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

Running title: Oak regeneration along climatic gradients.

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24   Abstract

25   • *Quercus* spp. is one of the most important tree genera in temperate deciduous forests from

26   biodiversity, economic and cultural perspectives. However, natural regeneration of oaks,

27   depending on specific environmental conditions, is still not sufficiently understood. Oak

28   regeneration dynamics are impacted by climate change, but these climate impacts will depend

29   on local forest management, and light and temperature conditions.

30   • Here, we studied germination, survival and seedling performance (i.e. aboveground biomass,

31   height, root collar diameter and specific leaf area) of four oak species (*Q. cerris, Q. ilex, Q.*

32   *robur* and *Q. petraea*). Acorns were sown across a wide latitudinal gradient, from Italy to

33   Sweden, and across several microclimatic gradients located within and beyond the species'

34   natural ranges. Microclimatic gradients were applied in terms of forest structure, distance to

35   the forest edge and experimental warming.

36   • We found strong interactions between species and latitude, as well as between microclimate

37   and latitude or species. The species thus reacted differently to local and regional changes

38   inmicroclimate; complex in comparison to simply structured forests seemed to benefit the

39   temperate *Q. robur* and *Q. petraea* in southern regions, whereas the Mediterranean *Q. ilex*

40   and *Q. cerris* performed better in simply structured forests with a reduced microclimatic

41   buffering capacity. The experimental warming treatment only enhanced height and

42   aboveground biomass of Mediterranean species.

43   • Our results showed that local gradients in light and temperature play a key role in the initial

44   stages of oak regeneration, however one also needs to consider the species-specific responses

45   to forest structure and the macroclimatic context.

46

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 and Hipp, 2020). They 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, they 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 value 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

73 agricultural lands (Bobiec et al., 2011, 2018; Demeter et al., 2021). Hence, for successful seedling

74 establishment specific microclimatic conditions are required (Von Lüpke, 1998; Mölder et al., 2019),

75 but we still lack information on how light, temperature and humidity affect the regeneration success

76 of different oak species.

77 The macroclimate, defined as free-air conditions, largely affects tree growth and determines species

78 distributions based on temperature and precipitation patterns (Bonan, 2008; Elith and Leathwick,

79 2009). Seedlings' climate niches, however, are more limited than those of adult trees (Grubb, 1977;

80 Bell et al., 2014; Leuschner and Meier, 2018; Caron et al., 2021). Therefore, it is still unclear how

81 regeneration of important tree species such as oaks will respond to climate change and extreme

82 weather events. Moreover, specific abiotic conditions are likely determined by both the regional

83 macroclimate as well as the microclimate (i.e. local climatic conditions shaped by the surrounding

84 vegetation and topography; Geiger et al., 2009). Microclimatic gradients can, for instance, occur near

85 forest edges, where temperature decreases and humidity increases towards the forest core (Schmidt

86 et al., 2019; Meeussen et al., 2021). Likewise, forest management interventions that lead to reductions

87 in canopy cover such as thinning can create an increase in light and temperature at the forest floor

88 (Kovács et al., 2017; Zellweger et al., 2019; Meeussen et al., 2021). Via the temperature buffering

89 effect of the canopy, microclimatic conditions near the forest floor are stabilized (De Frenne et al.,

90 2013), which might facilitate regeneration of oaks and protect seedlings against extreme temperatures

91 and drought. To better understand natural oak regeneration, more research is necessary to figure out

92 how local and large-scale climatic gradients interact and determine the regeneration success of

93 different oak species in a warming world. Also, warming experiments in the field can be very useful

94 to test oak recruitment under future temperature scenarios in alternative macroclimatic and

95 microclimatic contexts. However, to date no one has experimentally manipulated temperature in situ

96 to better understand the factors affecting oak regeneration in different forest types and along edge-to-

97 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 and 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 provide valuable insights on how species perform outside their natural range and 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 variation in life history. In total, 1024 acorns were sown, distributed across five sites along a *c.* 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 species. We hypothesized 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* performed better in warmer environments (both micro- and macroclimates), whereas the northern species *Q. robur* and *Q. petraea* benefitted from locally buffered (cooler) microclimatic conditions,

123   especially in the more southern regions, such as can be found in the forest interior or in complex

124   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 (**Figure 1a**) and extend from the southern part of Sweden and Norway towards South-Italy, Turkey, the Balkan and the northern part of Spain and Portugal in 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 and Caudullo, 2016; de Rigo et al., 2016) (**Figure 1a**). Both species grow on a wide variety of soils and are relatively resistant to drought (Barbero et al., 1992; Praciak, et al., 2013). Q*uercus ilex* can also survive low winter temperatures down to -20°C for shorter periods (Knopf, 2002). Q*uercus ilex* is an evergreen and more shade-tolerant species (de Rigo and Caudullo, 2016), whereas *Q. robur*, *Q. petraea* and *Q. cerris* are deciduous and light-demanding tree species (Eaton et al., 2016, de Rigo et al., 2016). As seedlings however, *Q. cerris* and *Q. petraea* are a bit more tolerant to shade in comparison to *Q. robur* which has a very low shade tolerance (Leuschner and Meier, 2018).

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 (i.e. temperature difference of 8.2°C,

