, microclimate, and biotic interactions by using individual acorn protectors, by seeding in fenced, open areas, and by weeding. We hypothesized that seedling emergence and early growth would be conditioned by i) seed-batch quality, including germination potential and acorn mass; ii) species-specific traits, specifically SLA; iii) local weather conditions across the germination and early-growth stages; and iv) site-level soil properties. In addition, we hypothesized that v) the response to soil and weather would differ among the four most represented oak species in our experiment, namely *Quercus robur* L., *Q. cerris* L., *Q. ilex* L., and *Q. petraea* (Matt.) Liebl. Moreover, we investigated at which level —that of seed batches, species, sites, or plots within sites— the greatest additional variation remained. Ultimately, this study aims to shed light on the factors that modulate the natural and assisted regeneration of a major European tree genus, thereby contributing to the conservation and restoration of various types of ecosystems and their associated biodiversity and ecosystem services.

2. Methods

2.1. Study design

In autumn 2021, we established a coordinated, distributed experiment to evaluate the drivers of oak regeneration across Europe. A collaborative network of 45 experimental *sites* was established across 15 countries spanning latitudinally from southern Spain to southern Norway and longitudinally from western Portugal to Latvia (Fig. 1). This produced climatic gradients across sites, with a range in average temperature and cumulative precipitation during the study year in Jan-Mar of −3.0–12.0 °C and 62–400 mm, respectively; in Apr-Jun of 9.8–21.1 °C and 11–342 mm; and in Jul-Sep of 15.0–28.2 °C and 18–267 mm (monthly weather data obtained from the NASA POWER database; see Data availability statement). Soil characteristics varied across sites (see Section 2.3), as well as species identities (Fig. 1). Across all sites, a common, standardized protocol was followed to ensure methodological consistency (Leverkus et al., 2021).

Two experimental *cohorts* were established: cohort A, seeded in autumn-winter 2021–22; and cohort B, seeded in autumn-winter 2022–23. Each site involved either one of these cohorts or both. Cohort B was not contemplated initially but was added *ad-hoc* to compare the results of different seeding years and to enable the inclusion of sites that were established with delay (e.g., for logistical constraints or due to low acorn availability in the first year). Each site used a minimum of one local oak species, with some sites featuring two or three species within a given cohort. Each seeded species within a cohort and site was termed a *case*. For example, a site with three species, each seeded in two cohorts, had six cases. The study comprised a total of 97 cases, with 78 cases in cohort A and 19 cases in cohort B. The total number of cases per species varied considerably, ranging from 1 to 24 (Table S1).

All sites were located on open areas, such as abandoned fields, clearcut forests, or disturbed areas, and with a maximum slope of 10 %. Highly degraded or polluted areas, such as roadsides or mines, were excluded. Sites had to be near a mature population of the target oak species and ecologically suitable for its regeneration. Sites could not contain shrubs or trees, and they were either fenced or otherwise

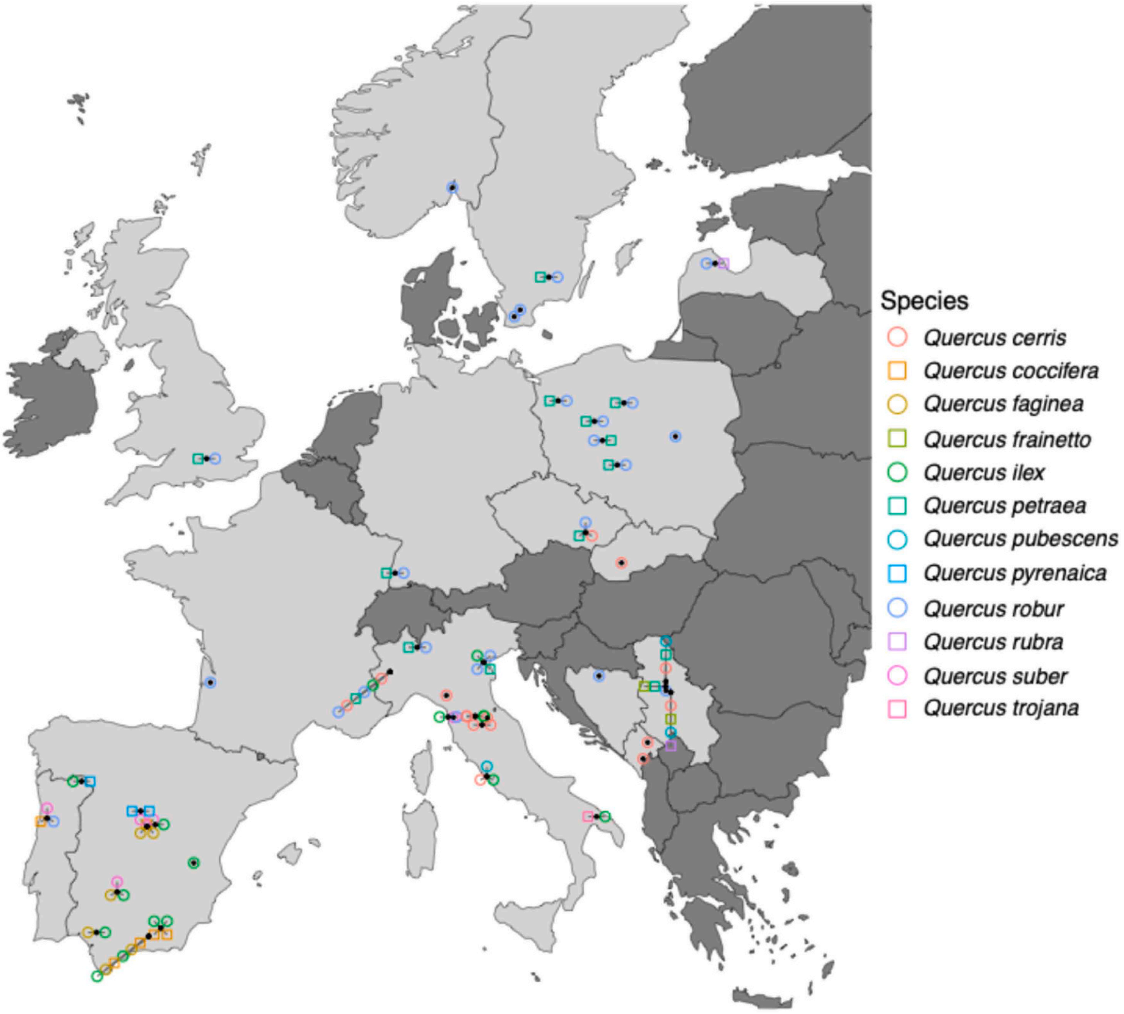

Fig. 1. Location of the study sites (black dots) across 15 countries, indicating the species tested in the corresponding cases (i.e., species tested in one cohort and site). On sites where more than one case was established, case symbols are separated from the site location and linked with a line for clarity. Species shown twice at one site indicate that it was tested in both cohorts. Across the study, the species encompassed a spectrum of ecological strategies from more conservative evergreen species (three species), through marcescent ones (four species), to more acquisitive deciduous species (five species), which was reflected in different values of species-level SLA (Table S1).

protected from medium- (e.g., rabbits) to large-sized (e.g., red deer) herbivores (Fig. 2).

At each site, four *plots* of 1.5 × 1.5 m were established for each case (Leverkus et al., 2021). A hypothetical site with four cases (e.g., three species tested in cohort A and one species in cohort B) thus contained 16 seeded plots. The plots of a given site were marked first and then randomly allocated to a particular species. The plots within a site were required to have a minimum distance of 1 m and a maximum of 100 m from each other. A buffer strip of at least 0.5 m was maintained between the outer plots and the site fence.

Each plot contained nine *seeding points* distributed in three rows, and each point was marked with a stick. Two acorns were seeded at each seeding point, 10 cm apart from each other. This resulted in 4 plots x 9 points x 2 acorns = 72 acorns seeded per case. In total, the field study followed 6984 acorns (see Fig. 2).

