





RESEARCH ARTICLE

Initial oak regeneration responses to experimental warming along microclimatic and macroclimatic gradients

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ABSTRACT

- *Quercus* spp. are one of the most important tree genera in temperate deciduous forests in terms of biodiversity, economic and cultural perspectives. However, natural regeneration of oaks, depending on specific environmental conditions, is still not sufficiently understood. Oak regeneration dynamics are impacted by climate change, but these climate impacts will depend on local forest management and light and temperature conditions.
- Here, we studied germination, survival and seedling performance (*i.e.* aboveground biomass, height, root collar diameter and specific leaf area) of four oak species (*Q. cerris*, *Q. ilex*, *Q. robur* and *Q. petraea*). Acorns were sown across a wide latitudinal gradient, from Italy to Sweden, and across several microclimatic gradients located within and beyond the species' natural ranges. Microclimatic gradients were applied in terms of forest structure, distance to the forest edge and experimental warming.
- We found strong interactions between species and latitude, as well as between microclimate and latitude or species. The species thus reacted differently to local and regional changes in light and temperature; in southern regions the temperate *Q. robur* and *Q. petraea* performed best in plots with a complex structure, whereas the Mediterranean *Q. ilex* and *Q. cerris* performed better in simply structured forests with a reduced microclimatic buffering capacity. The experimental warming treatment only enhanced height and aboveground biomass of Mediterranean species.
- Our results show that local microclimatic gradients play a key role in the initial stages of oak regeneration; however, one needs to consider the species-specific responses to forest structure and the macroclimatic context.

INTRODUCTION

Quercus spp. (oak) is one of the largest and evolutionary most important tree genera worldwide, with over 450 different species across the Northern Hemisphere (Jones, 1974; Nixon, 2006; Gil-Pelegrín *et al.* 2017; Kremer & Hipp, 2020). Oaks are one of the most important tree genera both in forests and agricultural landscapes across Europe (Eaton *et al.* 2016; Mitchell *et al.* 2019). Oaks are not only one of the most abundant tree species in many temperate deciduous forests, but also contribute to numerous ecosystem services, such as wood production, are key species for biodiversity conservation and are of high cultural value (Eaton *et al.* 2016; Mitchell *et al.* 2019; Mölder *et al.* 2019).

Both the economic (Hanewinkel *et al.* 2013) as well as the ecological and cultural values associated with oak forests are under pressure due to climate change and other forest disturbances, such as pests and pathogens (Thomas *et al.* 2002; Mitchell *et al.* 2019). For instance, defoliation of *Quercus robur*

and *Q. petraea* has been shown to significantly increase over time, predominantly as a result of drought impacts (Sousa-Silva *et al.* 2018), sometimes followed by pathogen outbreaks, such as the processionary moth, or *vice versa* (Tomlinson *et al.* 2015; Godefroid *et al.* 2019). The combined impact of both abiotic (*i.e.* extreme weather conditions) and biotic (*e.g.* insect defoliators) stressors have subsequently triggered increasing incidences of oak decline across Europe (Thomas *et al.* 2002).

Moreover, the long-term persistence of these keystone species remains uncertain as natural regeneration is impacted. Already more than 100 years ago, Watt (1919) wrote on the causes of failure of natural regeneration of oak and, since then, alarming signals have been noticed across Europe (*e.g.* Palmer *et al.* 2004; Petritan *et al.* 2013). Besides issues with pathogens, predators, browsers and insects, successful oak regeneration depends on a specific set of abiotic conditions (Annighöfer *et al.* 2015; Kamler *et al.* 2016). Neither open nor shaded habitats, such as closed forests, are optimal for oak regeneration (Bobiec *et al.* 2018). Due to management changes many of the

traditional semi-open wooded landscapes have disappeared (Vera, 2000). Oak seedlings are generally more abundant in large forest gaps, in coppiced and coppice-with-standards forests, or in forest transition zones near agricultural lands (Bobiec *et al.* 2011, 2018; Demeter *et al.* 2021). Hence, for successful seedling establishment specific microclimate conditions are required (Von Lüpke, 1998; Mölder *et al.* 2019), but we still lack information on how light, temperature and humidity affect the regeneration success of different oak species.

The macroclimate, defined as free-air conditions, largely affects tree growth, and determines species distributions based on temperature and precipitation patterns (Bonan, 2008; Elith & Leathwick, 2009). Seedling climate niches, however, are more limited than those of adult trees (Grubb, 1977; Bell *et al.* 2014; Leuschner & Meier, 2018; Caron *et al.* 2021). Therefore, it is still unclear how regeneration of important tree species, such as oaks, will respond to climate change and extreme weather events. Moreover, specific abiotic conditions are likely determined by both the regional macroclimate as well as the microclimate (*i.e.* local climate conditions shaped by the surrounding vegetation and topography; Geiger *et al.* 2009). Microclimatic gradients can, for instance, occur near forest edges, where temperature decreases and humidity increases towards the forest core (Schmidt *et al.* 2019; Camille *et al.* 2021). Likewise, forest management interventions that lead to reductions in canopy cover, such as thinning, can create an increase in light and temperature at the forest floor (Kovács *et al.* 2017; Zellweger *et al.* 2019; Camille *et al.* 2021). Because of the temperature buffering effect of the canopy, microclimate conditions near the forest floor are stabilized (De Frenne *et al.* 2013), which might facilitate regeneration of oaks and protect seedlings against extreme temperatures and drought. To better understand natural oak regeneration, more research is necessary to understand how local and large-scale climate gradients interact and determine the regeneration success of different oak species in a warming world. Also, warming experiments in the field can be very useful to test oak recruitment under future temperature scenarios in alternative macroclimatic and microclimatic contexts. However, to date, no one has experimentally manipulated temperature *in situ* to better understand the factors affecting oak regeneration in different forest types and along edge-to-core gradients across Europe.

Knowledge on the preferred set of abiotic conditions might, however, not be enough to enhance natural regeneration of oaks in a warming world. Many tree species might not be able to adapt or migrate as fast as the shifting environmental conditions (Svenning & Skov, 2004; Lenoir *et al.* 2008), leading to time-lag dynamics and therefore putting pressure on future forest resilience, biodiversity and ecosystem services (Iverson *et al.* 2004; Bertrand *et al.* 2011). Besides providing management guidelines regarding the preservation of local microclimatic conditions, a potential solution could thus be to translocate species to climatically more suitable locations to help them track the shifting isotherms (*i.e.* assisted migration; Leech *et al.* 2011). Both *in-situ* warming experiments as well as translocation experiments beyond the actual range margins, which are both currently lacking for many tree species (Saxe *et al.* 2001), can gain us valuable insights on how species perform outside their natural range, and will help conserve important species and forest functions threatened by climate change (Gaston, 2003; Lee-Yaw *et al.* 2016).

Here we assessed the germination, survival and seedling performance (the latter quantified as aboveground biomass, height, root collar diameter and specific leaf area) of four economically and ecologically important oak species (*Q. cerris*, *Q. ilex*, *Q. petraea* and *Q. robur*), as different species will respond differently due to variations in life history. In total, 1024 acorns were sown, distributed across five sites along a *ca.* 2000-km broad latitudinal gradient from Italy to Sweden. Along the latitudinal gradient with varying macroclimate, seedlings were subject to varying microclimatic conditions determined by local factors, including forest management and distance to the forest edge. Lastly, we experimentally manipulated microclimates by means of a warming treatment to test how experimental warming affected the initial stages of natural regeneration of the different oak species. We developed hypotheses to find different germination, survival and performance signals of the four species along our macro- and microclimatic gradients. We expected that the southern species, *Q. ilex* and *Q. cerris*, would perform better in warmer environments (both micro- and macroclimates), whereas the northern species, *Q. robur* and *Q. petraea*, would benefit from locally buffered (cooler) microclimate conditions, especially in the more southern regions, such as can be found in the forest interior or in complex forests.

MATERIAL AND METHODS

Study species

We selected four native European oak species for the experiment: *Q. robur*, *Q. petraea*, *Q. ilex* subsp. *Ilex* and *Q. cerris* (family Fagaceae). The sessile oak (*Q. petraea*) and the pedunculate oak (*Q. robur*) are two very common and important deciduous tree species in the temperate part of the continent, and even (co-)dominate many European temperate deciduous, mixed forests (Eaton *et al.* 2016). Their ranges largely overlap (Fig. 1a) and extend from the southern part of Sweden and Norway towards south Italy, Turkey, the Balkans and the northern part of Spain and Portugal to the south (Eaton *et al.* 2016). However, *Q. robur* has a slightly larger distribution range and performs better in continental climates. *Quercus petraea*, on the other hand, is more drought-tolerant, is often found on rocky soils and on slopes or hills, and prefers more Atlantic climates (Eaton *et al.* 2016). Turkey oak (*Q. cerris*) and holm oak (*Q. ilex*) are native to southern Europe, with distribution mainly in the Mediterranean Basin. *Quercus ilex* can be found in the western and central parts of the Mediterranean Basin, whereas *Q. cerris* is mainly present in Italy and the Balkans (de Rigo & Caudullo, 2016; de Rigo *et al.* 2016) (Fig. 1a). Both species grow on a wide variety of soils and are relatively resistant to drought (Barbero *et al.* 1992; Praciak, 2013). *Quercus ilex* can also survive low winter temperatures, down to -20°C for short periods (Knopf, 2002). *Quercus ilex* is an evergreen and more shade-tolerant species (de Rigo & Caudullo, 2016), whereas *Q. robur*, *Q. petraea* and *Q. cerris* are deciduous and light-demanding species (de Rigo *et al.* 2016; Eaton *et al.* 2016). As seedlings, however, *Q. cerris* and *Q. petraea* are slightly more tolerant to shade in comparison to *Q. robur*, which has very low shade tolerance (Leuschner & Meier, 2018).