CHELSA, 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 (**Figure 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**).
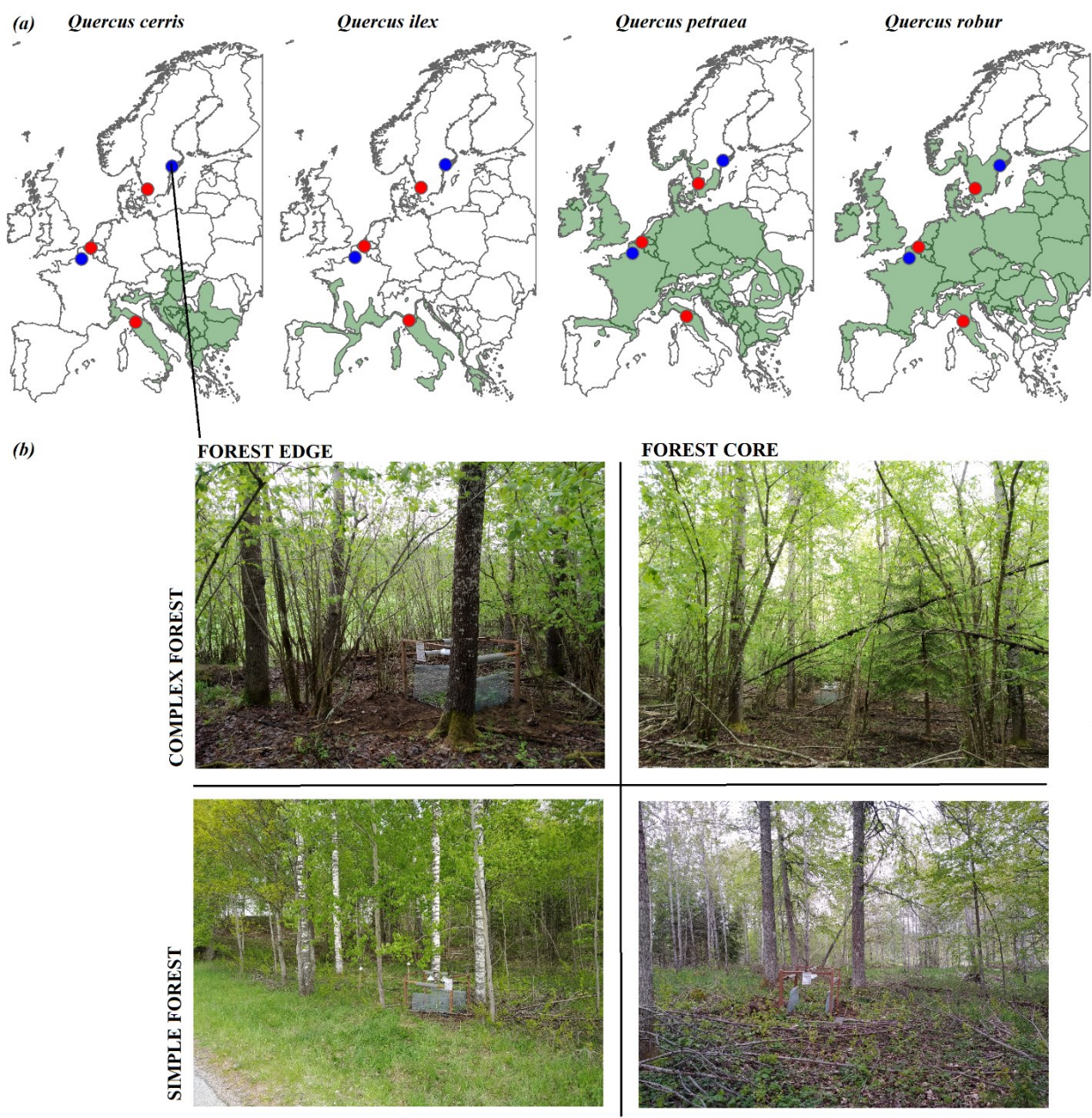
Figure 1: (a) Distribution maps of the four species. The red and blue circles represent the different regions involved in

the experiment. Red circles are the regions equipped with experimental warming and control plots. Blue circles are the

regions equipped with control plots. Distribution maps are from: http://www.euforgen.org/species/ (b) Pictures of the

160 microclimatic gradients (here in Stockholm): two forest edges and two forest core plots were selected of which each time

161 one was located in a "simple" (or more open) forest (bottom) and one in a more "complex" (or dense) forest (top). In

162 regions represented by a red dot, additional plots with experimental warming were established at the four locations.

163

164 In all five sites, four experimental locations were established: we included variation in forest structure

165 and distance to the forest edge to be able to study the effect of the local microclimate (i.e. sub-canopy

166 gradients in light, humidity and temperature) on the initial regeneration stages of oak (**Figure 1b**).

167 Two forest stands were selected with a different forest structure as differences in vegetation structure

168 will affect the forest microclimate (Frey et al., 2016; Kovács et al., 2017; Meeussen et al., 2021). The

169 first stand, hereafter referred to as 'complex forest', was always a vertically dense and multi-layered

170 forest stand with a well-developed shrub layer in the understorey (i.e. at least more than 15%) and a

171 closed upper canopy layer (canopy cover preferably above 90%). A second stand type represented a

172 'simple forest' which was composed only of a single tree layer, had a higher canopy openness (canopy

173 cover below 70%) and no or few shrubs in the understorey (i.e. a maximum shrub cover of 45%).

174 Moreover, in each of these stands, two plots were established (n = 20 plots across the five sites),

175 forming a second microclimatic gradient determined by distance to the edge (Meeussen et al., 2021).

176 The centre of the first plot was located at a distance of roughly 2-5 m from the edge whereas the

177 second plot lied at least 50-100 m towards the core of the forest patch. The studied edges were all

178 bordered by a matrix of agricultural land and were approximately south-oriented, as edge orientation

179 due to the impact of direct radiation, is known to affect the microclimate and edge width (Chen et al.,

180 1995; Matlack, 1993). Further details on the study design, forest structure and site selection are

181 available in De Pauw et al. (2021) and in **Table S1**.

182 In three sites, i.e. Southern Sweden, Belgium and Central Italy, an experimental warming treatment

183 was installed (for feasibility reasons, this was not possible at the other two sites). We therefore

184 doubled the number of plots present at those three locations. This led to a total of 32 plots (i.e. five

185 sites with four plots per site, among which three sites had an additional set of four plots with

186 experimental warming: 20 plots for control *vs.* 12 plots for warming treatment). The warming

187 treatment was applied both day and night during the growing seasons of 2019 (from installation in

188 May to the 30th of September) and 2020 (from the 1st week of February to the 1st week of September)

189 making use of two infrared heater arrays of 100 W per experimental plot (Elstein - Werk M Steinmetz

190 GmbH & Co KG, Northeim, Germany) located approximately 85 cm above the ground (see Nijs et

191 al., 1996; Kimball, 2005; Kimball et al., 2008; for a discussion on the advantages and drawbacks of