2.2. Seed collection, storage, and germination testing

For each site, we collected a minimum of 500 acorns per case from at least 10 mother trees (with a similar number of seeds from each tree), which were placed in 50 μm-thick polyethylene bags for transportation and storage. We intended to collect all acorns from locally growing trees, but low acorn production impeded this in some cases (see Medina et al., 2024 for details on acorn origin and collection methods).

After collection, acorns were air-dried for 24 h in the lab and then stored at 1–4 °C. The bags were stored open without piling in a refrigerator for the shortest time possible, with periodical inspections for rottenness. The acorns were then tested for viability with the flotation test (Bonfil, 1998). Viable acorns were divided into three groups: 72 acorns used for seeding (see Section 2.4), 72 acorns for a treatment that is not described in this paper, and 150 acorns posted to the University of Granada for assessment of seed batch quality.

At the University of Granada, the 150 acorns were inspected, refrigerated, and subjected to quality assessment within one week of reception. The procedure included measuring the dry weight of 50 acorns per batch, as well as testing for germination on the remaining 100 acorns. For the germination test, each batch of acorns was split in half, and the acorns were placed on two trays covered in silica sand. The two trays were then placed in separate germination chambers, which were maintained at a constant temperature of 20 °C. The acorns were watered three times per week, and germination was assessed over an 8-week period. For more detailed methods on acorn germination testing, see Medina et al. (2024).

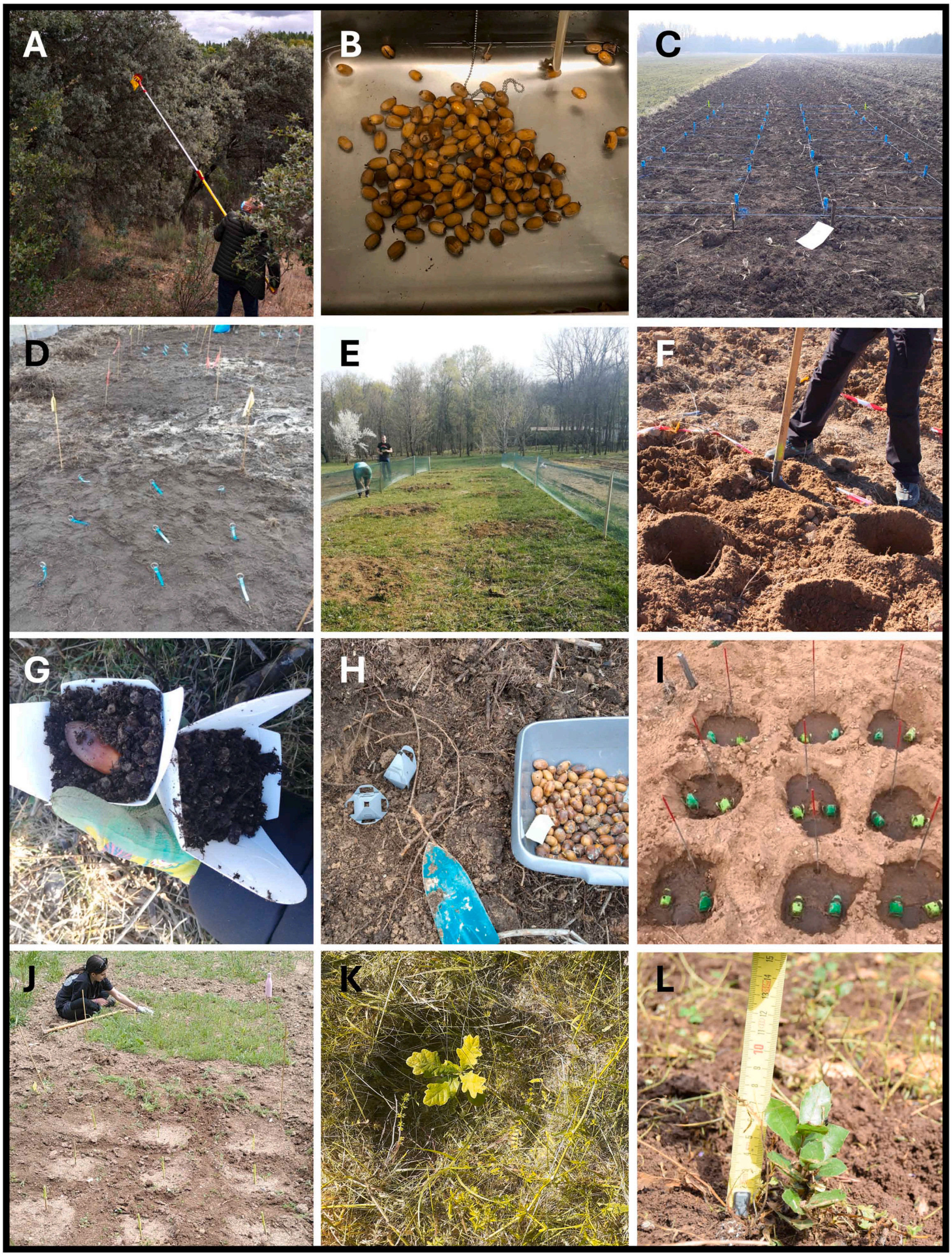

Fig. 2. Photos from the fieldwork. **A)** Acorn collection; Parque Natural de Montesinho (Portugal); Photographer: Maria Sameiro Patrício. **B)** Flotation test; Store Ranvik (Norway); Photographer: Kjersti Holt Hanssen. **C)** Site identification; Mahovljani, Laktasi (Bosnia and Herzegovina); Photographer: Branislav Cvjetkovic. **D)** Plot establishment; Pierroton (France); Photographer: Alba Lázaro-González. **E)** Site fencing; ArbKos (Serbia); Photographer: Ivona Kerkez. **F)** Hole digging; Universidad de Alcalá (Spain); Photographer: Pedro Villar Salvador. **G)** Preparation of seed-shelter; Calci (Italy); Photographer: Barbara Mariotti. **H)** Seeding; Training Forest Enterprise Masarykův Les Křtiny (Czech Republic); Photographer: Lenka Ehrenbergerová. **I)** Irrigation; Becerra (Spain); Photographer: Alexandro B. Leverkus. **J)** Weeding; Technical University of Madrid (Spain); Photographer: Juan Oliet. **K)** Seedling emergence; Flugplatz Freiburg (Germany); Photographer: Klaus Kremer. **L)** Plant measurements; Riserva Naturale Orientata Murge Orientali (IT 33 RNO-MO) (Italy); Photographer: Paola Mairota.

2.3. Soil analyses

At each site, we collected one composite soil sample from three 20 cm-deep holes dug at randomly located points within the site. The soil from the three sub-samples was mixed, and 1 kg of the mixture was placed in a polyethylene bag and taken to the lab. The sample was dried at air temperature for a minimum of one week and then posted to the University of Granada along with the acorn samples.

Upon receipt, the soil samples were dried again at ambient temperature in the laboratory. Before the analyses, the samples were homogenized and passed through a 2 mm sieve. Soil texture was analyzed using the standard pipette methods of Robinson-Köhn or Andreasen (Pansu and Gautheyrou, 2006). The available water (determined by subtracting soil humidity at 33 kPa from soil humidity at 1500 kPa) was calculated using the membrane method (Richards and Weaver, 1944). Total C and N were determined by dry combustion using an elemental analyzer (LECO® TruSpec CN, St. Joseph, MI, USA). Extractable P was determined by colorimetry by the Olsen method (Olsen and Sommers, 1982) and measured by a UV/visible spectrophotometer (Thermo Helios Alpha UV/Vis Spectrophotometer, Thermo Fisher Scientific, Waltham, MA, USA). Total organic carbon (TOC) was evaluated with the method proposed by Walkley and Black (1934), through oxidation with potassium dichromate. $CaCO_3$ content was analyzed as the amount of carbon dioxide emitted during the reaction of $CaCO_3$ with HCl (Bascomb, 1961). Soil pH was determined using a glass electrode with a soil-to-water ratio of 1:2.5 (Jackson, 1964), and the same ratio was employed for the determination of electrical conductivity.