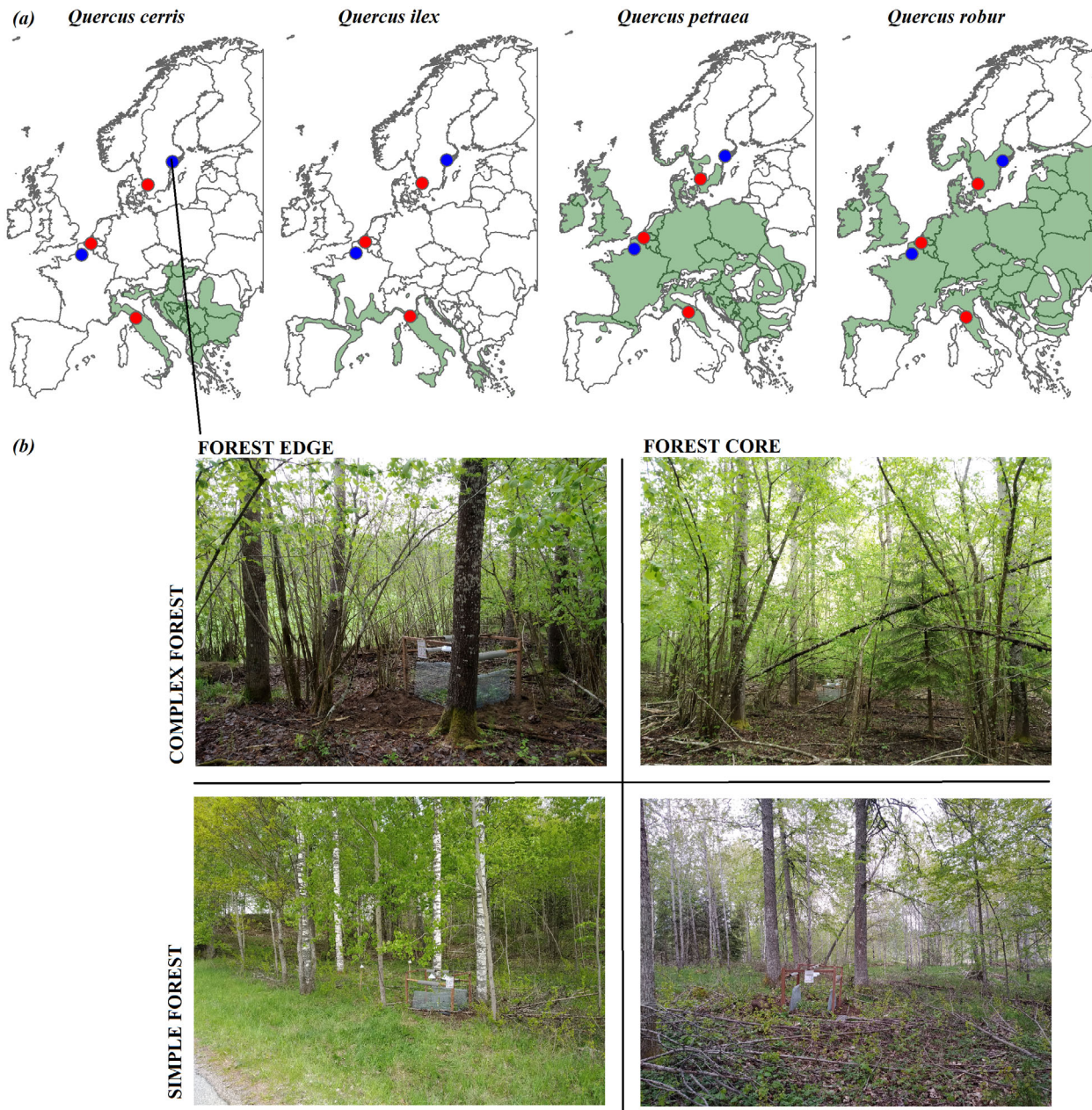


Fig. 1. (a) Distribution maps of the four oak species. The red and blue circles represent the different regions in the experiment. Red circles are regions with experimental warming and control plots. Blue circles are regions with control plots. Distribution maps are from: <http://www.euforgen.org/species/>. (b) Microclimatic gradients (in Stockholm): two forest edges and two forest core plots were selected, located in a 'simple' (or more open) forest (bottom) and in a more 'complex' (or dense) forest (top). In regions represented by a red dot, additional plots with experimental warming were established at the four locations.

Study design

We included both macroclimatic and microclimatic gradients, as well as experimental warming, replicated along each of the macroclimatic and microclimatic gradients in our study. To be able to study the effect of macroclimatic variation on initial oak regeneration, we planted acorns of the four studied species along a 1,800-km wide latitudinal gradient (covering a temperature difference of 8.2°C, Karger et al. 2017; Table S1) crossing the temperate forest biome in Europe. Along this south–north gradient, five experimental

sites were selected in deciduous forests: Florence in central Italy, Amiens in northern France, Ghent in Belgium, Halmstad in southern Sweden and Stockholm in central Sweden (Fig. 1a). The tree layer in most experimental sites was dominated by *Q. robur* or *Q. petraea*, but with diverse species co-occurring in the different sites (Table S1).

In all five sites, four experimental locations were established: we included variation in forest structure and distance to the forest edge to be able to study the effect of the local microclimate (i.e. sub-canopy gradients in light, humidity and temperature) on the initial regeneration stages of oak (Fig. 1b). Two

forest stands were selected with a different forest structure as differences in vegetation structure will affect the forest microclimate (Frey *et al.* 2016; Kovács *et al.* 2017; Camille *et al.* 2021). The first stand, hereafter referred to as ‘complex forest’, was always a vertically dense and multi-layered forest stand with a well-developed shrub layer (*i.e.* at least > 15%) and a closed upper canopy layer (*i.e.* canopy cover preferably > 90%). A second stand type represented a ‘simple forest’, which was composed only of a single tree layer, had a higher canopy openness (canopy cover < 70%) and no or few shrubs in the understorey (*i.e.* maximum shrub cover of 45%). Moreover, in each of these stands, two plots were established ($n = 20$ plots across the five sites), forming a second microclimatic gradient determined by distance to the edge (Camille *et al.* 2021). The centre of the first plot was located at a distance of roughly 2–5 m from the edge, whereas the second plot was at least 50–100 m towards the core of the forest patch. The studied edges were all bordered by a matrix of agricultural land and were approximately oriented towards the south, as edge orientation due to the impact of direct radiation is known to affect the microclimate and edge width (Matlack, 1993; Chen *et al.* 1995). Further details on the study design, forest structure and site selection are available in De Pauw *et al.* (2021) and in Table S1.

In three sites, *i.e.* southern Sweden, Belgium and central Italy, an experimental warming treatment was installed (for feasibility reasons, this was not possible at the other two sites). We therefore doubled the number of plots present at those three locations. This led to a total of 32 plots (five sites with four plots per site, among which three sites had an additional set of four plots with experimental warming: 20 plots for control *versus* 12 plots for warming treatment). The warming treatment was applied both day and night during the growing seasons of 2019 (from installation in May to the 30 September) and 2020 (from the first week of February to the first week of September), using two infrared heater arrays of 100 W per experimental plot (Elstein – Werk M Steinmetz, Northeim, Germany) located approximately 85 cm above the ground (see Nijs *et al.* 1996; Kimball, 2005; Kimball *et al.* 2008; for discussion on the advantages and drawbacks of infrared heaters in climate change experiments).

To quantify the amount of warming and the temperature differences along microclimatic and macroclimatic gradients, soil temperature measurements were taken hourly, from September 2019 until September 2020, with Lascar temperature loggers (EasyLog EL-USB-1, accuracy from -35°C to $+80^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$). The loggers were buried in each plot, immediately next to the oaks in the soil, in a protective plastic tube at a depth of 5 cm. A linear-mixed effect model with all design variables (*i.e.* site, forest structure, distance to edge and treatment) as fixed effects and with sensor ID as random effect, showed that the soil temperature in the warming treatment was significantly elevated by $0.89 \pm 0.16^{\circ}\text{C}$ (parameter estimate and SD, $P < 0.001$) compared to the control treatment (see also Fig. S1; which shows an illustrative example of temperatures in all experimental locations in Belgium during the first 2 weeks of June) and that the soil moisture content was decreased by 7%. Moreover, on average, the air temperature in these experimental locations was 0.62°C higher in simply structured forests in comparison to complex forests. Also, near the edge, the air temperature slightly increased, although not significantly, but the soil water content was significantly lower in edge plots

compared to core plots (on average, a decrease of 8%) (De Pauw *et al.* 2021).

Acorns were bought from the tree nursery Sylva-Van Hulle® (Belgium; www.sylva.be) and stratified in a cold environment (fridge $\pm 4^{\circ}\text{C}$) until the day of sowing. Immediately before sowing, the acorns were hydrated in a bucket of water for 2 h. Floating and damaged (*e.g.* visible weevil exit holes) acorns were discarded. Subsequently, the acorns were weighed, placed in a container (7 cm \times 7 cm and 15-cm deep) and covered with a thin layer of potting soil. To avoid an effect of soil conditions on oak germination and growth, all acorns were sown in containers filled with the same potting soil, consisting of 85% peat and 15% coconut fibre, pH-KCl 5.0–6.5. Per plot, 32 containers were installed, divided across two rows (Fig. S2). Each row thus contained four acorns of the four selected oak species, randomly distributed along the row. In total, 1024 acorns (32 plots \times 32 acorns per plot) were planted for the experiment. The containers were placed in closed cages (mesh: 6.4 mm \times 6.4 mm; see Fig. S2) to protect the acorns from rodents.

Acorns of *Q. robur* and *Q. ilex* were sown in the spring of 2019 (between the end of April for the southern regions and the beginning of June for the more northern regions). Acorns of *Q. cerris* and *Q. petraea* were sown 1 year later in the winter/spring of 2020 (in February for the more southern regions and in April for the more northern regions) because of germination failure for *Q. petraea* in 2019 and because no acorns of *Q. cerris* were commercially available in 2019 in many European countries. The oak species differed in provenance, similar to their original distribution area. *Quercus cerris* and *Q. ilex* came, respectively, from Hungary and Spain, whereas acorns of *Q. petraea* came from England and those of *Q. robur* were of Belgian origin. Per species, we kept the provenance uniform, as it was not our intention to study the effect of tree provenance on germination and seedling performance. While we are aware that provenance effects can exist in trees, including more provenances was simply not feasible given our study extent.

Data collection

Twice a year, once during the growing season and once at the end of summer, the following characteristics and traits were measured and determined to assess the germination, survival and performance status of the different species.

To quantify germination and survival, for each container ($n = 1024$), we determined if a seedling was present (no measurement periods in 2019 and two measurement periods in 2020 for *Q. cerris* and *Q. petraea* and two measurements in 2019 and two in 2020 for *Q. robur* and *Q. ilex*). If seedlings were present throughout the experiment, the acorn was considered as germinated (germination = 1), regardless of the period and of future survival. For those acorns that germinated during the experiment, we subsequently also checked seedling survival at the end of the experiment (August/September 2020) (survival = 1).