192 infrared heaters in climate change experiments). To quantify the amount of warming and the

193 temperature differences along microclimatic and macroclimatic gradients, soil temperature

194 measurements occurred hourly, from September 2019 until September 2020, with lascar temperature

195 loggers (EasyLog EL-USB-1, accuracy at -35 to +80 °C: ± 0.5 °C). The loggers were buried in each

196 plot immediately next to the oaks in the soil in a protective plastic tube at a depth of 5 cm. A linear-

197 mixed effect model with all design variables (i.e. site, forest structure, distance to the edge and

198 treatment) as fixed effects and with sensor ID as random effect, showed that the soil temperature in

199 the warming treatment was significantly elevated by 0.89 ± 0.16 °C parameter estimate and S.D., $p <$

200 0.001) compared to the control treatment (see also Figure S1; which shows, as an illustrative example,

201 of the temperatures in all experimental locations in Belgium during the first two weeks of June) and

202 that the soil moisture content decreased by 7% Moreover, on average, the air temperature in the

203 experimental locations was 0.62°C higher in simply structured forests in comparison to complex

204 forests. Also near the edge, the air temperature slightly increased although not significant but the soil

205 water content was significantly lower in edge plots compared to core plots (on average a decrease of

206 8%) (De Pauw et al., 2021).

207 Acorns were bought from the tree nursery Sylva-Van Hulle® (Belgium; www.sylva.be) and stratified

208 in a cold environment (i.e. fridge ± 4 °C) until the day of sowing. Right before sowing, the acorns

209 were hydrated in a bucket of water for two hours. Floating and damaged (e.g. visible weevil exit

210 holes) acorns were discarded. Subsequently, the acorns were weighed, placed in a container (7 cm by

211 7 cm and 15 cm deep) and covered by a thin layer of potting soil. To avoid an effect of soil conditions

212   on oak germination and growth, all acorns were sown in containers filled with the same potting soil,

213   consisting of 85% peat and 15% coconut fibre with a pH-KCl of 5-6.5. Per plot 32 containers were

214   installed, divided across two rows (**Figure S2).** Each row thus contained four acorns of the four

215   selected oak species randomly distributed along the row. In total, 1024 acorns (32 plots × 32 acorns

216   per plot) were planted for the experiment. The containers were placed in closed cages (meshes 6.4

217   mm by 6.4 mm) (see **Figure S2**) to protect the acorns against rodents. Acorns of *Q. robur* and *Q. ilex*

218   were sown in the spring of 2019 (between the end of April for the southern regions and the beginning

219   of June for the more northern regions). Acorns of *Q. cerris* and *Q. petraea* were sown one year later

220   in the winter/spring of 2020 (in February for the more southern regions and in April in the more

221   northern regions) because of germination failure for *Q. petraea* in 2019 and because no acorns of *Q.*

222   *cerris* were commercially available in 2019 in many European countries. The oak species differed in

223   provenance, similar to their original distribution area. *Quercus cerris* and *Q. ilex* came respectively

224   from Hungary and Spain whereas acorns of *Q. petraea* came from England and finally, those of *Q.*

225   *robur* had a Belgian origin. Per species, we kept the provenance uniform as it was not our intention

226   to study the effect of tree provenance on germination and seedling performance. While we are aware

227   that provenance effects can exist in trees, including more provenances was simply not feasible given

228   our study extent.

229

230   Data collection

231   Twice a year, once during the growing season and once at the end of the summer, the following

232   characteristics and traits were measured and determined to assess the germination, survival and

233   performance status of the different species.

234   To quantify germination and survival, for each container (n = 1024), we determined if a seedling was

235   present (no measurement periods in 2019 and 2 measurement periods in 2020 for *Q. cerris* and *Q.*

236   *petraea* and 2 measurements in 2019 and 2 in 2020 for *Q. robur* and *Q. ilex*). If seedlings were present

237   during the course of the experiment, the acorn was considered as germinated (germination = 1),

238   regardless of the period and of future survival. For those acorns that germinated during the

239   experiment, we subsequently also checked seedling survival at the end of the experiment

240   (August/September 2020) (survival = 1).

241   We also measured plant height (cm) of the germinated individuals using a foldable ruler. The height

242   was defined as the shortest distance between the upper boundary of the main photosynthetic tissues

243   (youngest fully expanded or expanding leaf) of the oak and the ground level (Pérez-Harguindeguy et

244   al., 2013) without stretching the plants axis. Besides the height, we also measured the diameter at root

245   collar (DRC, mm), as close to the ground as possible, using a digital caliper. At the end of the

246   experiment, we collected the largest healthy-looking leaf of each individual, avoiding leaves with

247   obvious symptoms of pathogen or herbivore attack. These leaves were dried for 48 hours at 40 °C

248   and subsequently, their dry weight was determined. All leaves were also scanned with a LI-3000C

249   Portable Area Meter in combination with a LI-3050C Transparent Belt Conveyor Accessory (LI-COR

250   Environmental, Nebraska, USA) to measure their one-sided area. The ratio of total leaf area to total

251   leaf dry mass or specific leaf area (SLA, mm^2 mg^{-1}) was calculated as a response variable. Finally, in

252   August 2020 at the end of the experiment, we also cut the whole seedling directly above the soil and

253   dried it for 48 hours at 65 °C to determine the total aboveground biomass of each individual (mg).

254   For four of our metrics (i.e. germination, survival, biomass and SLA) we thus only have one value

255   per acorn in our dataset, whereas for diameter at root collar and plant height multiple repeated

256   measurements of the different surveys were available.

257   Data analysis

258   The effect of macroclimatic and microclimatic gradients, including the warming treatment, on the

259   initial regeneration stages of the four studied oak species was modelled in R (R core Team 2020).