2.4. Soil preparation, acorn protection, seeding, and site maintenance

Soil preparation involved removing vegetation from the plots and excavating a hole of 40 × 40 × 40 cm at each seeding point, which was done either manually or mechanically (Fig. 2). The acorns were soaked in water for 24 h for rehydration and taken to the field. The precise timing of seeding varied across sites, depending on seed availability and local phenology, and it roughly spanned from October to March for both cohorts.

Before seeding, acorns were placed inside *seed shelters*, which consist of plastic boxes filled with soil from the site, which aim to protect acorns from rodents and other granivores (Castro et al., 2015). The shelter's upper and lower openings, with a 1-cm diameter, are large enough to allow the exit of the stem or root yet small enough to impede the entrance of rodents or birds or the removal of the acorn. A puncture line at one edge opens the whole device as the stem and root grow wider. The shelters were buried in such a way that their upper opening was 0.5–1 cm beneath the soil surface, so that the acorns were buried at a total depth of ca. 3–4 cm. Each seed point received 2 L of water immediately after seeding (Fig. 2). Finally, seed points were marked to allow the identification of each of the two plants.

After seeding, fences were maintained, and spontaneous vegetation was regularly cleared from the sites when it covered 80 % of the plot surface.

2.5. Measurements

After the first growing season following seeding (i.e., at a point in time that varied across the geographic gradient, but roughly between September and October), we monitored the emergence of the two acorns per seed-point and measured seedling growth. We measured stem height (from the root collar to the apex) and root-collar diameter. All seedlings were measured in those seed points in which one seedling emerged, but only the tallest individual was measured in those cases where two seedlings emerged at the seed point. As this constituted a potential source of bias (for taller plants at seed points with two emerged individuals vs. those where only one emerged) we accounted for this statistically by including whether there was selection of the taller seedling as a factor in the model for seedling growth (see Section 2.6). The database thus contains measurements for one individual per seed point if either one or two live individuals were present, or no measurement if no seedling was present.

With the seedling measurements, we estimated the seedling Stem Volume Index (SVI) as:

$$\mathrm{SVI} = \sum\nolimits_{i=1}^{n} h_i d_i^2$$

where n is the number of stems of an individual, h_i is the height of stem i, and d_i is its diameter (both in mm). The resulting values were divided by 1000 to convert the units into cm^3.

All the field data were collected by participants and submitted to the coordination team at the University of Granada.

2.6. Statistical analyses

We used mixed-effects models to account for the different scales at which the drivers of the responses were measured, as well as the levels of autocorrelation among the response data resulting from the experimental design (Zuur et al., 2009). The response variable seedling emergence consisted of the proportion of acorns per seed point that produced a seedling by the end of the first summer. For this variable, we fitted generalized mixed-effects models with a binomial distribution and a logit link function. Seedling growth, estimated as SVI (see Section 2.5), was analyzed using linear mixed-effects models, after log-transformation to better meet model assumptions and after the removal of one outlier.

For both response variables, the fixed effects included cohort (a two-level factor), acorn dry weight, acorn germination percentage, two soil variables, species-level SLA obtained from publicly available databases (Díaz et al., 2022, 2016; Tavşanoğlu and Pausas, 2018; see Table S1), and weather variables obtained from the NASA POWER database (see Data availability statement). Acorn dry weight and germination consisted of one mean value per acorn batch. Acorn weight data were missing in two of the 84 acorn batches, so we performed multiple imputation (20 datasets) using species, cohort, site ID, and germination percentage as predictors. We then used the mean of the 20 imputed values for the analysis. To create two main uncorrelated soil variables, we ran a Principal Components Analysis (PCA) with the following variables: percentage of gravel, coarse silt, fine silt, clay, sand, available water, total C, total N, $CaCO_3$, organic C, and organic matter, P concentration, and pH; all variables were standardized by subtracting the mean and dividing by the standard deviation before the PCA. Regarding the weather variables, we tested the effect on seedling emergence of the mean monthly temperature and the cumulative precipitation (which includes rain and snow, expressed in water equivalent) of the winter months (January to March) of the study year, as this was the post-seeding period that could most strongly influence emergence. For SVI, the weather variables tested were the cumulative mean monthly precipitation of the winter, the spring, and the summer (which showed little correlation with each other; Fig. S1), and the mean monthly temperature of the whole period (Jan–Sep, values were combined because the temperatures of the three seasons were highly correlated). In addition, for SVI, we also included as a predictor a two-level factor indicating whether one or two seedlings had emerged at each seed point (see the reasoning in Section 2.5). To improve model performance, the weather and acorn-level predictors were standardized by subtracting their means and dividing by their standard deviations. In both models, the random effects were specified to account for autocorrelation resulting from the spatial arrangement of the experiment (random intercepts for site and for plot within site), the origin of the acorns (random intercept for acorn batch), and species identity (random intercept for species).

We checked for multicollinearity in the models through Variance Inflation Factors (VIF) and removed or merged collinear variables before selecting the predictors described above. The resulting models included only variables with a VIF lower than 4, which is considered a moderate degree of collinearity (Craney and Surles, 2002). The significance of the fixed effects in the models was assessed through a stepwise simplification procedure, in which non-significant terms were sequentially removed from the model until only significant terms remained (Crawley, 2013). Significance was evaluated at $p \leq 0.05$ using likelihood ratio tests at each step.

Additionally, we fitted models for seedling emergence and SVI using only the subset of the data consisting of species present in at least 10 sites, namely *Q. cerris*, *Q. ilex*, *Q. petraea*, and *Q. robur*. The objective was to determine whether responses to soil and weather variables varied by species identity. For this, we tested interactions between species and the two soil PCA axes, as well as between species and the weather variables. As species was treated as a fixed effect in this model, it was excluded from the random effects, and species-level SLA was not tested here. The remaining model structure followed that described above.

Finally, to assess the degree to which the data from individual sites may have influenced model outcomes, we conducted a "leave-one-out" sensitivity analysis on the models of the whole dataset. For this, individual sites were sequentially removed from the data, and the general model was re-fitted each time.

Analyses were run in R version 4.4.1 (R Core Team, 2024), with the packages *lme4* (Bates et al., 2015) and *mice* (van Buuren and Groothuis-Oudshoorn, 2011).

3. Results

3.1. Soils

The first four axes of the PCA explained 82.0 % of the total variance, with 37.2 % captured by PC1, 21.3 % by PC2, 15.4 % by PC3, and 8.1 % by PC4 (Fig. S2). The first axis was strongly and negatively correlated with sand content, and positively with available water and all other soil particle size classes. Axis 2 was most negatively associated with soil organic matter but also with P, total N and total C, and positively related to pH, clay and $CaCO_3$ concentration (Fig. 3, Table S2).

3.2. Seedling emergence

Of the 3492 seeding points, 985 (28.2 %) showed no emergence, 1176 (33.7 %) produced one emerged seedling, and 1331 (38.1 %) produced two emerged seedlings after the first growing season. The probability of seedling emergence was affected by the two acorn-batch variables (acorn mass and germination probability), the two weather variables (winter precipitation and mean monthly temperature), seeding cohort, and the second soil PC axis, yet not by the first soil PC axis or species-level SLA (Table 1).