We also measured plant height (cm) of the germinated individuals using a foldable ruler. The height was defined as the shortest distance between the upper boundary of the main photosynthetic tissues (youngest fully expanded or expanding leaf) of the oak and ground level (Pérez-Harguindeguy *et al.* 2013), without stretching the plants axis. Besides height, we also measured the diameter at the root collar (DRC, mm), as close to the ground as possible, using a digital caliper. At the

end of the experiment, we collected the largest healthy-looking leaf of each individual, avoiding leaves with obvious symptoms of pathogen or herbivore attack. These leaves were dried for 48 h at 40°C and subsequently their dry weight was determined. All leaves were also scanned with a LI-3000C Portable Area Meter in combination with a Li-3050C Transparent Belt Conveyor Accessory (Li-Cor Environmental, Lincoln, NE, USA) to measure the one-sided area. The ratio of total leaf area to total leaf dry mass, the specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$), was calculated as a response variable. Finally, in August 2020, at the end of the experiment, we also cut the whole seedling directly above the soil and dried it for 48 h at 65°C to determine total aboveground biomass of each individual (mg).

For four of our metrics (*i.e.* germination, survival, biomass and SLA) we thus only have one value per acorn in our dataset, whereas for diameter at root collar and plant height, multiple repeated measurements of the different surveys were available.

Data analysis

The effect of macroclimatic and microclimatic gradients, including the warming treatment, on the initial regeneration stages of the four studied oak species was modelled in R (R core Team 2020). Due to the hierarchical structure of the data, we used (generalized) linear mixed-effect models and the *glmer* function from the package *lme4* (Bates *et al.* 2015). The response variables 'germination' and 'survival' were modelled with a binomial distribution, while DRC, SLA, plant height and biomass were modelled with a Gaussian distribution. To determine the optimal model structure, both for random as well as fixed effects, the protocol described by Zuur *et al.* (2009) was followed. First, the optimal random structure was determined (*i.e.* using the beyond optimal model containing all desired fixed effects and interaction effects). The selected random structure was a combination of: (1) a single variable that combined the site, forest structure and distance to the edge of the experimental plot (*i.e.* a factor with 20 levels such as for instance "Belgium_simple_edge"), and (2) individual ID (*i.e.* the specific container/acorn individual) for the repeated measurements (*i.e.* DRC and plant height), both as random intercepts. This random structure was used for all models as it reflected the optimal structure for all but one model. For germination, the optimal structure was one without random effects, but for the sake of simplicity and since AIC values differed only in six units, we decided to select the same random structure for all models.

For each response variable, two models were constructed. In a first model, including data from all experimental locations, we tested the impact of the fixed effects latitude (as a continuous predictor for site), forest stand structure (a factor variable with two levels: complex *versus* simple stands), distance to the edge (a factor variable with two levels: forest edge *versus* core) and species (a factor variable with four levels: *Q. ilex*, *Q. petraea*, *Q. robur* or *Q. cerris*) on the initial regeneration stages of oak. In a second model, we used a subset of the data containing only information of the sites with an experimental warming treatment (*i.e.* central Italy, Belgium and southern Sweden) and in this model, we also added experimental warming (a factor variable with two levels: control *versus* warming) to the model as an additional fixed effect. Two-way interaction terms were included between all the fixed effects. Moreover, the weight of the acorn was added as covariate to each model, as

acorn mass is known to affect germination and growth (*e.g.* Tilki, 2010; Kormanik *et al.* 2011). Continuous predictor variables like latitude and acorn weight were standardized to allow for a comparison of model coefficients. The response variable biomass was log-transformed prior to the analyses as it showed issues with homoscedasticity due to a strong right-skewed distribution. Subsequently, *via* a manual backward model, selection of non-significant interactions and main effects were removed from the model. Finally, restricted maximum likelihood was employed to assess the parameters, and the model fit was determined as the variance explained by the fixed effects (*i.e.* marginal R^2) and the combination of random and fixed effects (*i.e.* conditional R^2) (Nakagawa & Schielzeth, 2013).

RESULTS

Germination and survival

Among the 1024 acorns we sowed, 741 germinated (~ 72%) during the course of the experiment. Of those, 493 seedlings (~ 66%) were still alive at the end of the experiment (Table 1). Strong differences between species were found; almost 91% of the acorns of *Q. ilex* germinated, whereas for *Q. cerris* we found a germination percentage of only 52%. Approximately 99% of the acorns of *Q. ilex* and *Q. robur* germinated during the first year of the experiment. Higher survival rates were noted for *Q. ilex* and *Q. cerris* (both ~ 85%), whereas for *Q. robur* and *Q. petraea* survival rates were ~ 41% and ~ 72%, respectively.

Germination rates of heavier acorns were higher, whereas there was no effect of acorn weight on survival (Table 2). We found significant interaction effects between latitude and species for both germination and survival (Table 2). These interactions showed, first, that germination success increased for *Q. cerris* and *Q. petraea* towards the north, whereas it decreased towards the north for *Q. ilex* and *Q. robur*. Moreover, for survival, besides a latitude–species interaction, additional interactions between both stand structure and species as well as between stand structure and latitude were found (Fig. 2, Table 2). These indicated that complex forests, in comparison to simple forests, favoured the survival of seedlings in warmer regions. In simply structured stands, survival strongly increased towards colder regions for *Q. cerris*, *Q. petraea* and *Q. robur*, whereas there was only a weak increase for *Q. ilex*. In complex stands, however, the increase in survival for *Q. robur* towards northern regions was weaker, and we even found a decrease in survival of *Q. ilex* seedlings towards northern regions (Fig. 2, Table 2). We did not find an additional impact or interaction effect of the warming treatment on the survival rate of the seedlings, and neither on the germination success of the acorns. Acorn germination was, however, higher in the forest core (Fig. S3, Table 2).

Seedling performance

In general, we found higher biomass (log-transformed) for the Mediterranean species (*Q. ilex* and *Q. cerris*) in southern regions in comparison to northern regions, whereas for *Q. robur* and *Q. petraea* we found the opposite trend. Besides the latitude–species interaction, there was a positive significant interaction between stand structure and latitude on the biomass, and there was a type–species interaction; in general,

Table 1. Average seedling characteristics of the four oak species at the end of the experiment (August 2020) across macroclimatic (latitude) and microclimatic (stand structure, distance to the edge, warming) gradients.

Species	Acorns germinated (n = 256 per species sown in total)	Seedlings surviving at end of experiment	Aboveground biomass (mg) (mean ± SD)	Plant height (cm) (mean ± SD)	Diameter at root collar (mm) (mean ± SD)	Specific leaf area (mm ² mg ⁻¹) (mean ± SD)
<i>Q. cerris</i> ^a	134	115	466.22 ± 276.23	18.6 ± 6.9	2.40 ± 0.60	23.95 ± 5.73
<i>Q. ilex</i>	234	199	1056.02 ± 964.23	23.1 ± 9.4	2.66 ± 0.91	13.99 ± 3.86
<i>Q. petraea</i> ^a	170	123	227.23 ± 163.55	13.6 ± 5.5	1.93 ± 0.49	22.96 ± 6.15
<i>Q. robur</i>	203	83	358.73 ± 491.01	20.6 ± 8.4	2.21 ± 0.82	25.08 ± 4.75

^a*Quercus cerris* and *Q. petraea* were monitored for only one growing season, whereas *Q. robur* and *Q. ilex* were monitored during two growing seasons.

Table 2. Impact of macroclimate (latitude), microclimate (forest structure and distance to edge), species and their interaction effects, as well as the impact of acorn weight, on germination, survival and characteristics of oak seedlings. Complex forests, forest cores and *Q. ilex* were used as reference forest structure, reference distance to the edge and reference species for the model intercept parameter.

	Germination	Survival	Aboveground biomass (mg, log-transformed)	Plant height (cm)	Diameter at root collar (cm)	Specific leaf area (mm ² mg ⁻¹)
Latitude (°N)	↓		↓***	↓***	↓	↑
Forest structure (simple compared to complex)		↓	↑**		↑	↓**
Edge-to-core gradient (edge plot compared to interior)	↓*				↑	
<i>Q. cerris</i>	↓***	↓	↓***	↓***	↓***	↑***
<i>Q. petraea</i>	↓***	↓***	↓***	↓***	↓***	↑***
<i>Q. robur</i>	↓***	↓***	↓***	↓	↓***	↑***
Acorn weight (mg)	↑*		↑***	↑***	↑***	
Lat: Simple structure		↑*	↑*		↑	
Lat: <i>Q. cerris</i>	↑*	↑***	↑	↑***	↑*	↑
Lat: <i>Q. petraea</i>	↑**	↑***	↑***	↑***	↑***	↓*
Lat: <i>Q. robur</i>	↑	↑**	↑**	↑***	↑***	↓
Simple structure: <i>Q. cerris</i>		↑	↓		↑	
Simple structure: <i>Q. petraea</i>		↑	↓*		↓*	
Simple structure: <i>Q. robur</i>		↑*	↑		↓	
Edge plot: <i>Q. cerris</i>					↓*	
Edge plot: <i>Q. petraea</i>					↓	
Edge plot: <i>Q. robur</i>					↑	
Marginal R ²	0.23	0.50	0.48	0.19	0.26	0.55
Conditional R ²	0.30	0.64	0.56	0.42	0.53	0.66

The direction of the effect size is depicted by an arrow (relative to zero for continuous variable and relative to the intercept parameter, or reference, for factor variables like forest structure, distance to the edge and species) and significance of effect size is indicated with asterisks (**P* < 0.05, ***P* < 0.01, ****P* < 0.001). Results of models with significant experimental warming effects can be found in the appendix, Table S1.

biomass was higher in simple forests, except for *Q. petraea*, but in southern regions seedling biomass was higher in complex forest stands, whereas in northern regions seedling biomass was higher in simple forest stands (Table 2, Fig. 3).

For DRC and plant height, we again found strong and significant interaction terms between species and latitude: *Q. ilex* seedlings had a lower DRC and plant height in northern regions, whereas for the other oaks, DRC and plant height increased towards the north (Table 2). We also found interactions for DRC between species and microclimate, both in terms of stand structure and distance to the edge. The diameter was generally higher near the edge, except for *Q. cerris*, and generally higher in simple forest stands, except for *Q. petraea* (Fig. 4a, Table 2).