260   Due to the hierarchical structure of the data, we used (generalized) linear mixed-effect models and

261   the '*glmer*' function from the package '*lme4*' (Bates et al., 2015). The response variables

262   'germination' and 'survival' were modelled with a binomial distribution while DRC, SLA, plant

263   height and biomass were modelled with a Gaussian distribution. To determine the optimal model

264   structure both for random as well as fixed effects, the protocol described by Zuur et al. (2009) was

265   followed. Firstly, the optimal random structure was determined (i.e. starting from the beyond optimal

266   model). The selected random structure was a combination of (1) a single variable that combined the

267   site, forest structure and distance to the edge of the experimental plot, and (2) individual ID (i.e. the

268   specific container/acorn individual) for the repeated measurements (i.e. DRC and plant height) both

269   as random intercepts. This random structure was used for all models as it reflected the optimal

270   structure for all but one model. For germination, the optimal structure was one without random

271   effects, but for the sake of simplicity and since AIC-values did differ only 6 units, we decided to

272   select the same random structure for all models.

273   For each response variable two models were constructed. In a first model, using the data from all

274   plots and treatments, we tested the impact of the fixed effects latitude (as a continuous predictor for

275   site), forest stand structure (a factor variable with two levels: complex *vs*. simple stands), distance to

276   the edge (a factor variable with two levels: forest edge *vs*. core) and species (a factor variable with

277   four levels: *Q. ilex, Q. petraea*, *Q. robur* or *Q. cerris*) on the initial regeneration stages of oak. In a

278   second model, we used a subset of the data containing only information of the sites with an

279   experimental warming treatment (i.e. Central Italy, Belgium and Southern Sweden) and in this model,

280   we also added experimental warming (a factor variable with two levels: control *vs*. warming) to the

281   model as an additional fixed effect. Two-way interaction terms were included between all the fixed

282   effects. Moreover, the weight of the acorn was added as covariate to each model, as acorn massis

283   known to affect germination and growth (e.g. Tilki, 2010; Kormanik et al., 2011). Continuous

284   predictor variables like latitude and acorn weight were standardized to allow for a comparison of

285   model coefficients. The response variable biomass was log-transformed prior to the analyses as it

286   showed a strong right-skewed distribution. Subsequently, via a manual backward model selection

287   non-significant interactions and main effects were removed from the model. Finally, restricted

288   maximum likelihood was employed to assess the parameters and the model fit was determined as the

289   variance explained by the fixed effects (i.e. marginal R^2) and the combination of random and fixed

290   effects (i.e. conditional R^2) (Nakagawa and Schielzeth, 2013).

Results

292 Germination and survival

293 Among the 1024 acorns we sowed, 741 germinated (~ 72%) during the course of the experiment. Of

294 those, 493 seedlings (~ 66%) were still alive at the end of the experiment (**Table 1**). Strong differences

295 between species were found; almost 91% of the acorns of *Q. ilex* germinated whereas for *Q. cerris*

296 we found a germination percentage of only 52%. Approximately, 99% of the acorns of *Q. ilex* and *Q.*

297 *robur* germinated during the first year of the experiment. Higher survival rates were noted for *Q. ilex*

298 and *Q. cerris* (both ~ 85%) whereas for *Q. robur* and *Q. petraea* survival rates were ~ 41% and ~

299 72%, respectively.

300 **Table 1:** Average seedling characteristics of the oak species at the end of the experiment (August 2020) across

301 macroclimatic (i.e. latitude) and microclimatic (i.e. stand structure, distance to the edge, warming) gradients.

Species	Acorns germinated (n = 256 per species sown in total)	Seedlings surviving at the end of the experiment	Aboveground biomass (mg) (Mean ± sd)	Plant height (cm) (Mean ± sd)	Diameter at root collar (mm) (Mean ± sd)	Specific leaf area (mm² mg⁻¹) (Mean ± sd)
*Q. cerris**	134	115	466.22 ± 276.23	18.6 ± 6.9	2.40 ± 0.60	23.95 ± 5.73
Q. ilex	234	199	1056.02 ± 964.23	23.1 ± 9.4	2.66 ± 0.91	13.99 ± 3.86
*Q. petraea**	170	123	227.23 ± 163.55	13.6 ± 5.5	1.93 ± 0.49	22.96 ± 6.15
Q. robur	203	83	358.73 ± 491.01	20.6 ± 8.4	2.21 ± 0.82	25.08 ± 4.75

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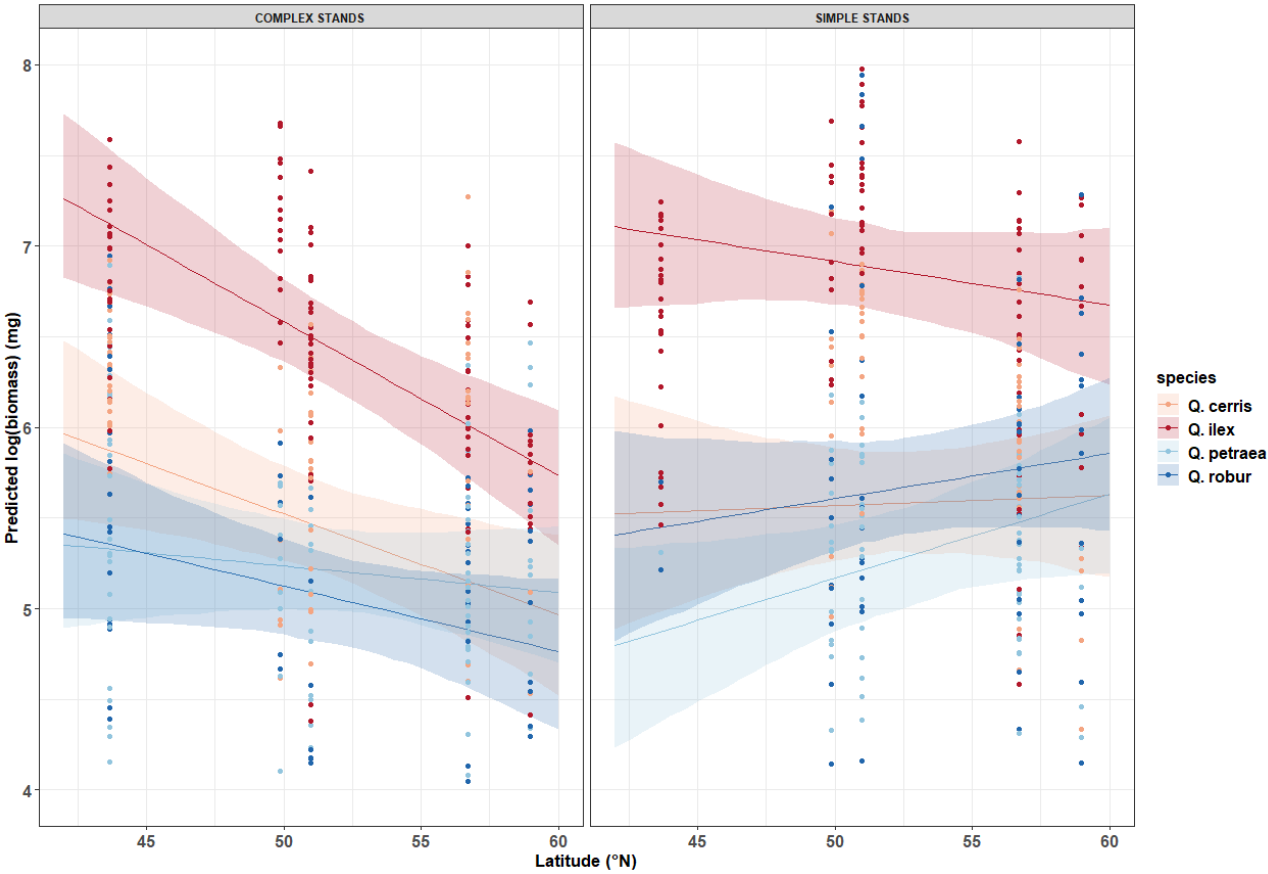303 two growing seasons.