The relationship between the probability of emergence and both the germination potential and the mean acorn dry weight of the acorn batch was positive (Figs. 4a, 4b). The association with the second soil PC axis was negative (Fig. 4c). Surprisingly, seedling emergence was negatively correlated both with mean monthly winter temperature and cumulative winter precipitation (Figs. 4d, 4e). In addition, emergence rates in cohort B were higher than in cohort A (Fig. 4f). Nearly two-thirds of the total variance was explained by the model, and two-thirds of the explained variance corresponded to the random effects (Table 1). Of the variance explained by the random effects, around half was associated with acorn batch, one-third with the site, nearly 10 % with plot, and a negligible amount with species identity (Table 1). The sensitivity analysis revealed that the direction and magnitude of all effects remained robust even after excluding individual sites from the model (Appendix S1, Fig. S3).

3.3. Seedling growth

Seedling growth, estimated as SVI, was affected by the dry mass and germination potential of the acorn batch, as well as by the average monthly temperature of the study period (Jan-Sep) and precipitation in the winter months. As with seedling emergence, the relationship of SVI with the acorn-batch variables was positive, while its relationship with the two weather variables –mean monthly temperature in Jan-Sep and cumulative precipitation in the winter months– was negative (Fig. 5). The remaining variables, namely cohort, species-level SLA, the two main

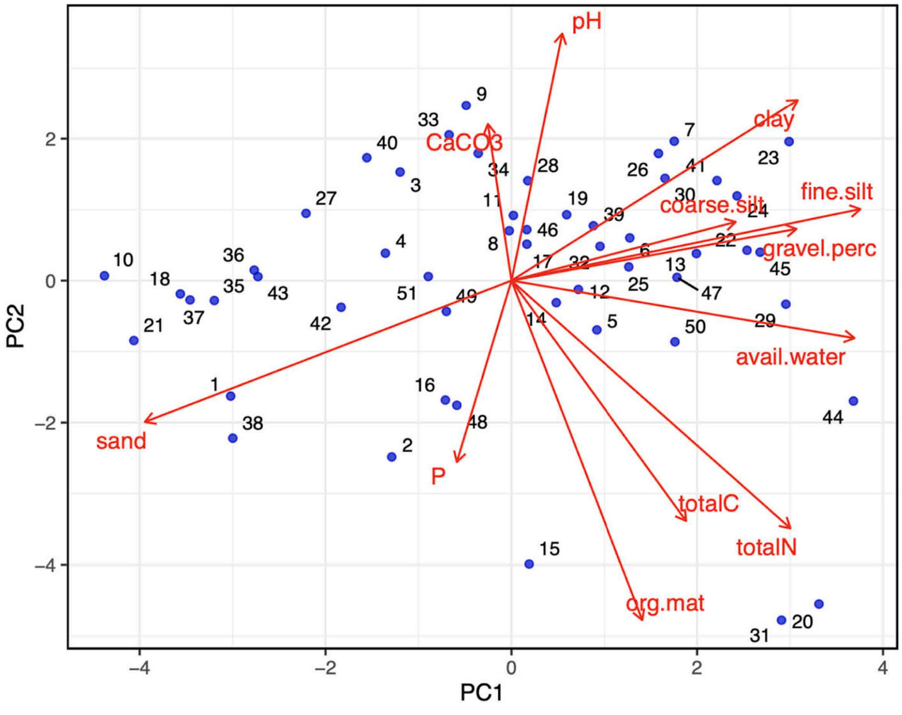

Fig. 3. PCA of soil properties across the experiment. The numbered points represent the soil samples from each site (see associated database), and the arrows show the relative loadings of the soil variables on the first and second principal components, which jointly account for 58.5 % of the total variance.

Table 1
Mixed-effects models for the probability of emergence and seedling volume index after the first growing season.

		Emergence probability[1]		**Seedling volume index**[2]	
Predictor	**df**	χ^2	**P**[3]	χ^2	**P**[3]
Cohort	1	6.14	**< 0.05**	1.02	0.31
SLA[4,5]	1	1.05	0.30	0.03	0.87
Soil PC1	1	1.06	0.30	0.85	0.36
Soil PC2	1	4.30	**< 0.05**	0.40	0.53
Germin. Potential[4]	1	12.31	**< 0.001**	4.22	**< 0.05**
Acorn dry weight[4]	1	14.26	**< 0.001**	11.25	**< 0.001**
Mean monthly temperature[4,6]	1	15.12	**< 0.001**	6.07	**< 0.05**
Winter precipitation[4]	1	9.00	**< 0.01**	5.15	**< 0.05**
Spring precipitation[4]	1	-	-	1.70	0.19
Summer precipitation[4]	1	-	-	0.26	0.61
N emerged seedlings[7]	1	-	-	48.73	**< 0.001**
R^2[*]		**R**^{2}		**R**^{2}	
Marginal (fixed effects)		0.22		0.11	
Conditional (fixed and random effects)		0.63		0.63	
Random effects[8]		**%**		**%**	
Site		36.0		55.3	
Plot within site		9.2		4.3	
Seed batch		53.5		17.4	
Species		1.3		23.0	

[1] Model based on 3492 observations distributed across 180 plots at 45 sites with 86 seed batches from 12 species.

[2] Model based on 1966 observations across 166 plots at 42 sites with 72 seed batches from 11 species (for 3 *cases*, no growth data were recorded despite the presence of seedlings); SVI was log-transformed.

[3] P-values in bold indicate statistical significance.

[4] Standardized variables.

[5] For emergence, SLA was tested on the full model yet excluding the species-level random effect due to model overparametrization.

[6] Mean monthly temperature of Jan–Mar for emergence; of Jan–Sep for SVI.

[7] Dummy variable indicating whether 1 or 2 seedlings had emerged at the seeding point because in the latter case only the taller one was measured; for details, see Section 2.5.

[8] Percentage of explained variance stemming from each level.

[*] Proportion of total variance explained in the simplified model, which included all the random effects and the significant fixed effects; calculation based on Nakagawa et al., (2017).

soil PC axes, and precipitation in spring and in summer, had no significant effect on SVI (Table 2). The observed effect of the number of emerged seedlings was a procedural bias control and is thus not informative.

3.4. Response of the most abundant species

When analyzing only those species present in at least 10 sites, the emergence of seedlings was again affected by the soil PC2 axis, the two acorn-batch variables, and the two weather variables (Table 2), and these effects aligned with those of the general model. Additionally, a significant interaction was observed between the soil PC1 axis and species, suggesting species-specific responses of emergence to soil texture and water availability. Whereas *Q. petraea, Q. ilex,* and *Q. robur* showed no clear association with this axis, the association was strongly negative for *Q. cerris* (Fig. 6). Cohort did not have a significant effect on emergence in this model, nor did the interaction between species and soil PC2 or between species and any weather variable.

The growth of the four most represented species showed significant effects of the same predictors as in the general model described in Section 3.3. Additionally, there was a significant interaction between species and soil axis PC2 (Table 2). The association between this axis and SVI was neutral for *Q. petraea* and *Q. robur*, negative for *Q. ilex*, and positive for *Q. cerris* (Fig. 6).

4. Discussion

Seed quality metrics were decisive in explaining seedling emergence and early growth across 12 oak species seeded within the current range of conspecific adult populations at 45 European sites. Local soil properties and weather during the study period contributed to explaining variation across a broad geographic gradient spanning latitudinally from southern Spain to southern Norway and longitudinally from western Portugal to Latvia, whereas species-level effects were limited to idiosyncratic differences in the response of the four most represented oak species to soil, and species-averaged SLA did not explain heterogeneity in either seedling emergence or growth. The distributed and experimental approach of this experiment, strengthened by a common study protocol, provides a broad perspective of the drivers of oak recruitment and valuable insights for forestry and ecological restoration with a major tree genus.

4.1. Importance of seed and species traits

There was strong support for our first hypothesis, namely that germination potential and acorn mass would explain variation in seedling emergence and early growth. Acorn dry weight showed a positive association with both seedling emergence and first-year growth, although the effect was most pronounced for seedling emergence. The relationship between seed size and emergence, which has been documented in many studies (Devetaković et al., 2019; Gómez, 2004; Lázaro-González et al., 2023b), may result from the reduced risk of desiccation in larger acorns. As these seeds are highly sensitive to water loss (Xia et al., 2022), even a relatively short period of water shortage may result in emergence failure, particularly for small acorns.