Seedlings of *Q. ilex* had the lowest SLA. Although, again, species reacted differently along the latitudinal gradient. For most species, we found an increase in SLA towards higher

latitudes, except for *Q. petraea* seedlings, which decreased their SLA towards the north. Moreover, for all species the SLA was lower in simply structured forests (Fig. 4b, Table 2).

Simulating climate warming, by increasing the air temperature, did not affect SLA or DRC in our experiment. If treatment was included in the models for plant height and biomass, we did however find a significant interaction between warming and species. This interaction indicated that the height and biomass of *Q. robur* were reduced under warming, whereas the seedlings of *Q. ilex* and *Q. cerris* grew taller and had more biomass in comparison to the control plots (Table S2).

DISCUSSION

We found that macroclimate (*i.e.* latitude) and species identity had a strong interactive effect on the germination success, survival rate and performance level of oak seedlings. However, also

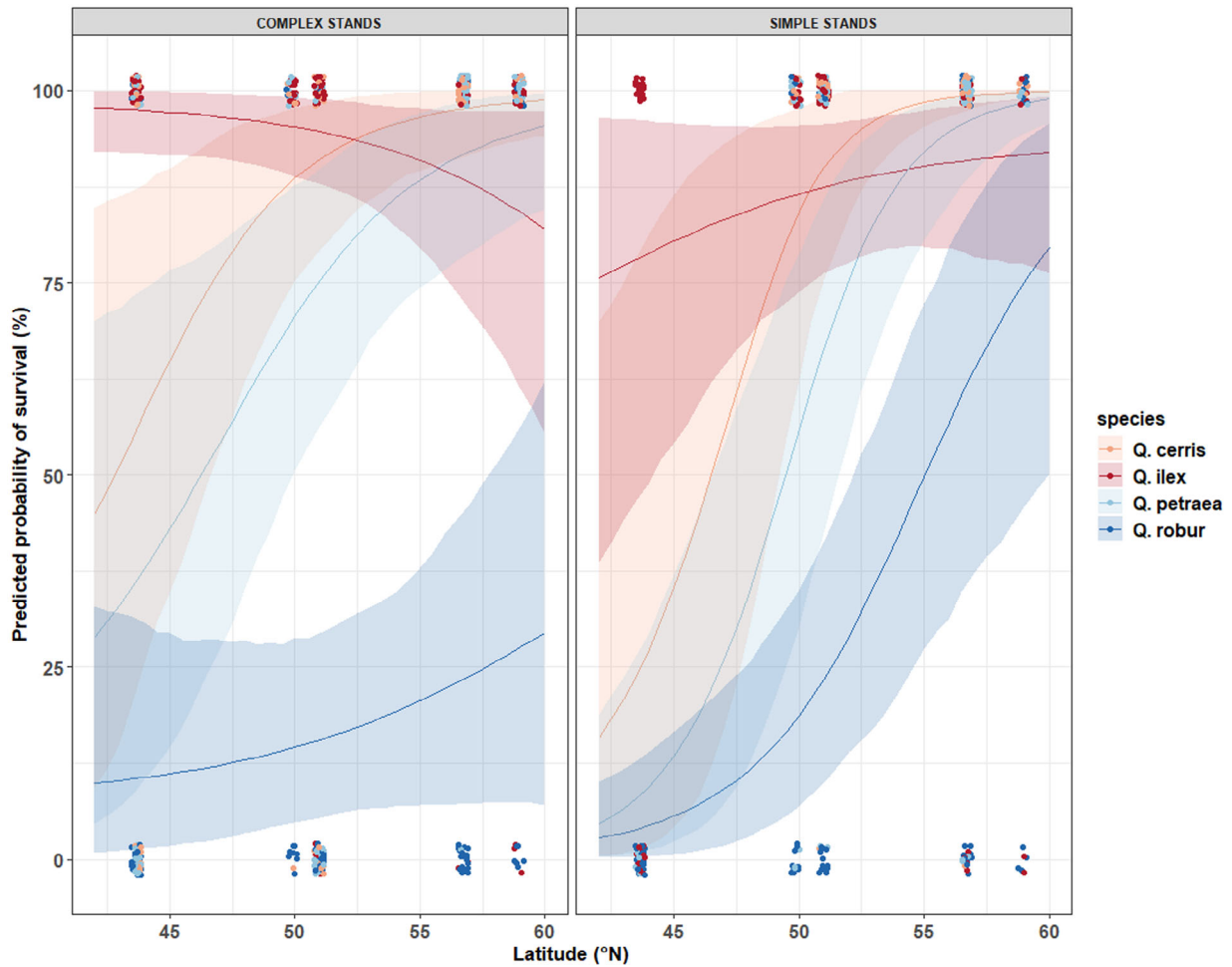


Fig. 2. Predicted probabilities of survival for the four studied oak species (species are shown in different colours) as a function of latitude ($^{\circ}$ N) for two forest types (left: complex forests; right: simply structured forest). The dots represent the raw data points (with 0 = no survival and 100 = survival) and the shaded areas show the 95% prediction intervals. A small amount of noise (*i.e.* via the ‘jitter’ function in R) was added to the raw data points along the x - and y -axis to improve clarity.

microclimatic conditions (*i.e.* temperature, light availability and soil moisture) had an important impact on the initial stages of oak regeneration, with the direction of the effect often depending on the studied species. In general, experimental warming did not significantly alter oak recruitment, except for a positive effect on plant height and biomass for *Q. ilex* and *Q. cerris* and a negative effect on plant height and biomass for *Q. robur*.

Germination and survival

Seedling germination was higher in the forest interior in comparison to the edge, and this was valid across the whole latitudinal gradient as well as for all species studied. Forest edges are characterized by a different structure (*i.e.* higher stem density; Camille *et al.* 2020), altered microclimatic conditions (*i.e.* warmer and drier; Chen *et al.* 1995; Davies-Colley *et al.* 2000; Camille *et al.* 2021), higher nutrient deposition (De Schrijver *et al.* 2007; Wuyts *et al.* 2008) and a different understorey plant, animal and soil microbiota community composition (*e.g.* De Smedt *et al.* 2019; Govaert *et al.* 2020), which can all affect the regeneration and establishment of tree species (Meiners *et al.*

2002). However, an improved germination rate in the forest core contrasts with previous studies finding a higher germination rate at forest edges or in more open landscapes (Wales, 1972; Meiners *et al.* 2002; Götmark, 2007; Bobiec *et al.* 2018). Reduced emergence in the forest interior could be related to stronger shading by canopy trees and, therefore, especially shade-intolerant species could have higher emergence near forest edges (Wales, 1972; Meiners *et al.* 2002). Oaks are shade-intolerant but, on the other hand, they have large seeds rich in nutrients which give them a ‘kick start’ for growth. This is also shown by the significant positive effect of acorn weight on germination rate and thus might also explain the high germination rate in the forest interior. Moreover, after already a few dry years, the spring and/or summer of 2019 and 2020 were also very dry in all regions (Barbosa *et al.* 2020) and since our forest edges were characterized by a lower soil moisture content (De Pauw *et al.* 2021), these drought effects might lead to higher germination in the forest interior.

Furthermore, the latitude–species interaction found for germination, whereby *Q. robur* germinated better in the south and *Q. cerris* in the north, is rather counterintuitive, as the former

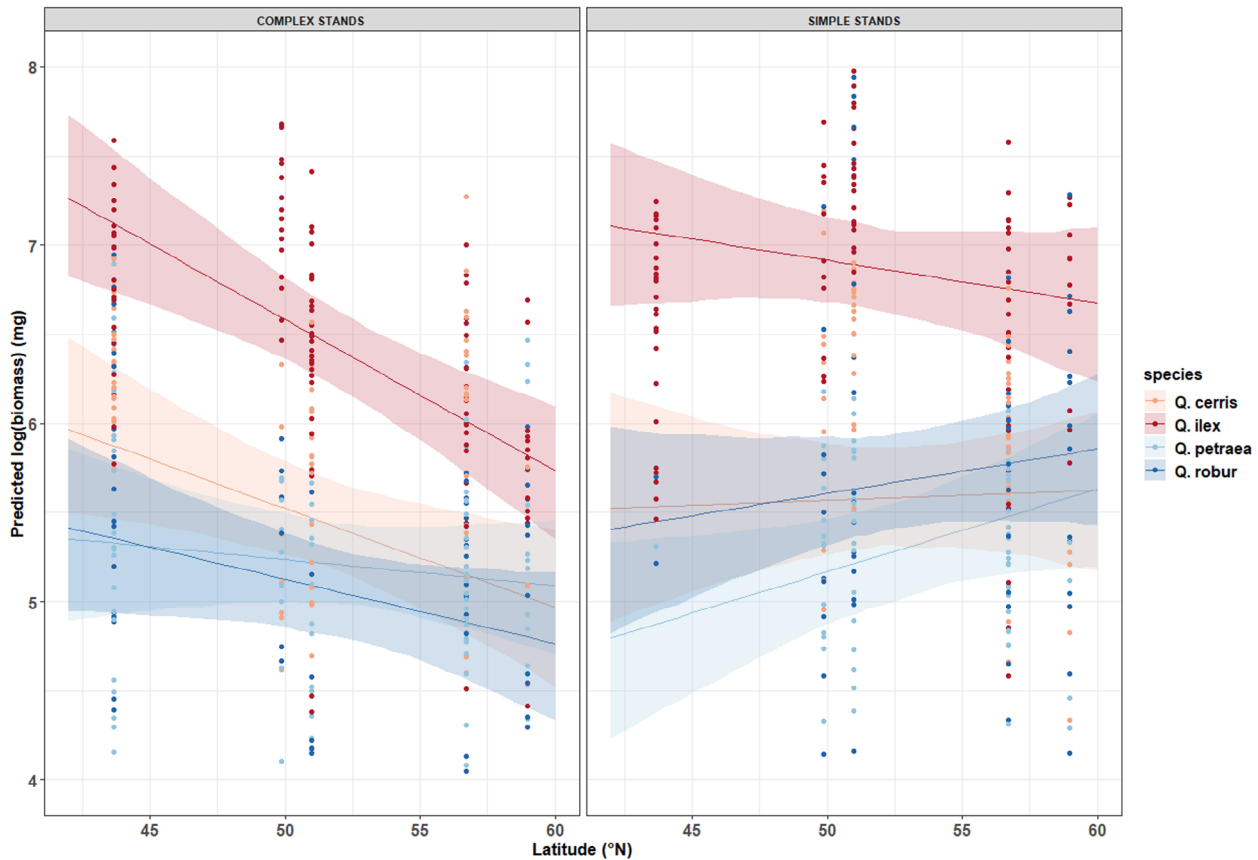


Fig. 3. Predicted biomass (log-transformed) of the four oaks (species shown in different colours) as a function of latitude (°N) for the two forest types (left: complex forests; right: simply structured forests). The dots represent raw data points and shaded areas are 95% prediction intervals.

has a more southern distribution range than the latter. We speculate that these patterns are related to the fact that these species were planted in 2020, whereas *Q. ilex* and *Q. robur* were planted in 2019 and show, as expected, higher germination in the south and north, respectively. These trends thus, although not conclusive, might reflect annual variation in weather conditions rather than species-specific germination trends. Moreover, germination and growth during the first year, as discussed above, might be strongly impacted by the nutrients present in the acorn.