304

305 Germination rates of heavier acorns were higher, whereas we found no effect of acorn weight on

306 survival (**Table 2**). We found significant interaction effects between latitude and species for both

307 germination and survival (**Table 2**). These interactions showed, firstly, that germination success

308 increased for *Q. cerris* and *Q. petraea* towards the north, whereas it decreased towards the north for

309 *Q. ilex* and *Q. robur*. Moreover, for survival, besides a latitude-species interaction, additional

310 interactions between both stand structure and species as well as between stand structure and latitude

311 were found (**Figure 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 (**Figure 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 (**Figure S3, Table 2**).
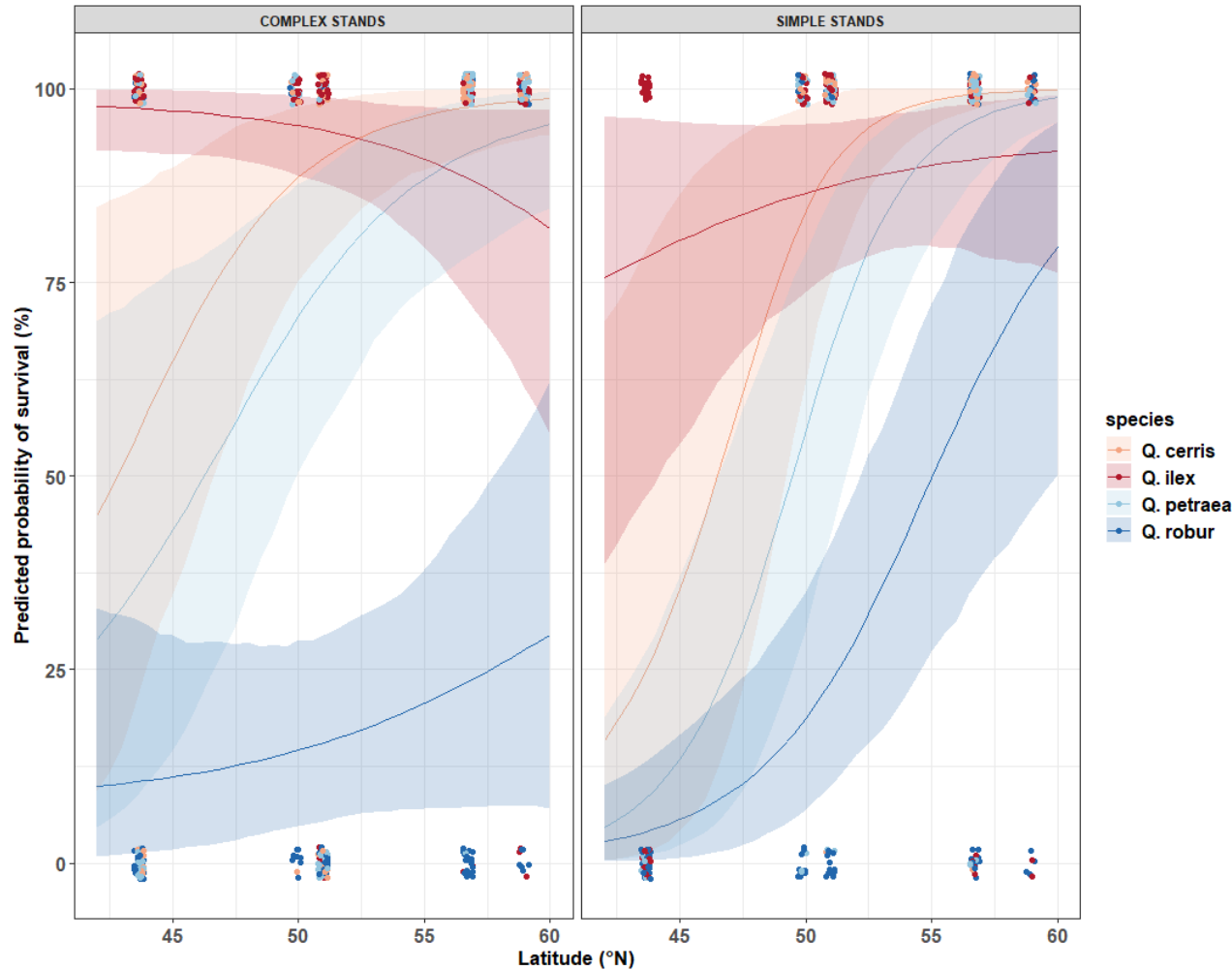
Figure 2: Predicted probabilities of survival for the four studied oak species (species are shown in different colours) as a function of latitude (°N) for two forest types (left: complex forests; right: simply structured forest). The dots represent the raw data points (with 0 = no survival and 100 = survival) and the shaded areas show the 95% prediction intervals. A small amount of jittering was added to the raw data points along the x and y-axis to improve clarity.