Positive relationships between acorn size and growth have been reported extensively as well (Dey et al., 2008; Löf et al., 2019; but see Clark and Schlarbaum, 2018). However, our study –conducted under full-light conditions– may have underestimated the magnitude of the growth dependence on seed size, which tends to be greatest under low light conditions, which are more typical for the regeneration of most oak species (Quero et al., 2007). The positive seed size-growth relationship can be attributed to a greater availability of reserves after germination, the escape from size-dependent mortality (Quero et al., 2007), and an earlier germination and emergence of large seeds (Gómez, 2004). Additionally, high seed mass can increase the tolerance to stressors other than desiccation, such as waterlogging, in some species (Pérez-Ramos and Marañón, 2009). By affecting growth, the implications of seed size may carry over to subsequent development stages, as larger seedlings tend to show higher survival and performance (Andivia et al., 2021). Such implications may also increase in the future, as warming experiments have found that greater acorn size can partly compensate for reductions in seedling performance due to hotter and/or drier climate for different oak species (Badano and Sánchez-Montes de Oca, 2022; Lázaro-González et al., 2023b).

Under natural conditions, there may also be negative selection pressure on acorn size (Gómez, 2004), for example through granivory (Pérez-Ramos and Marañón, 2008) and seed dispersal (Schupp, 1995). The benefits of heavier acorns for regenerating oaks, therefore, apply under conditions of adequate dispersal (or seeding) and low seed predation. Further, the effects of today's positive seed-size selection on the future dynamics after tree maturity are still largely unknown (Leverkus and Navarro, 2021). It is worth noting that the high inter- and intraspecific diversity of oaks (Kremer and Hipp, 2020) in traits such as seed size underlies their capacity to overcome multiple selective pressures (Gómez, 2004), including the adaptation to climate change (Schroeder et al., 2021). Therefore, besides the directed selection of traits for stand regeneration to address the recommendations derived from this and other studies, restoration should also strive to maintain sufficient diversity –by also retaining apparently less successful trait values– to enhance the adaptive potential of populations to future environmental

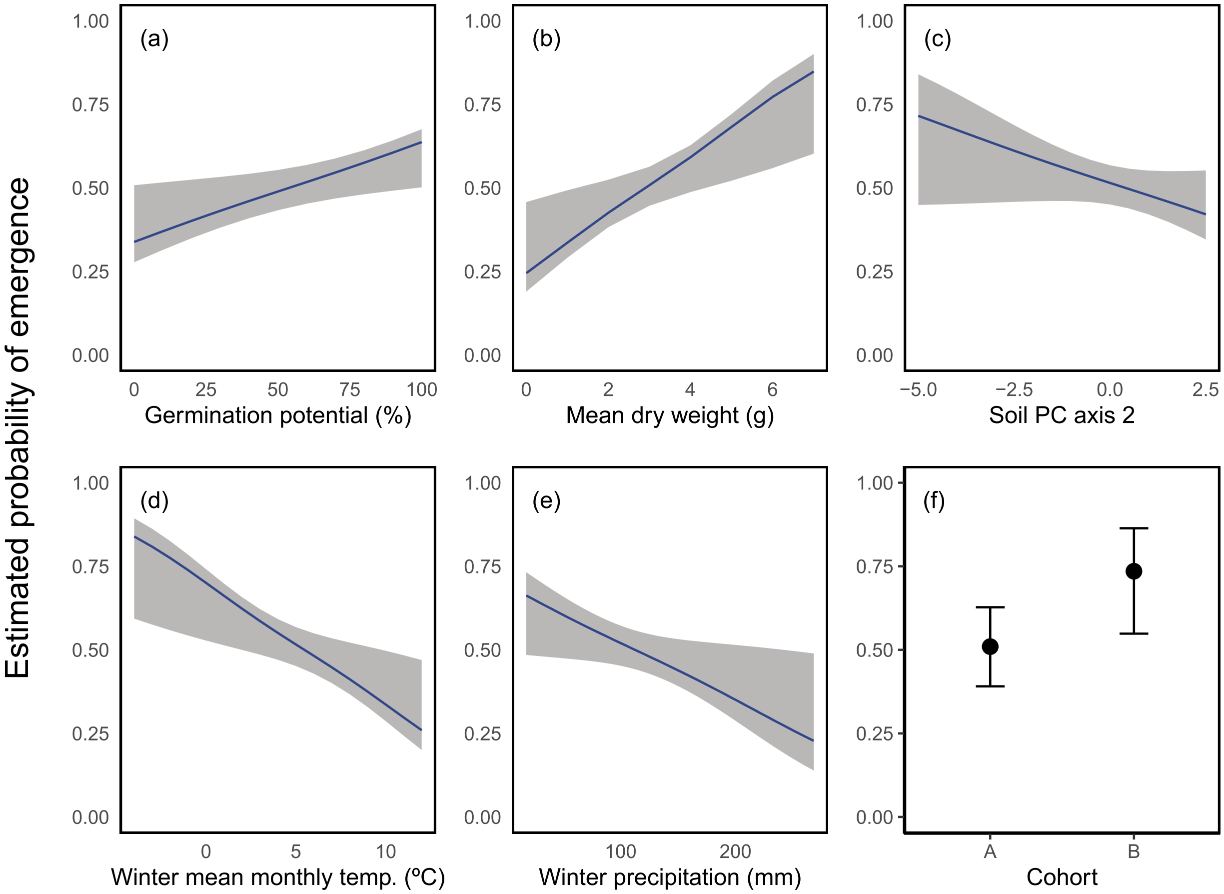

Fig. 4. Predicted effect of the significant explanatory variables on the probability of emergence. Predictors (a) and (b) were measured in the lab for each acorn batch; (c) was based on soil analyses at the site level (see Fig. 3); (d) and (e) are the weather of the study year from remotely-sensed data; and (f) refers to the year of seeding. For each variable, the predicted responses are averaged over the remaining significant predictors shown in Table 1. The gray shaded areas in (a–e) are 95 % confidence bands, and the error bars in (f) indicate 95 % confidence intervals.

changes.

In addition to acorn size, germination potential was positively associated with both seedling emergence and growth, although the association was strongest with seedling emergence. While differences in germination across species (Ceccon et al., 2016) and within species (Gómez, 2004) are also related to seed size, in our experiment, the two predictors – seed size and germination – affected emergence independently of each other. The relationship between seed germination and seedling emergence was foreseen, as the former is embedded in the latter. However, it should be noted that germination potential was measured under controlled conditions considered to be optimal (Jain and Gupta, 2005). Germination in the field experiment may also have been influenced by environmental factors such as soil moisture (Urbieta et al., 2008) or the use of seed protectors (Leverkus et al., 2015). The actual germination in the field may therefore differ from that measured in the germination chambers, but it still showed a strong effect. Finally, the positive, albeit weaker, relationship between germination potential and early growth is likely to have been mediated by genetic effects associated with acorn quality (Clark and Schlarbaum, 2018).