For survival, we found an increased probability to persist towards colder macroclimates, except for *Q. ilex* in complex forests. A lower survival rate in warm regions might be related to drought stress and this especially for *Q. robur* and *Q. petraea*, as our most southern region was approximately located at the warm range margin of these species (Urli *et al.* 2014; Eaton *et al.* 2016). Moreover, the survival rate of *Q. ilex*, a species with a high tolerance to drought (Lobo *et al.* 2018), was not lower in southern regions, and even increased towards the south in complex forest stands. In general, the survival in southern regions was also higher in complex forests, whereas in the north we found higher survival in simply structured forests. This might reflect the importance of the buffering effect of dense forests in warm environments, creating less environmental stress due to more humid and cooler conditions in complex forests (De Frenne *et al.* 2019; Zellweger *et al.* 2019; Camille *et al.* 2021), and thus protecting young seedlings from desiccation (Aussenac, 2000; Badano *et al.* 2015). Whereas in cold

environments, simply structured forests provided a warmer and brighter environment, as was also the case in our experiment (see also De Pauw *et al.* 2021). Finally, the overall high mortality rates of *Q. robur* might be related to its susceptibility to oak powdery mildew (Marçais & Desprez-Loustau, 2014), which we also observed in our study, and the fact that this species was monitored for two consecutive years whereas *Q. petraea* and *Q. cerris* were only monitored for one growing season.

Performance

Towards colder macroclimates, both plant height and diameter at root collar (DRC) increased, except for *Q. ilex*, which performed better in warmer macroclimates. We suggest that this species–latitude interaction might be caused by the temperature and drought tolerance of the different oak seedlings along the gradient. Under dry conditions, temperate species are more likely to invest in their root biomass instead of aboveground biomass (expressed here as plant height and stem diameter) (Van Hees, 1997). Indeed, along the latitudinal gradient, we also detected an interaction between species identity and macroclimate for aboveground biomass; seedlings of the two Mediterranean oak species had a higher biomass in southern regions. Although, along the macroclimatic gradient, also the forest structure interactively affected the oak biomass: a simple forest structure led to a higher biomass for oak seedlings probably related to the higher light availability. This was especially

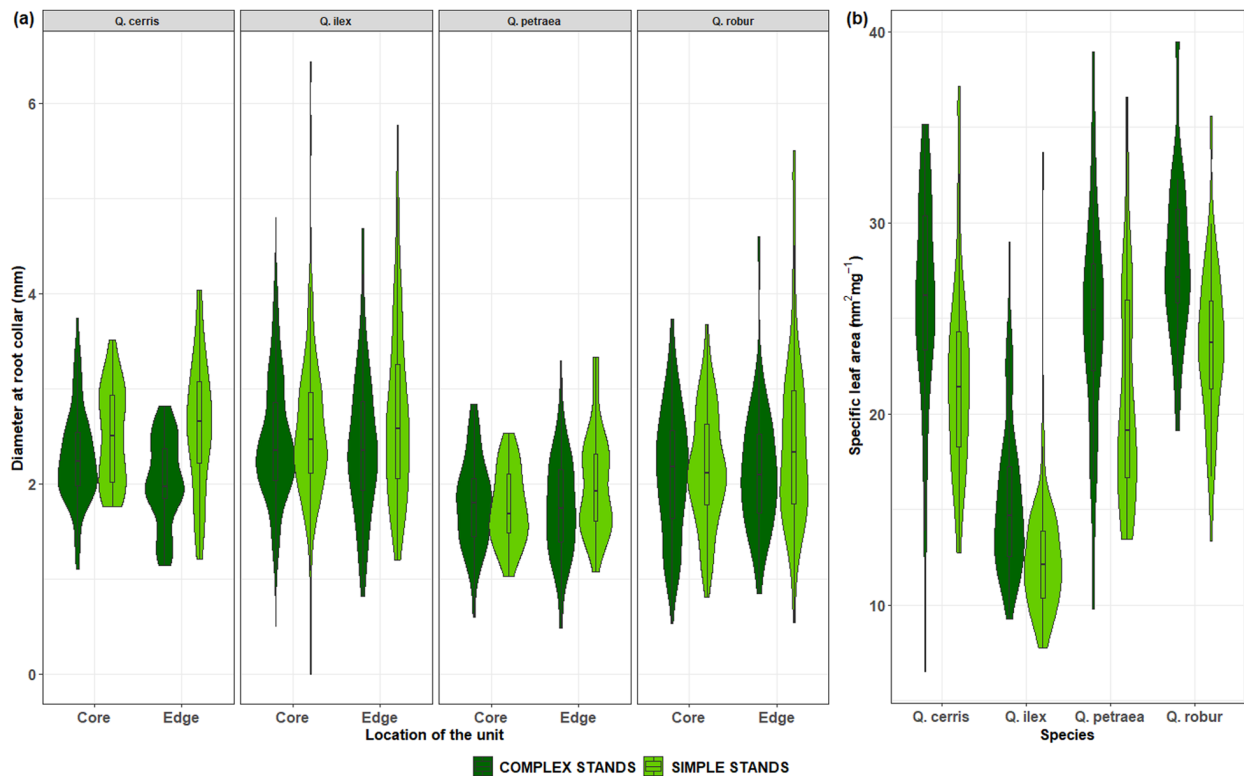


Fig. 4. (a) Violin plots of root collar diameter (mm) of the different oak species (shown in the subpanels) across the microclimatic gradients formed by stand structure (complex versus simple forest stands, visualized in dark and light green, respectively) and the distance to the edge of the experimental plot (in the core versus at the edge of the forest). Boxes show median and interquartile range. (b) Violin plot of the impact of stand structure, represented again in dark and light green, on specific leaf area (mm² mg⁻¹) for the oak species.

the case for northern regions, as in the south we found a higher biomass in complex stands in comparison to simple stands (except for *Q. petraea*).

Also, DRC was affected by the vegetation structure, with a higher DRC in simple stands (except for *Q. petraea*) and near edges (except for *Q. cerris*). These trends are all probably related to enhanced microclimatic growing conditions (*i.e.* trade-off between water availability and warmth/light) in open, simply structured forest patches or near edges. Previous studies found a higher growth, biomass and height near forest edges or under increased light intensities (Meiners *et al.* 2002; Lhotka & Stringer, 2013; Sevillano *et al.* 2016). Microclimate conditions in simply structured forests or near forest edges might also be more representative of traditional management practices, leading to semi-open woody landscapes, which are known to have had enhanced *Quercus* reproduction in the past in relation to more shade-tolerant species (Watt, 1919; Bobiec *et al.* 2018). Moreover, the positive effect of a low canopy cover might also favour the survival and growth of oaks affected by mildew, which was the case for many seedlings in our experiment. This fungus tends to reduce the shade and drought tolerance of seedlings and, therefore, has the potential to reduce the regeneration capacity of oaks in forest environments (Lonsdale, 2015; Bobiec *et al.* 2018; Demeter *et al.* 2021).

Finally, SLA values were lower in simply structured forests and at low latitudes (except for *Q. petraea* for which the SLA slightly decreased towards the north). Also, significantly lower SLA values for *Q. ilex* were expected, since this species is

adapted to dry Mediterranean climates and characterized by small, thick and coriaceous leaves, allowing the tree to reduce its transpiration (de Rigo & Caudullo, 2016). Traits such as SLA, besides representing a different ecological strategy, are not only influenced by global but also by local environmental factors (Wright *et al.* 2004; De Pauw *et al.* 2021; Govaert *et al.* 2021). Hence, higher SLA values in complex forests might be a reaction to lower light intensity (*i.e.* higher canopy closure), as plants growing in shade need to have larger leaves to capture sufficient light for their photosynthesis (Sevillano *et al.* 2016; Buajan *et al.* 2017). Besides, a lower SLA value in southern regions might be a mechanism to reduce water stress as a response to a higher vapour pressure deficit.

Experimental warming and transplant experiment beyond range limits

In warm and dry climates, the Mediterranean species *Q. ilex* and *Q. cerris* clearly performed better, with a higher biomass and height, and higher survival rates. Moreover, even when transplanted beyond their coldest range limits, both species still performed well, and their survival rates remained high (especially for *Q. ilex*). *Quercus ilex* was able to maintain the highest biomass and DRC, even in our Swedish plots. However, one must keep in mind that *Q. cerris* and *Q. petraea* were only monitored for one growing season and were not exposed to winter conditions along the gradient. Frost is known to affect seedling performance and survival and might limit species

distribution at the northern range margin (Hofmann *et al.* 2014; Bianchi *et al.* 2019). Survival and performance results of these latter two species could thus be strongly altered if we had studied them during two consecutive growing seasons. Besides frost, latitudinal patterns might also be related to other species-specific drivers, such as phenological differences, light quality and quantity, drought or herbivory patterns along the gradients (Ducousso *et al.* 1996; Collet *et al.* 1998; Sevillano *et al.* 2016; Moreira *et al.* 2021).