Seedling performance

In general, we found a 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 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, Figure 3**).

Figure 3: Predicted biomass (log-transformed) of the 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 the raw data points and the shaded areas the 95% prediction intervals.

Table 2: The impact of macroclimate (i.e. latitude), microclimate (i.e. forest structure and distance to the edge), species and their interaction effects, as well as the impact of acorn weight, on the germination, survival and characteristics of oak seedlings. Complex forests, forest cores, and *Q. ilex* were used as the reference forest structure, reference distance to the edge and reference species for the model intercept parameter. The direction of the effect size is depicted by an arrow (i.e. 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 the significance of the 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**.

	Germination	Survival	Aboveground biomass (mg, log-transformed)	Plant height (cm)	Diameter at root collar (cm)	Specific leaf area (mm² mg⁻¹)
Latitude (°N)	↓	↓	↓***	↓***	↓	↑
Forest structure (simple compared to complex)		↓	↑**		↑	↓**
Edge-to-core gradient (edge plot compared to interior)	↓*				↑	
Q. cerris	↓***	↓	↓***	↓***	↓***	↑***
Q. petraea	↓***	↓***	↓***	↓***	↓***	↑***
Q. robur	↓***	↓***	↓***	↓	↓***	↑***
Acorn weight (mg)	↑*		↑***	↑***	↑***	
Lat : Simple structure		↑*	↑*		↑	
Lat : *Q. cerris*	↑*	↑***	↑	↑***	↑*	↑
Lat : *Q. petraea*	↑**	↑***	↑***	↑***	↑***	↓*
Lat : *Q. robur*	↑	↑**	↑**	↑***	↑***	↓
Simple structure : *Q. cerris*		↑	↓		↑	
Simple structure: *Q. petraea*		↑	↓*		↓*	
Simple structure: *Q. robur*		↑*	↑		↓	
Edge plot : *Q. cerris*					↓*	
Edge plot: *Q. petraea*					↓	
Edge plot: *Q. robur*					↑	
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

344 For DRC and plant height, we again found strong and significant interaction terms between species

345 and latitude: *Q. ilex* seedlings had a lower DRC and plant height in northern regions, whereas for the

346 other oaks, DRC and plant height increased towards the north (**Table 2**). We also found interactions

347 for DRC between species and microclimate, both in terms of stand structure and distance to the edge.

348 The diameter was generally higher near the edge, except for *Q. cerris*, and generally higher in simple

349 forest stands, except for *Q. petraea* (**Figure 4a, Table 2**).

350 Seedlings of *Q. ilex* had the lowest SLA. Though, again species reacted differently along the

351 latitudinal gradient. For most species, we found an increase in SLA towards higher latitudes, except

352 for *Q. petraea* seedlings which decreased their SLA towards the north. Moreover, for all species the

353 SLA was lower in simply structured forests (**Figure 4b, Table 2**).

354 Simulating climate warming by warming the air temperature, did not affect SLA or DRC in our

355 experiment. If treatment was included in the models for plant height and biomass, we did however

356 find a significant interaction between warming and species. This interaction indicated that the height

357 and biomass of *Q. robur* were reduced under warming whereas the seedlings of *Q. ilex* and *Q. cerris*

358 grew taller and had more biomass in comparison to the control plots (**Table S2**).
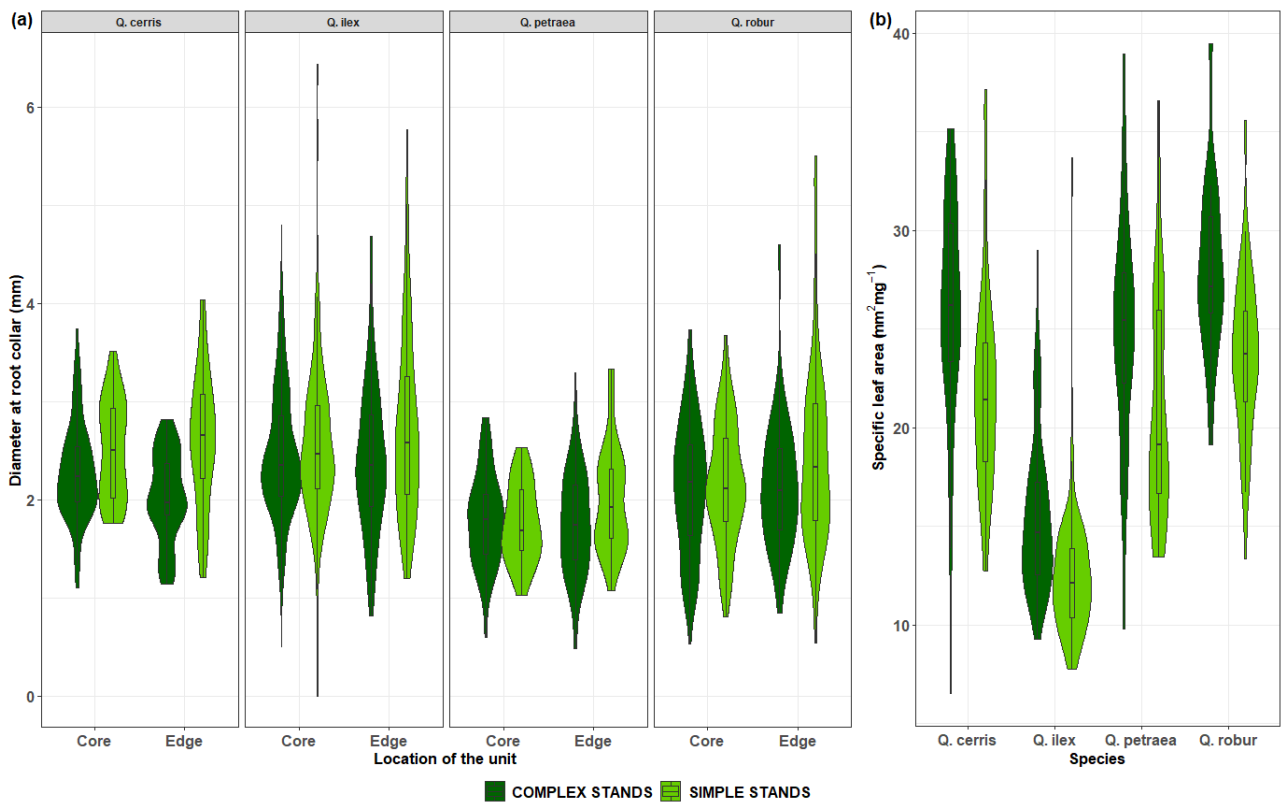
359