Our second hypothesis, namely that differences in SLA at the species level would explain heterogeneity in seedling emergence and early growth, was not supported by the data. SLA is known to be strongly related to the trade-off between acquisitive and conservative ecological strategies (Poorter et al., 2009), which are in turn related to plant growth rates. Our hypothesis was based on the conception that the more acquisitive species, with high SLA, are positively related to early seedling growth (Modrzyński et al., 2015). The lack of such an effect could result from several mutually non-exclusive mechanisms. First, the strong association of growth with the resources contained in the acorn during the first months after germination (Quero et al., 2007) may have led to a response associated with acorn mass rather than with species-level ecological strategy (as derived from SLA). Second, under full light conditions, such as those in our experiment, seedlings tend to invest more carbohydrates in root growth than in aboveground biomass and thus produce smaller leaves (Reich et al., 1998), which may have masked differences in stem volume growth across the SLA spectrum. Third, as SLA exhibits strong plastic responses to light (Reich et al., 1998), SLA data collected exclusively under full-light conditions may be necessary to match the experimental conditions and thus better relate to the measured responses. Fourth, deciduous species tend to be more plastic to environmental drivers than evergreen ones (Stotz et al., 2022), and, considering that the species-level SLA values may have partly been measured under some degree of shade, the stronger plastic response of deciduous species may have homogenized the response across species with variable functional strategies in the experiment. And fifth, intraspecific variation in SLA across source populations and individuals may have reduced the capacity to explain responses at the species level.

Species effects on seedling emergence were also low when considering the random effects, as just 1 % of their associated variance was explained by species identity. This contrasted with the seed batch, which explained more than half of the random-effects variance. This highlights that seed quality was the most important factor in explaining emergence across our experiment, and its underlying causes deserve further attention. Conversely, for seedling growth, species and seed batch were similarly important in explaining additional variance; however, the main source of variance in growth was related to spatial heterogeneity,

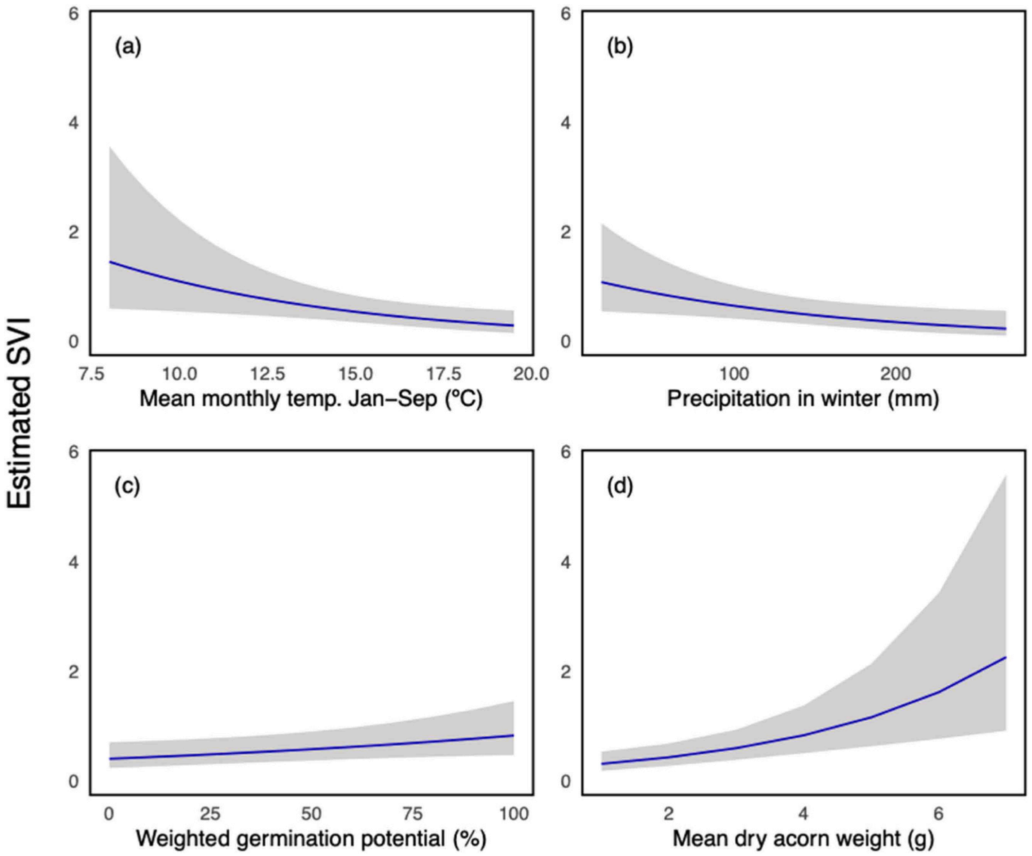

Fig. 5. Predicted effect of the significant explanatory variables on seedling stem volume index. Panels (a) and (b) show the effect of weather during the study year obtained from remotely-sensed data, and (c) and (d) the effect of two acorn quality variables measured in the lab for each acorn batch. For each variable, the predicted responses are averaged over the remaining significant predictors in Table 1. The gray shaded areas are 95 % confidence bands.

as suggested by the random effect of site.

4.2. Weather and soil drive seedling emergence and growth across geographic gradients

Weather conditions during the study year modulated seedling emergence and growth, in agreement with our third hypothesis. In partial disagreement with hypothesis 5, the response of seedling emergence and growth to weather was consistent across the four main oak species. This was surprising given the Mediterranean distribution of *Q. ilex* and *Q. cerris*, compared to the temperate distribution of *Q. robur* and *Q. petraea* (San-Miguel-Ayanz et al., 2016). However, we highlight that the first and more abundant cohort of our experiment was initiated in late 2021, so that seedling emergence occurred during an extreme drought year across the European Mediterranean region (Garrido-Perez et al., 2024). This may explain why sites experiencing higher temperatures were associated with lower emergence and growth, in addition to the cohort effect. Although the effect of precipitation was tested independently, warmer sites were also correlated with a drier summer (Fig. S1), which is characteristic of the Mediterranean climate (Blondel et al., 2010). The effect of temperature in our study is also consistent with the results by Meeussen et al. (2022), who found that the survival probability of four major oak species (*Q. cerris*, *Q. ilex*, *Q. petraea*, and *Q. robur*) increased with latitude from northern Italy to southern Sweden in stands that were at least partly open (although in their study the trend in growth was the opposite for *Q. ilex*). Our results suggest that emergence and growth were generally lower in the Mediterranean biome than in other biomes in Europe, supporting the conclusion that colder weather tends to be more favorable for emergence and seedling recruitment and that drought constitutes a regeneration risk.

Considering that the experimental sites were situated near adult oaks of the same species, our results also suggest that sites with higher temperatures generally reduced their regeneration potential, regardless of the acorn quality and species identity. Warming experiments have revealed local negative effects of temperature increase on the performance of oaks, for instance *Q. ilex* and *Q. faginea* in Spain (Lázaro-González et al., 2023b) and *Q. viminea* and *Q. eduardii* in Mexico (Badano and Sánchez-Montes de Oca, 2022), highlighting similarities between the large-scale spatial temperature gradient in our experiment and the effects of local temperature increase. The effects of temperature gradients in our experiment, however, may have been partly masked by the likely existence of local adaptations across source populations (Kremer and Hipp, 2020), as local adaptations play an important role in producing genetic differentiation in functional traits and fitness (Ramírez-Valiente et al., 2022). In addition, recent evidence suggests that epigenetic mechanisms can also mediate population responses to environmental variation, either reinforcing or buffering genetic differentiation (Bossdorf et al., 2008). Such environmentally induced changes in gene expression may further contribute to variation in functional traits and fitness, potentially obscuring the direct effects of temperature gradients.

It was surprising to find a negative association between seedling emergence and winter precipitation. For seedling growth, precipitation in winter, but not in spring or summer, explained differences across sites as well. Although this finding appears to contradict the above discussion of drought effects, a potential explanation could lie in the negative effects of waterlogging on seedling emergence, as has been observed for species such as *Q. suber* and *Q. pyrenaica* (Acácio et al., 2024; Urbieta et al., 2008). Waterlogging can reduce the probability of germination (Pérez-Ramos and Marañón, 2009) and induce seedling mortality

Table 2
Mixed-effects models for the probability of emergence and SVI after the first growing season for *Q. cerris*, *Q. ilex*, *Q. petraea,* and *Q. robur*.