Rather unexpectedly, we only found a limited impact of our experimental warming treatment on the germination, survival and performance of our four studied oak species. More specifically, we found a negative effect on plant height and biomass for *Q. robur*, whereas this effect was positive for both *Q. cerris* and *Q. ilex*. *Quercus robur* is generally known to be less shade-tolerant than *Q. cerris* and *Q. petraea* (Leuschner & Meier, 2018) and thus might better regenerate in open conditions, as demonstrated in previous research (Demeter *et al.* 2021). Consistently, in the northern regions, we found a strong increase in the survival rate of *Q. robur* in simple and relatively more open forests in comparison with more complex and darker forests. This species thus requires sufficient light to grow but might also be more sensitive to heat and drought compared to the other oak species. The Mediterranean species, on the other hand, are better adapted to heat and drought (*e.g. via* their leaf characteristics or their provenance; de Rigo & Caudullo, 2016; Bert *et al.* 2020), and therefore could benefit from the additional warmth, especially at locations beyond their northern edge. Moreover, stronger effects might be expected if the degree of warming were higher and for long-term warming experiments, since the seedlings might also experience time-lags in response to the warming treatment (Bertrand *et al.* 2011; De Pauw *et al.* 2021). Therefore, in our rather short-term experiment, other drivers, such as the nutrients available in the acorn and the microclimate, could have had a stronger impact on the observed patterns than the warming treatment. Differences in microclimate due to vegetation characteristics were, on average, approximately of the same magnitude as the observed temperature increase under the warming treatment (De Pauw *et al.* 2021).

Even though we did not find a strong impact of the warming treatment, climate change still could strongly affect natural tree regeneration at a local scale, as we found significant impacts of the macroclimate itself, as well as more complex macroclimate–microclimate (*i.e. via* forest structure and edge distance) interactions. The latter highlights the importance of local microclimate buffering and appropriate forest management to limit the impact of rising temperatures in the understorey of forest interiors.

Potential management implications

Successful natural oak regeneration is complex and largely context dependent. Both species identity and macroclimate determine the outcome, while microclimate conditions and management interventions may locally alter these influences on initial oak regeneration. Moreover, conditions enhancing or limiting acorn germination differ from those for survival, growth or biomass accumulation. Such conditions might differ further from the growth requirements in later growing stages or for adult trees (Morin *et al.* 2007; Annighöfer *et al.* 2015; Leuschner & Meier, 2018). Therefore, successful regeneration

requires constant as well as species- and location-specific monitoring and farsighted, proactive management interventions to control the local climate and light availability, and thus the initial regeneration success.

We show that the local microclimate, via the impact of management and distance to the edge, is key for the initial stages of regeneration and establishment of oaks. With the local microclimate, we do not only refer to temperature and soil moisture conditions, but also to the impact of light availability at the forest floor, which has been shown in previous studies to be an important driver of oak regeneration processes (*e.g.* Théry, 2001; Sevillano *et al.* 2016). Previous studies found that neither fully exposed sites nor light-limited sites led to successful regeneration of oaks (Puerta-Piñero *et al.* 2007; Bobiec *et al.* 2018). Simply structured forests, forest edges or natural and human-induced canopy gaps, might provide an important regeneration niche for oak species, thanks to the higher canopy openness and thus warmer temperatures and increased light availability in the understorey (Aussenac, 2000; Davies-Colley *et al.* 2000; Camille *et al.* 2021). However, optimal light conditions for oak regeneration will depend on the focal species and will require management interventions as the forest floor microclimate will be influenced by both the macroclimate and the local forest structure (Aussenac, 2000; De Frenne *et al.* 2019; Camille *et al.* 2021). The detected macroclimate–forest structure interactions, as found for biomass and survival, show that such trade-offs in microclimatic requirements exist along the studied latitudinal gradient. An increased light availability (and subsequently forest floor temperature) might benefit the initial regeneration stages and seedling performance in northern regions, whereas in southern regions managers might want to keep forest stands dense and closed to improve moisture retention and avoid a detrimental impact of drought on growth and survival of oak seedlings.

In this experiment, we unfortunately only had the opportunity to test the initial regeneration responses of four ecologically and economically important European oaks. It would be very interesting to include a more ecologically and phylogenetically diverse set of oak species in future research. Furthermore, performance of the four studied oak species might also have been affected by their provenance, as this is known to play a key role in regeneration and growth dynamics (*e.g.* Deans & Harvey, 1996; Arend *et al.* 2011). In the future, it would therefore be interesting to include acorns from different provenances, covering their natural range, in the experimental design and to explore differences within and between provenances and species.

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DATA AVAILABILITY STATEMENT

Data related to this manuscript are available on Figshare: <https://doi.org/10.6084/m9.figshare.19248527>.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Foliage ABA levels (black circles) and leaf water potential (white circles) through time in a drought that induced visible signs of leaf necrosis on the final day of measurement. In some species both foliage ABA levels and leaf

water potential data are presented as means and standard errors ($n = 3$ plants).

Figure S2. Left: overview of and experimental plot (without warming treatment) with two rows 16 oak seedling containers protected by a cage. Right: row with acorns right before planting (top) and a germinating *Q. ilex* (bottom).

Figure S3. Predicted probabilities of germination (%) of the acorns (the four selected oak species are all shown in a different subpanel) in function of the distance to the edge of the plot (at the edge or in the core of the forest).

Table S1. Overview and characteristics of the 20 experimental locations.

Table S2. The impact of macroclimate (i.e. latitude °N), microclimate (i.e. forest structure and distance to the edge), experimental warming, species and their interaction effects, as well as the impact of acorn weight, on the biomass and natural height of oak seedlings.

REFERENCES

- Anngihöfer P., Beckschäfer P., Vor T., Ammer C. (2015) Regeneration Patterns of European Oak Species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in Dependence of Environment and Neighborhood. *PLoS One*, **10**, e0134935. <https://doi.org/10.1371/journal.pone.0134935>.
- Arend M., Kuster T., Günthardt-Goerg M.S., Dobbertin M. (2011) Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiology*, **31**, 287–297.
- Aussenac G. (2000) Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*. <https://doi.org/10.1051/forest:2000119>.
- Badano E.I., Samour-Nieva O.R., Flores J., Douterlungne D. (2015) Microclimate and seedling predation as drivers of tree recruitment in human-disturbed oak forests. *Forest Ecology and Management*, **356**, 93–100. <https://doi.org/10.1016/j.foreco.2015.07.031>.
- Barbero M., Loisel R., Quézel P. (1992) *Quercus ilex* L. ecosystems: function, dynamics and management. In: Romane F., Terradas J.I. (Eds), *Advances in vegetation science*, Vol 13. Springer, Dordrecht, the Netherlands, pp 19–34.
- Barbosa M.F.P., Masante D., Arias-Muñoz C., Cammalleri C., De Jager A., Magni D., Mazzeschi M., McCormick N., Naumann G., Spinoni J., Vogt J. (2021) Droughts in Europe and Worldwide 2019–2020, EUR 30719 EN. Publications Office of the European Union, Luxembourg.
- Bates D., Mächler M., Bolker B., Walker S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bell D.M., Bradford J.B., Lauenroth W.K. (2014) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, **23**, 168–180. <https://doi.org/10.1111/GEB.12109>.
- Bert D., Lebourgeois F., Ponton S., Musch B., Ducousso A. (2020) Which oak provenances for the 22nd century in Western Europe? Dendroclimatology in common gardens. *PLoS One*, **15**, e0234583. <https://doi.org/10.1371/journal.pone.0234583>.
- Bertrand R., Lenoir J., Piedallu C., Riofrío-Dillon G., de Ruffray P., Vidal C., Pierrat J.-C., Gégout J.-C. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, **479**, 517–520. <https://doi.org/10.1038/nature10548>.
- Bianchi E., Bugmann H., Bigler C. (2019) Early emergence increases survival of tree seedlings in Central European temperate forests despite severe late frost. *Ecology and Evolution*, **9**, <https://doi.org/10.1002/ece3.5399>.
- Bobiec A., Jaszcz E., Wojtunik K. (2011) Oak (*Quercus robur* L.) regeneration as a response to natural dynamics of stands in European hemiboreal zone. *European Journal of Forest Research*, **130**, 785–797. <https://doi.org/10.1007/s10342-010-0471-3>.
- Bobiec A., Reif A., Öllerer K. (2018) Seeing the oak-cape beyond the forest: a landscape approach to the oak regeneration in Europe. *Landscape Ecology*, <https://doi.org/10.1007/s10980-018-0619-y>.
- Bonan G.B. (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449. <https://doi.org/10.1126/science.1155121>.
- Buajan S., Jinfu L., Zhongsheng H.E., Xueping F., Muhammad A. (2017) The effect of light on micro-environment and specific leaf area within the gap, subtropical forest, China. *Pakistan Journal of Botany*, **49**, 273–282.
- Caron M.M., Zellweger F., Verheyen K., Baeten L., Hédl R., Bernhardt-Römermann M., Berki I., Brunet J., Decocq G., Díaz S., Dirnböck T., Durak T., Heinken T., Jaroszewicz B., Kopecký M., Lenoir J., Macek M., Malicki M., Mális F., Nagel T.A., Perring M.P., Petřík P., Reczyńska K., Pielech R., Schmidt W., Świerkosz K., Teleki B., Wulf M., Frenne P.D. (2021) Thermal differences between juveniles and adults increased over time in European forest trees. *Journal of Ecology*, **109**, 3944–3957. <https://doi.org/10.1111/1365-2745.13773>.
- Chen J., Franklin J.F., Spies T.A. (1995) Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications*, **5**, 74–86. <https://doi.org/10.2307/1942053>.
- Collet C., Ningre F., Frochot H. (1998) Modifying the microclimate around young oaks through vegetation microclimate: Effects on seedling growth and branching. *Forest Ecology and Management*, **110**, 249–262. [https://doi.org/10.1016/S0378-1127\(98\)00284-9](https://doi.org/10.1016/S0378-1127(98)00284-9).
- Davies-Colley R.J., Payne G.W., Van Elswijk M. (2000) Microclimate gradients across a forest edge. *New Zealand Journal of Ecology*, **24**, 111–121.
- Deans J.D., Harvey F.J. (1996) Frost hardness of 16 European provenances of sessile oak growing in Scotland. *Forestry*, **69**, 5–11.
- Demeter L., Molnár Á.P., Öllerer K., Csóka G., Kiš A., Vadász C., Horváth F., Molnár Z. (2021) Rethinking the natural regeneration failure of pedunculate oak: The pathogen mildew hypothesis. *Biological Conservation*, <https://doi.org/10.1016/j.bioccon.2020.108928>.
- Ducousso A., Guyon J., Krémer A. (1996) Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt) Liebl.). *Annales Des Sciences Forestières*, **53**, 775–782. <https://doi.org/10.1051/FOREST:19960253>.
- Eaton E.G.S.D.J., Caudullo G., Oliveira S., De Rigo D. (2016). *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threats. European Atlas of Forest Tree Species, 160–163. European Commission, Luxembourg.
- Elith J., Leathwick J.R. (2009) Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697. <https://doi.org/10.1146/ANNUREV.ECOLSYS.110308.120159>.
- De Frenne P., Rodríguez-Sánchez F., Coomes D.A., Baeten L., Verstraeten G., Vellend M., Bernhardt-Römermann M., Brown C.D., Brunet J., Cornelis J., Decocq G.M., Dierschke H., Eriksson O., Gilliam F.S., Hedl R., Heinken T., Hermy M., Hommel P., Jenkins M.A., Kelly D.L., Kirby K.J., Mitchell F.J.G., Naaf T., Newman M., Peterken G., Petrik P., Schultz J., Sonnier G., Van Calster H., Waller D.M., Walther G.-R., White P.S., Woods K.D., Wulf M., Graae B.J., Verheyen K. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, **110**, 18561–18565. <https://doi.org/10.1073/pnas.1311190110>
- De Frenne P., Zellweger F., Rodríguez-Sánchez F., Schaffers B.R., Hylander K., Luoto M., Vellend M., Verheyen K., Lenoir J. (2019) Global buffering of temperatures under forest canopies. *Nature Ecology and Evolution*, **3**, 744–749. <https://doi.org/10.1038/s41559-019-0842-1>.