Figure 4: (a) Violin plots of the root collar diameter (mm) of the different oak species (shown in the subpanels) across the microclimatic gradients formed by stand structure (complex *vs*. simple forest stands, visualized by dark and light green colours, respectively) and the distance to the edge of the experimental plot (in the core *vs*. at the edge of the forest). Boxes show the median and interquartile range. (b) Violin plot of the impact of stand structure, represented again by dark and light green hues, on the specific leaf area ($mm^2 mg^{-1}$) for the oak species.

365

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 microclimatic conditions and light availability 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 to all species we studied. Forest edges are characterized by a different structure (i.e. higher stem density; Meeussen et al., 2020), altered microclimatic conditions (i.e. warmer and drier; Chen et al., 1995; Davies-Colley et al., 2000; Meeussen et al., 2021), higher nutrient depositions (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 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). A reduced emergence in the forest interior could be related to a stronger shading by canopy trees and therefore especially shade-intolerant species could have a 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 might thus explain the high germination rate in the forest interior as well. Moreover, after already a few dry years, the spring and/or summer of 2019 and 2020 were very dry as well in all regions

391   (Barbosa et al., 2020) and since our forest edges were characterized by a lower soil moisture content

392   (De Pauw et al., 2021), these drought effects might cause a higher germination in the forest interior.

393   Also, the latitude-species interaction found for germination, whereby we found that *Q. robur*

394   germinated better in the south and *Q. cerris* in the north, is rather counterintuitive as the former has

395   a more southern distribution range than the latter. We speculate that these patterns are related to the

396   fact that these species were planted in 2020, whereas *Q. ilex* and *Q. robur* were planted in 2019 and

397   show as expected more a higher germination in the south and north respectively. The trends thus,

398   although not conclusive, might reflect annual variation in weather conditions rather than species-

399   specific germination trends. Moreover, germination and growth during the first year, as discussed

400   above, might be strongly impacted by the nutrients present in the acorn.

401   For survival, we found an increased probability to persist towards colder macroclimates, except for

402   *Q. ilex* in complex forests. A lower survival rate in warm regions might be related to drought stress

403   and this especially for *Q. robur* and *Q. petraea* as our most southern region was approximately located

404   at the warm range margin of these species (Urli et al., 2014; Eaton et al., 2016). Moreover, the survival

405   rate of *Q. ilex,* a species with a high tolerance to drought (Lobo et al., 2018), was not lower in southern

406   regions and even increased towards the south in complex forest stands. In general, the survival in

407   southern regions was also higher in complex forests, whereas in the north we found higher survival

408   rates in simply structured forests. This might reflect the importance of the buffering effect of dense

409   forests in warm environments, creating less environmental stress due to more humid and cooler

410   conditions in complex forests (De Frenne et al., 2019; Zellweger et al., 2019; Meeussen et al., 2021),

411   and thus protecting young seedlings from withering (Aussenac, 2000; Badano et al., 2015). Whereas

412   in cold environments, simply structured forests provide a warmer and brighter environment, as was

413   also the case in our experiment (see also De Pauw et al., 2021). Finally, the overall high mortality

414   rates of *Q. robur* might be related to its susceptibility to oak powdery mildew (Marçais and Desprez-

415   Loustau, 2014) which we also observed in our study.

416   Performance

417 Towards colder macroclimates, both plant height and diameter at root collar (DRC) increased, except

418 for *Q. ilex* which performed better in warmer macroclimates. We suggest that this species-latitude

419 interaction might be caused by the temperature and drought tolerance of the different oak seedlings

420 along the gradient. Under dry circumstances, temperate species are more likely to invest in their root

421 biomass instead of aboveground biomass (i.e. expressed here as plant height and stem diameter) (Van

422 Hees, 1997). Indeed, along the latitudinal gradient, we also detected an interaction between species

423 identity and macroclimate for aboveground biomass; seedlings from the two Mediterranean oak

424 species had a higher biomass in southern regions. Though, along the macroclimatic gradient, also the

425 forest structure interactively affected the biomass: a simple forest structure led to a higher biomass

426 for oak seedlings. But this was especially the case for northern regions, as in the south we found a

427 higher biomass in complex stands in comparison to simple stands (except for *Q. petraea*). Also, DRC

428 was affected by the vegetation structure with a higher DRC in simple stands (except for *Q. petraea*)

429 and near edges (except for *Q. cerris*). These trends are all probably related to enhanced microclimatic

430 growing conditions (i.e. trade of between water availability and warmth) and light availability in open,

431 simply structured forest patches or near edges. Previous studies already found a higher growth,

432 biomass and height near forest edges or under increased light intensities (Meiners et al., 2002; Lhotka

433 and Stringer, 2013; Sevillano et al., 2016). Microclimatic conditions and light availability in simply

434 structured forests or near forest edges might also be more representative of those of traditional

435 management practices leading to semi-open woody landscapes, which are known to have enhanced

436 *Quercus* reproduction in the past over more shade-tolerant species (Watt, 1919; Bobiec et al., 2018).

437 Moreover, the positive effect of a low canopy cover might also favour the survival and growth of

438 oaks affected by mildew, which was the case for many seedlings in our experiment. The fungus tends

439 to reduce the shade and drought-tolerance of seedlings and therefore has the potential to reduce the

440 regeneration capacity of oaks in forest environments (Lonsdale, 2015; Bobiec et al., 2018; Demeter

441 et al., 2021).