		Emergence probability[1]		Seedling volume index[2]	
Predictor[3]	**df**	χ^2	**P**	χ^2	**P**
Cohort	1	3.52	0.06	0.59	0.44
Species	3	-	-	-	-
Soil PC1	1	-	-	0.07	0.79
Soil PC2	1	8.73	**< 0.01**	-	-
Germin. potential[6]	1	7.38	**< 0.01**	4.45	**< 0.05**
Acorn dry weight[6]	1	10.88	**< 0.001**	5.96	**< 0.05**
Mean monthly temperature[5,6]	1	20.99	**< 0.001**	7.75	**< 0.01**
Winter precipitation[6]	1	7.57	**< 0.01**	8.44	**< 0.01**
Spring precipitation[6]	1	-	-	2.77	0.10
Summer precipitation[6]	1	-	-	0.33	0.57
PC1 × species	3	8.26	**< 0.05**	3.63	0.30
PC2 × species	3	3.41	0.33	12.09	**< 0.01**
Temp[5,6] × species	3	3.30	0.35	6.08	0.11
Winter precip[6] × species	3	5.46	0.14	6.43	0.09
Spring precip[6] × species	3	-	-	3.54	0.32
Summer precip[6] × species	3	-	-	6.62	0.08
N emerged seedlings[7]	1	-	-	42.58	**< 0.001**
$\mathbf{R^2}$[*]		$\mathbf{R^2}$		$\mathbf{R^2}$	
Marginal (fixed effects)		0.25		0.23	
Conditional (fixed and random effects)		0.53		0.62	
Random effects[4]		**%**		**%**	
Site		62.8		62.5	
Plot within site		19.4		5.1	
Seed batch		17.8		32.4	

[1] Based on 2484 observations distributed across 168 plots at 42 sites with 58 seed batches from 4 species.

[2] Based on 1649 observations distributed across 158 plots at 40 sites with 55 seed batches from 4 species; SVI was log-transformed.

[3] Terms without a result were either not relevant for a given response (interactions) or not tested because they were included in interactions (main effects).

[4] Percentage of explained variance stemming from each random effect.

[5] Mean monthly temperature of Jan-Mar for emergence and of Jan-Sep for SVI.

[6] Standardized variables.

[7] Dummy variable indicating whether 1 or 2 seedlings had emerged at the seeding point because in the latter case only the taller one was measured; for details, see Section 2.5.

[*] Proportion of total variance explained in the simplified model, which included all the random effects and the significant fixed effects; calculation based on Nakagawa et al. (2017).

(Urbieta et al., 2008). Besides, it can delay seedling emergence (Kühne and Bartsch, 2007; Pérez-Ramos and Marañón, 2009) and reduce early seedling growth (Murphy et al., 2024, but see Kühne and Bartsch, 2007). As our study was conducted in open areas, the absence of trees may have exacerbated the effect of rainfall on soil water content, thereby increasing the likelihood and duration of anoxic soil conditions through waterlogging (Runyan et al., 2012); note, however, that we did not measure such process. On the other hand, the gradient from sites with well-drained sandy soils to other soil textures with a greater water holding capacity, identified in soil axis PC1, did not explain heterogeneity in seedling emergence or growth. The one exception was for *Q. cerris*, whose emergence was favored in well-drained soils. Other reported differences between species in the tolerance to soil oxygen deprivation, such as between *Q. robur* and *Q. petraea* (Murphy et al., 2024), were not apparent in our data, suggesting that waterlogging may only have occurred with some species and may only partly explain the negative association between precipitation and the measured responses.

Considering gradients in soil conditions, the first soil PCA axis provided no support for our fourth hypothesis. As PC1 was mainly related to soil texture, it likely reflects spatial variation inherent to geological and topographic factors, whereas PC2, correlated to soil nutrient concentrations and pH, is more likely to be a reflection of differences in vegetation, disturbance, and successional dynamics. The second PCA axis did confirm our fourth hypothesis, as seedling emergence was positively associated with soils with higher organic matter, total N, total C, and P concentration, and negatively associated with soil pH, clay content, and $CaCO_3$ concentration. However, the response in terms of growth to this soil axis was species-specific (supporting hypothesis 5), as only the growth of *Q. cerris* and *Q. ilex* correlated with this axis. We expected a stronger association between seedling emergence and soil water-holding capacity (note that clay content ranged between 2.9 % and 73.6 % across sites), as well as a stronger association between seedling growth and soil nutrient concentration and pH, but *Q. cerris* was the only species to exhibit such relationships. A deciduous species of eastern Mediterranean distribution, *Q. cerris* is considered moderately drought resistant and indifferent to soil type (Kostić et al., 2022), and it has a high capacity to adjust root growth under seasonal drought (Montagnoli et al., 2012). The evergreen *Q. ilex*, a paradigmatic species of the Mediterranean region (Blondel et al., 2010), is able to thrive under a variety of climates and is considered independent of soil substrate (Martín-Sánchez et al., 2022), although in our study it grew better on acidic soils with higher organic matter content. The lack of response of the temperate deciduous *Q. robur* and *Q. petraea,* which are mostly sympatric although with the latter preferring slightly drier soils than the

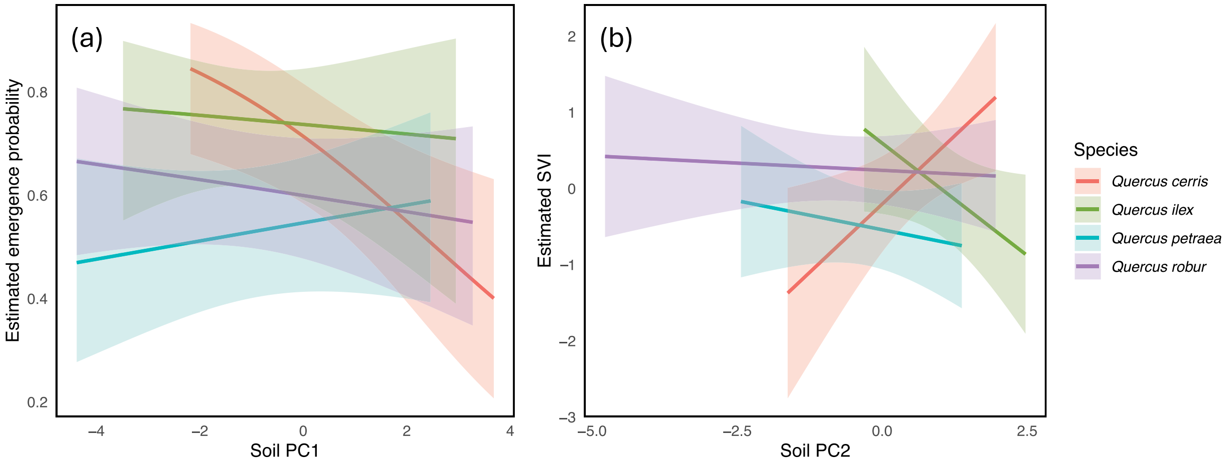

Fig. 6. Species-specific effects of soil conditions on (a) seedling emergence probability and (b) SVI for *Quercus cerris*, *Q. ilex*, *Q. petraea* and, *Q. robur*. The soil axis PC1 was associated with soil texture and water availability, and axis PC2 was positively related to soil pH and negatively to organic matter (see Fig. 1 and Table S2). The predicted responses are averaged over the remaining significant predictors in Table 2. The shaded areas are 95 % confidence bands.

first (Eaton et al., 2016), may suggest that weather played a stronger role across the range of soil conditions tested in the experiment, or that nonlinear responses to particular soil characteristics – for instance through thresholds in pH or clay content – governed species' responses to soils. Due to the scarcity of replicate sites of the remaining species, it was not possible to test whether they responded idiosyncratically to broad gradients in soil and weather.