- Frey S.J.K., Hadley A.S., Johnson S.L., Schulze M., Jones J.A., Betts M.G. (2016) Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, **2**, e1501392. <https://doi.org/10.1126/sciadv.1501392>.
- Gaston K.J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford, UK.
- Geiger R., Aron R.H., Todhunter P. (2009) *The climate near the ground*. Rowman & Littlefield, Washington, DC, USA.
- Gil-Pelegrin E., Peguero-Pina J.J., Sancho-Knapik D. (2017) Oaks and people: a long journey together. In: Gil-Pelegrin E., Peguero-Pina J. J., Sancho-Knapik D. (Eds), *Oaks Physiological Ecology. Exploring the Functional Diversity of Genus Quercus L.* Springer, Cham, Switzerland, pp 1–11.
- Godefroid M., Meurisse N., Groenen F., Kerdelhué C., Rossi J.-P. (2019) Current and future distribution of the invasive oak processionary moth. *Biological Invasions*, **222**, 523–534. <https://doi.org/10.1007/S10530-019-02108-4>.
- Götmark F. (2007) Careful partial harvesting in conservation stands and retention of large oaks favour oak regeneration. *Biological Conservation*, **140**, 349–358. <https://doi.org/10.1016/j.biocon.2007.08.018>.
- Govaert S., Meeussen C., Vanneste T., Bollmann K., Brunet J., Cousins S.A.O., Diekmann M., Graae B.J., Hedwall P.-O., Heinken T., Iacopetti G., Lenoir J., Lindmo S., Orczewska A., Perring M.P., Ponette Q., Plue J., Selvi F., Spicher F., Tolosano M., Vermeir P., Zellweger F., Verheyen K., Vangansbeke P., De Frenne P. (2020) Edge influence on understorey plant communities depends on forest management. *Journal of Vegetation Science*, **31**, 281–292. <https://doi.org/10.1111/jvs.12844>
- Govaert S., Meeussen C., Vanneste T., Brunet J., Calders K., Cousins S. A. O., De Pauw K., Diekmann M., Graae B., Hedwall P., Iacopetti G., Lenoir J., Lindmo S., Orczewska A., Ponette Q., Plue J., Sanczuk P., Selvi F., Spicher F., Verheyen K., Vangansbeke P., De Frenne P. (2021) Trait–micro-environment relationships of forest herb communities across Europe. *Global Ecology and Biogeography*, Major revisions.
- Grubb P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145. <https://doi.org/10.1111/j.1469-185x.1977.tb01347.x>.
- Hanewinkel M., Cullmann D.A., Schelhaas M.J., Naburs G.J., Zimmermann N.E. (2013) Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, **3**, 203–207. <https://doi.org/10.1038/nclimate1687>.
- Van Hees A.F.M. (1997) Growth and morphology of pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) seedlings in relation to shading and drought. *Annals of Forest Science*, **54**, 9–18. <https://doi.org/10.1051/forest:19970102>.
- Hofmann M., Jager M., Bruelheide H. (2014) Relationship between frost hardiness of adults and seedlings of different tree species. *iForest - Biogeosciences for*, **7**, 282. <https://doi.org/10.3832/IFOR1076-007>.
- Iverson L.R., Schwartz M.W., Prasad A.M. (2004) How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography*, **13**, 209–219. <https://doi.org/10.1111/j.1466-822X.2004.00093.x>.
- Jones E.W. (1974) Introduction. In: Morris M. G., Perring F. H. (Eds), *The British Oak*. Botanical Society of the British Isles, London, UK, pp 11–12.
- Kamler J., Dobrovolný L., Drimaj J., Kadavý J., Kneifl M., Adamec Z., Knott R., Martinik A., Plhal R., Zeman J., Hrbek J. (2016) The impact of seed predation and browsing on natural sessile oak regeneration under different light conditions in an over-aged coppice stand. *Iforest*, **9**, 569–576. <https://doi.org/10.3832/IFOR1835-009>.
- Karger D.N., Conrad O., Böhner J., Kawohl T., Kreft H., Soria-Auza R.W., Zimmermann N.E., Linder H.P., Kessler M. (2017) Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, **4**, 170122. <https://doi.org/10.1038/sdata.2017.122>
- Kimball B.A. (2005) Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology*, **11**, 2041–2056. <https://doi.org/10.1111/j.1365-2486.2005.1028.x>.
- Kimball B.A., Conley M.M., Wang S., Lin X., Luo C., Morgan J., Smith D. (2008) Infrared heater arrays for warming ecosystem field plots. *Global Change Biology*, **14**, 309–320. <https://doi.org/10.1111/j.1365-2486.2007.01486.x>.
- Knopf H.E. (2002) In: Roloff A., Weisgerber H., Lang U.M., Stimm B., Schutt P. (Eds), *Enzyklopadie der Holzgewächse: Handbuch und Atlas der Dendrologie*. Wiley, Berlin, Germany.
- Kormanik P.P., Sung S.S., Kormanik T.L., Schlarbaum S.E., Zarnoch S.J. (2011) Effect of acorn size on development of northern red oak 1–0 seedlings. *Canadian Journal of Forest Research*, **28**, <https://doi.org/10.1139/X98-152>.
- Kovács B., Tinya F., Ódor P. (2017) Stand structural drivers of microclimate in mature temperate mixed forests. *Agricultural and Forest Meteorology*, **234–235**, 11–21. <https://doi.org/10.1016/j.agrformet.2016.11.268>.
- Kremer A., Hipp A.L. (2020) Oaks: An evolutionary success story. *New Phytologist*, **226**, 987–1011.
- Leech S.M., Almuedo P.L., Neill G.O. (2011) Assisted Migration: Adapting forest management to a changing climate. *Journal of Ecosystem Management*, **12**, 18–34.
- Lee-Yaw J.A., Kharouba H.M., Bontrager M., Mahony C., Csörgő A.M., Noreen A.M.E., Li Q., Schuster R., Angert A.L. (2016) A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, **19**, 710–722. <https://doi.org/10.1111/ELE.12604>.
- Lenoir J., Gégout J.C., Marquet P.A., De Ruffray P., Brisse H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771. <https://doi.org/10.1126/SCIENCE.1156831>.
- Leuschner C., Meier I.C. (2018) The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees. *Perspectives in Plant Ecology, Evolution and Systematics*, **33**, 89–103. <https://doi.org/10.1016/J.PPEES.2018.05.003>.
- Lhotka J.M., Stringer J.W. (2013) Forest edge effects on *Quercus* reproduction within naturally regenerated mixed broadleaf stands. *Canadian Journal of Forest Research*, **43**, 911–918. <https://doi.org/10.1139/cjfr-2013-0231>.
- Lobo A., Torres-Ruiz J.M., Burlett R., Lemaire C., Parise C., Francioni C., Truffaut L., Tomášková I., Hansen J.K., Kjær E.D., Kremer A., Delzon S. (2018) Assessing inter- and intraspecific variability of xylem vulnerability to embolism in oaks. *Forest Ecology and Management*, **424**, 53–61. <https://doi.org/10.1016/J.FORECO.2018.04.031>.
- Lonsdale D. (2015) Review of oak mildew, with particular reference to mature and veteran trees in Britain. *Arboricultural Journal*, **37**, 61–84. <https://doi.org/10.1080/03071375.2015.1039839>.
- Von Lüpke B. (1998) Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *Forest Ecology and Management*, **106**, 19–26. [https://doi.org/10.1016/S0378-1127\(97\)00235-1](https://doi.org/10.1016/S0378-1127(97)00235-1).
- Marçais B., Desprez-Loustau M.L. (2014) European oak powdery mildew: Impact on trees, effects of environmental factors, and potential effects of climate change. *Annals of Forest Science*. <https://doi.org/10.1007/s13595-012-0252-x>.
- Matlack G.R. (1993) Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation*, **66**, 185–194. [https://doi.org/10.1016/0006-3207\(93\)90004-K](https://doi.org/10.1016/0006-3207(93)90004-K).
- Meeussen C., Govaert S., Vanneste T., Calders K., Bollmann K., Brunet J., Cousins S.A.O., Diekmann M., Graae B.J., Hedwall P.-O., Krishna M., Orczewska A., Iacopetti G., Lenoir J., Lindmo S., Ponette Q., Plue J., Selvi F., Spicher F., Tolosano M., Verbeeck H., Verheyen K., Vangansbeke P., De Frenne P. (2020) Structural variation of forest edges across Europe. *Forest Ecology and Management*, **462**, 117929. <https://doi.org/10.1016/j.foreco.2020.117929>
- Meeussen C., Govaert S., Vanneste T., Bollmann K., Brunet J., Calders K., Cousins S.A.O., De Pauw K., Diekmann M., Gasperini C., Hedwall P.-O., Hyländer K., Iacopetti G., Lenoir J., Lindmo S., Orczewska A., Ponette Q., Plue J., Sanczuk P., Selvi F., Spicher F., Verbeeck H., Zellweger F., Verheyen K., Vangansbeke P., De Frenne P. (2021) Microclimatic edge-to-interior gradients of European deciduous forests. *Agricultural and Forest Meteorology*, **311**, 108699. <https://doi.org/10.1016/j.agrformet.2021.108699>
- Meiners S.J., Pickett S.T.A., Handel S.N. (2002) Probability of tree seedling establishment changes across a forest-old field edge gradient. *American Journal of Botany*, **89**, 466–471. <https://doi.org/10.3732/ajb.89.3.466>.
- Mitchell R.J., Bellamy P.E., Ellis C.J., Hewison R.L., Hodgetts N.G., Iason G.R., Littlewood N.A., Newey S., Stockan J.A., Taylor A.F.S. (2019) Collapsing foundations: The ecology of the British oak, implications of its decline and mitigation options. *Biological Conservation*, **233**, 316–327. <https://doi.org/10.1016/j.biocon.2019.03.040>
- Mölder A., Meyer P., Nagel R.V. (2019). Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur*, *Q. petraea*) forests: An overview. *Forest Ecology and Management*. <https://doi.org/10.1016/j.foreco.2019.01.006>
- Moreira X., Abdala-Roberts L., De Frenne P., Galmán A., Gaytán Á., Lago-Núñez B., Meeussen C., Pulkkinen P., Rasmussen P.U., Ten Hoopen J.P.J.G., Timmermans B.G.H., Vázquez-González C., Bos N., Castagneryol B., Tack A.J.M. (2021) Effects of latitude and conspecific plant density on insect leaf herbivory in oak saplings and seedlings. *American Journal of Botany*, **108**, 172. –176. <https://doi.org/10.1002/ajb2.1596>
- Morin X., Améglio T., Ahas R., Kurz-Besson C., Lanta V., Lebourgeois F., Miglietta F., Chuine I. (2007) Variation in cold hardiness and carbohydrate concentration from dormancy induction to bud burst among provenances of three European oak species. *Tree Physiology*, **27**, 817–825. <https://doi.org/10.1093/TREEPHYS/27.6.817>.