4.3. Implications for management

Our findings indicate that, at a continental scale, seed quality metrics were key in defining seedling emergence and, to a lesser extent, seedling growth in 12 oak species native to or naturalized in Europe. For programs aimed at establishing, restoring, rejuvenating, or diversifying stands with oaks, selecting batches of large seeds is likely to increase seedling establishment through increased emergence probability, as well as competitiveness resulting from enhanced early growth. In addition to seed size, germination potential proved to be a seed-batch quality indicator associated not only with seedling emergence but also with growth, so both seed traits together may indicate the general quality of acorn batches. As selecting high-quality reproductive material is key for effective assisted regeneration (Löf et al., 2019), maintaining acorn batches separated and testing them for germination –for instance through a simplified procedure during short-term storage–, besides weighing them, constitutes a way of determining the quality of acorn batches for seeding across broad gradients. Additional drivers of oak regeneration, not tested here, include abiotic factors such as light (Quero et al., 2007) and microclimate (Meeussen et al., 2022), as well as biotic interactions through granivory (Gómez, 2004), herbivory (Crawley and Long, 1995), soil-borne pathogens (Domínguez-Begines et al., 2020), and competition (Navarro et al., 2023). Our recommendations are valid for open areas and hinge on controlling biotic interactions, and the economic implications of such actions must also be considered (see references in Lázaro-González et al., 2023a).

While species have different ecological requirements in terms of light, soil, climate, and other variables, we identified some common environmental drivers of seedling emergence and growth across oak species that may help select suitable sites for natural regeneration or seeding. Provided that species are within their potential distribution ranges, we found that sites with colder weather and drier conditions in winter may be most conducive to seedling emergence and early growth. Understanding these drivers may help identify sites that are adequate for natural regeneration and seeding. Under conditions where emergence and early growth are expected to be lower, it may be more cost-effective to devote additional resources to actions such as tree planting (Lázaro-González et al., 2023a), drone-based seeding (Castro et al., 2024), or even aerial planting (Lloyd et al., 2025). Finally, the results from the 2021–2022 drought year highlight that regeneration efforts should be spread across years to secure adequate seedling establishment at any given site.

5. Conclusions

While the early regeneration phases of oaks may be defined by species-specific requirements, our study found some common drivers of seedling emergence and first-year growth across 12 oak species – 11 native and one naturalized – across broad geographic gradients that encompass the distribution of adult oak stands. Acorn-batch quality, measured as mean acorn dry weight and germination potential, are positive indicators of emergence and early growth rates across species. Second, weather conditions define emergence and early growth rates, with higher mean monthly winter temperatures and/or precipitation associated with reduced emergence and growth. Third, emergence and early growth rates vary little across species, and not in a way that is consistent with species' ecological strategies as derived from SLA; therefore, species-specific information is required for accurate predictions. Fourth, early establishment responses to soil properties are mostly species-specific. Fifth, seeding in drought years produces poor regeneration, so expanding the period of regeneration is necessary to secure success. And sixth, high unexplained variance across sites implies that heterogeneity in outcomes should be expected in both natural regeneration and direct seeding, and that regeneration strategies should combine selective targeting of sites for active intervention with spatial spread to buffer against local-scale regeneration failure.

CRediT authorship contribution statement

Alexandro B. Leverkus: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **María Medina:** Writing – review & editing, Visualization, Project administration, Investigation, Data curation. **Alba Lázaro-González:** Writing – review & editing, Investigation. **Laura Levy:** Writing – review & editing, Project administration, Methodology, Investigation. **Olivia Lorente-Casalini:** Writing – review & editing, Data curation. **Marino P. Reyes Martín:** Writing – review & editing, Investigation. **Enrique Andivia:** Writing – review & editing, Methodology, Investigation. **Alessandro Bizzarri:** Writing – review & editing, Investigation. **Henrik Böhlenius:** Writing – review & editing, Investigation. **Vito E. Cambria:** Writing – review & editing, Investigation. **Claudia Cocozza:** Writing – review & editing, Investigation. **Branislav Cvjetković:** Writing – review & editing, Investigation. **Giovanbattista de Dato:** Writing – review & editing, Investigation. **Lenka Ehrenbergerová:** Writing – review & editing, Investigation. **Peter Ferus:** Writing – review & editing, Investigation. **Lorena Gómez-Aparicio:** Writing – review & editing, Investigation. **Arndt Hampe:** Writing – review & editing, Investigation. **Kjersti Holt Hanssen:** Writing – review & editing, Investigation. **Marcin Jakubowski:** Writing – review & editing, Investigation, Writing – review & editing, Investigation. **Ivona Kerkez Janković:** Writing – review & editing, Investigation. **Marcin Klisz:** Writing – review & editing, Investigation, Writing – review & editing, Investigation. **Wojciech Kowalkowski:** Writing – review & editing, Investigation. **Klaus Kremer:** Writing – review & editing, Investigation. **Jelena Lazarevic:** Writing – review & editing, Investigation. **Dagnija Lazdiņa:** Writing – review & editing, Methodology, Investigation. **Emanuele Lingua:** Writing – review & editing, Investigation. **Magnus Löf:** Writing – review & editing, Methodology, Investigation. **Manuel E. Lucas-Borja:** Writing – review & editing, Investigation. **Adrian Łukowski:** Writing – review & editing, Investigation. **Paula Maia:** Writing – review & editing, Investigation. **Paola Mairota:** Writing – review & editing, Investigation, Writing – review & editing, Investigation. **Alberto Maltoni:** Writing – review & editing, Investigation. **Barbara Mariotti:** Writing – review & editing, Investigation. **Raffaella Marzano:** Writing – review & editing, Investigation. **Lucia Mondanelli:** Writing – review & editing, Investigation. **Antonio Montagnoli:** Writing – review & editing, Investigation. **Maria Cristina Monteverdi:** Writing – review & editing, Investigation. **Francisco B. Navarro Reyes:** Writing – review & editing, Investigation. **Juan A. Oliet:** Writing – review & editing, Investigation. **Maria S. Patrício:** Writing – review & editing, Investigation. **Zoran Poduška:** Writing – review & editing, Investigation. **Vladan Popovic:** Writing – review & editing, Investigation. **Radosław Puchałka:** Writing – review & editing, Investigation. **Piotr Robakowski:** Writing – review & editing, Investigation, Writing – review & editing, Investigation. **Piotr Sewerniak:** Writing – review & editing, Investigation, Writing – review & editing, Investigation. **Carmen Ureña-Lara:** Writing – review & editing, Investigation. **Pedro Villar-Salvador:** Writing – review & editing, Methodology, Investigation. **Johanna Witzell:** Writing – review & editing, Investigation. **Nicolò Anselmetto:** Writing – review & editing, Investigation. **Jürgen Bauhus:** Writing – review & editing, Investigation. **Raquel Benavides:** Writing – review & editing, Investigation. **Paola Bolzon:** Writing – review & editing, Investigation, Writing – review & editing, Investigation. **María D. Carbonero Muñoz:** Writing –

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Declaration of Generative AI and AI-assisted technologies in the writing process

AI was used to speed up the statistical coding, yet the correctness of the procedures remains the authors' responsibility. AI was not used in the writing process.

Declaration of Competing Interest

ABL and JC declare being the inventors of the seed shelter, which was used in this study to test the drivers of seedling emergence in the absence of seed predation by small animals. However, this in no way defined the research that was done or the conclusions made.

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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.2025.123223.

Data availability

All the data underlying this work are available, as follows. (a) The data on seedling emergence can be found at https://hdl.handle.net/10481/107106. (b) The data on soil characteristics are available at https://hdl.handle.net/10481/107107. (c) The data on acorn batch germination potential and seed mass are available at doi:10.30827/Digibug.87318 and described in the associated data paper (Medina et al., 2024). (d) The weather data were obtained from the NASA Earth Science/ Applied Science Program, derived from MERRA-2, and available at https://power.larc.nasa.gov/. (e) The data on SLA were obtained from Díaz et al. (2022) and Tavşanoğlu and Pausas (2018) (see Table S1).

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