- Nakagawa S., Schielzeth H. (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>.
- Nijs I., Teughels H., Blum H., Hendrey G., Impens I. (1996) Simulation of climate change with infrared heaters reduces the productivity of *Lolium perenne* L. in summer. *Environmental and Experimental Botany*, **36**, 271–280. [https://doi.org/10.1016/0098-8472\(96\)01021-0](https://doi.org/10.1016/0098-8472(96)01021-0).
- Nixon K.C. (2006) Global and Neotropical Distribution and Diversity of Oak (genus *Quercus*) and Oak Forests. In: Kappelle M. (Ed), *Ecology and Conservation of Neotropical Montane Oak Forests*. Springer, Berlin, Germany, pp 3–13. https://doi.org/10.1007/3-540-28909-7_1.
- Palmer S.C.F., Mitchell R.J., Truscott A.M., Welch D. (2004) Regeneration failure in Atlantic oakwoods: The roles of ungulate grazing and invertebrates. *Forest Ecology and Management*, **192**, 251–265. <https://doi.org/10.1016/j.foreco.2004.01.038>.
- De Pauw K., Sanczuk P., Meeussen C., Depauw L., De Lombaerde E., Govaert S., Vanneste T., Brunet J., Cousins S.A.O., Gasperini C., Hedwall P.-O., Iacopetti G., Lenoir J., Plue J., Selvi F., Spicher F., Uria-Diez J., Verheyen K., Vangansbeke P., De Frenne P. (2022) Forest understorey communities respond strongly to light in interaction with forest structure, but not to microclimate warming. *New Phytologist*, **233**, 219–235. <https://doi.org/10.1111/nph.17803>
- Pérez-Harguindeguy N., Díaz S., Garnier E., Lavorel S., Poorter H., Jaureguiberry P., Bret-Harte M.S., Cornwell W.K., Craine J.M., Gurvich D.E., Urcelay C., Veneklaas E.J., Reich P.B., Poorter L., Wright I. J., Ray P., Enrico L., Pausas J.G., de Vos A.C., Buchmann N., Funes G., Quétier F., Hodgson J.G., Thompson K., Morgan H.D., ter Steege H., Sack L., Blonder B., Poschlod P., Vaieretti M.V., Conti G., Staver A. C., Aquino S., Cornelissen J.H.C. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167. <https://doi.org/10.1071/bt12225>
- Petritan A.M., Nuske R.S., Petritan I.C., Tudose N.C. (2013) Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)–European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains. *Romania. Forest Ecology and Management*, **308**, 67–75. <https://doi.org/10.1016/j.foreco.2013.07.045>.
- Praciak A. (2013) *The CABI encyclopedia of forest trees*. CABI, Wallingford, UK.
- Puerta-Piñero C., Gómez J.M., Valladares F. (2007) Irradiance and oak seedling survival and growth in a heterogeneous environment. *Forest Ecology and Management*, **242**, 462–469. <https://doi.org/10.1016/J.FORECO.2007.01.079>.
- R Core Team (2020) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- De Rigo D., Caudullo G. (2016). *Quercus ilex* in Europe: distribution, habitat, usage and threats. European Atlas of Forest Tree Species, 152–153. European Commission, Luxembourg.
- De Rigo D., Enescu C.M., Durrant T.H., Caudullo G. (2016). *Quercus cerris* in Europe: distribution, habitat, usage and threats. European Atlas of Forest Tree Species, 148–149. European Commission, Luxembourg.
- Saxe H., Cannell M.G.R., Johnsen Ø., Ryan M.G., Vourlitis G. (2001) Tree and forest functioning in response to global warming. *New Phytologist*, <https://doi.org/10.1046/j.1469-8137.2001.00057.x>.
- Schmidt M., Lischeid G., Nendel C. (2019) Microclimate and matter dynamics in transition zones of forest to arable land. *Agricultural and Forest Meteorology*, **268**, 1–10. <https://doi.org/10.1016/j.agrformet.2019.01.001>.
- De Schrijver A., Devlaeminck R., Mertens J., Wuyts K., Hermy M., Verheyen K. (2007) On the importance of incorporating forest edge deposition for evaluating exceedance of critical pollutant loads. *Applied Vegetation Science*, **10**, 293–298. <https://doi.org/10.1111/j.1654-109X.2007.tb00529.x>.
- Sevillano I., Short L., Grant J., O'Reilly C. (2016) Effects of light availability on morphology, growth and biomass allocation of *Fagus sylvatica* and *Quercus robur* seedlings. *Forest Ecology and Management*, **374**, 11–19. <https://doi.org/10.1016/j.foreco.2016.04.048>.
- De Smedt P., Baeten L., Proesmans W., Van de Poel S., Van Keer J., Giffard B., Martin L., Vanhulle R., Brunet J., Cousins S.A.O., Decocq G., Deconchat M., Diekmann M., Gallet-Moron E., Le Roux V., Liira J., Valdés A., Wulf M., Andrieu E., Hermy M., Bonte D., Verheyen K. (2019) Strength of forest edge effects on litter-dwelling macro-arthropods across Europe is influenced by forest age and edge properties. *Diversity and Distributions*, **25**, 963–974. <https://doi.org/10.1111/ddi.12909>
- Sousa-Silva R., Verheyen K., Ponette Q., Bay E., Sioen G., Titeux H., Van de Peer T., Van Meerbeek K., Muys B. (2018) Tree diversity mitigates defoliation after a drought-induced tipping point. *Global Change Biology*, **24**, 4304–4315. <https://doi.org/10.1111/gcb.14326>
- Svenning J.-C., Skov F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters*, **7**, 565–573. <https://doi.org/10.1111/J.1461-0248.2004.00614.X>.
- Théry M. (2001). Forest light and its influence on habitat selection. *Plant Ecology*, **153**, 251–261.
- Thomas F.M., Blank R., Hartmann G. (2002) Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology*, **32**, 277–307. <https://doi.org/10.1046/j.1439-0329.2002.00291.x>.
- Tilki F. (2010) Influence of acorn size and storage duration on moisture content, germination and survival of *Quercus petraea* (Mattuschka). *Journal of Environmental Biology*, **31**, 325–328.
- Tomlinson I., Potter C., Bayliss H. (2015) Managing tree pests and diseases in urban settings: The case of Oak Processionary Moth in London, 2006–2012. *Urban Forestry and Urban Greening*, **14**, 286–292. <https://doi.org/10.1016/J.UFUG.2015.02.009>.
- Urli M., Lamy J.-B., Sin F., Burlett R., Delzon S., Porté A.J. (2014) The high vulnerability of *Quercus robur* to drought at its southern margin paves the way for *Quercus ilex*. *Plant Ecology*, **216**, 177–187. <https://doi.org/10.1007/S11258-014-0426-8>.
- Vera F.W.M. (2000) Grazing ecology and forest history. CABI, Wallingford, UK, <https://doi.org/10.1079/9780851994420.0000>.
- Wales B.A. (1972) Vegetation analysis of north and south edges in a mature oak–hickory forest. *Ecological Monographs*, **42**, 451–471. <https://doi.org/10.2307/1942167>.
- Watt A.S. (1919) On the causes of failure of natural regeneration in british Oakwoods. *Journal of Ecology*, **7**, 173. <https://doi.org/10.2307/2255275>.
- Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J.H.C., Diemer M., Flexas J., Garnier E., Groom P.K., Gulias J., Hikosaka K., Lamont B.B., Lee T., Lee W., Lusk C., Midgley J.J., Navas M.-L., Niinemets Ü, Oleksyn J., Osada N., Poorter H., Poot P., Prior L., Pyankov V.I., Roumet C., Thomas S.C., Tjoelker M.G., Veneklaas E.J., Villar R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827. <https://doi.org/10.1038/nature02403>
- Wuyts K., De Schrijver A., Staelens J., Gielis L., Vandenberghe J., Verheyen K. (2008) Comparison of forest edge effects on throughfall deposition in different forest types. *Environmental Pollution*, **156**, 854–861. <https://doi.org/10.1016/j.envpol.2008.05.018>.
- Zellweger F., Coomes D., Lenoir J., Depauw L., Maes S.L., Wulf M., Kirby K.J., Brunet J., Kopecký M., Máliš F., Schmidt W., Heinrichs S., den Ouden J., Jaroszewicz B., Buyse G., Spicher F., Verheyen K., De Frenne P. (2019) Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, **28**, 1774–1786. <https://doi.org/10.1111/geb.12991>
- Zuur A., Ieno E., Walker N., Saveliev A., Smith G. (2009) Mixed effects modelling for nested data. In: Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A., Smith G.M. (Eds), *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY, USA, pp 101–142.