442 Finally, SLA values were lower in simply structured forests and at low latitudes (except for *Q. petraea*

443 for which the SLA slightly decreased towards the north). Also, significantly lower SLA values for *Q.*

444 *ilex* were expected since this species is adapted to dry Mediterranean climates and characterized by

445 small, thick and coriaceous leaves, allowing the tree to reduce its transpiration rate (de Rigo and

446 Caudullo, 2016). Traits such as SLA, besides resembling a different ecological strategy, are not only

447 influenced by global but also by local environmental factors (Wright et al., 2004; De Pauw et al.,

448 2021; Govaert et al., 2021). So, higher SLA values in complex forests might be a reaction to lower

449 light intensity as plants growing in shade need to have larger leaves to capture sufficient light for their

450 photosynthesis (Sevillano et al., 2016; Buajan et al., 2017). Besides, a lower SLA value in southern

451 regions might be a mechanism to reduce water stress as a response to a higher vapor pressure deficit.

452 *Experimental warming and transplant experiment beyond range limits*

453 In warm and dry climates, the Mediterranean species *Q. ilex* and *Q. cerris* clearly performed better

454 with a higher biomass and height, and higher survival rates. Moreover, even when being transplanted

455 beyond their coldest range limits, both species still performed well and their survival rates remained

456 high (especially for *Q. ilex*). *Quercus ilex* was able to maintain the highest biomass and DRC, even

457 in our Swedish plots. However, one must keep in mind that *Q. cerris* and *Q. petraea* were only

458 monitored for one growing season and were not exposed to winter conditions along the gradient. Frost

459 is known to affect seedling performance and survival, and might limit species distribution at the

460 northern range margin (Bianchi et al., 2019; Hofmann et al., 2014). Survival and performance results

461 of those latter two species could thus be strongly altered if we would have studied them during two

462 consecutive growing seasons. Besides frost, latitudinal patterns might also be caused by other species-

463 specific drivers such as phenological differences, the light quality and quantity, drought or herbivory

464 patterns along the gradients (Ducousso et al., 1996; Collet et al., 1998; Sevillano et al., 2016; Moreira

465 et al., 2021).

466 Rather unexpectedly, we only found a limited impact of our experimental warming treatment on the

467 germination, survival and performance of our four studied oak species. More specifically, we found

468   a negative effect on plant height and biomass for *Q. robur*, whereas this effect was positive for both

469   *Q. cerris* and *Q. ilex*. *Quercus robur* is generally known as less shade tolerant than *Q. cerris* and *Q.*

470   *petraea* (Leuschner and Meier, 2018) and might thus better regenerate in open conditions, as it was

471   demonstrated in previous research (Demeter et al., 2021). Consistently, in the northern regions, we

472   found a strong increase in the survival rate of *Q. robur* in simple and relatively more open forests in

473   comparison with more complex and darker forests. This species thus requires sufficient light to grow

474   but might also be more sensitive to heat and drought compared to the other tree species. The

475   Mediterranean species, on the other hand, are better adapted to heat and drought (such as via their

476   leaf characteristics or their provenance; de Rigo and Caudullo, 2016; Bert et al., 2020) and therefore

477   could benefit from the additional warmth, especially at locations beyond their northern edge.

478   Moreover, stronger effects might be expected if the degree of warming would be higher and for long-

479   term warming experiments since the seedlings could also experience time-lags in response to the

480   warming treatment (Bertrand et al., 2011; De Pauw et al., 2021). Therefore, in our rather short-term

481   experiment, other drivers such as the nutrient available in the acorn and the microclimate, could have

482   had a stronger impact on the observed patterns than the warming treatment. Differences in

483   microclimate due to vegetation characteristics were on average approximately of the same magnitude

484   than the observed temperature increase under the warming treatment (De Pauw et al., 2021).

485   Even though we did not find a strong impact of the warming treatment, climate change still could

486   strongly affect natural tree regeneration at a local scale as we found significant impacts of the

487   macroclimate itself as well as more complex macroclimate-microclimate (i.e. via forest structure and

488   edge distance) interactions. The latter stress the importance of local microclimate buffering and

489   thoughtful forest management to limit the impact of rising temperatures in the understorey of forest

490   interiors.

491   Potential management implications

492   Successful natural oak regeneration is complex and largely context dependent. Both species identity

493   and macroclimate determine the outcome, while microclimate conditions and management

494 interventions may locally alter these influences on initial oak regeneration. Moreover, conditions

495 enhancing or limiting acorn germination, differ from those for survival, growth or biomass

496 accumulation. And these conditions might differ in turn from the growth requirements in later

497 growing stages or those of adult trees (Morin et al., 2007; Annighöfer et al., 2015; Leuschner and

498 Meier, 2018). Therefore, successful regeneration requires constant as well as species and location

499 specific monitoring and forehanded management interventions to control the local climate and light

500 availability and herewith the initial regeneration success.

501 We suggest that light is key for the initial stages of regeneration and establishment of oaks (see also

502 e.g. Théry, 2001; Sevillano et al., 2016). Previous studies showed that neither fully exposed sites or

503 light limited sites led to a successful regeneration for oaks (Puerta-Piñero et al., 2007; Bobiec et al.,

504 2018). Simply structured forests, forest edges or natural and human-induced canopy gaps, might

505 provide an important regeneration niche for oak species thanks to warmer microclimate conditions

506 and more light availability in the understorey (Aussenac, 2000; Davies-Colley et al., 2000; Meeussen

507 et al., 2021). However, optimal light conditions for oak regeneration will depend on the focal species

508 and will require management interventions as the forest-floor microclimate will be influenced by both

509 the macroclimate and the local forest structure (Aussenac, 2000; De Frenne et al., 2019; Meeussen et

510 al., 2021). The detected macroclimate-forest structure interactions, as found for biomass and survival,

511 showed that such trade-offs in microclimatic requirements exist along the studied latitudinal gradient.

512 An increased light availability (and subsequently forest-floor temperature) might benefit the initial

513 regeneration stages and seedling performance in northern regions whereas in southern regions

514 managers might want to keep forest stands dense and closed to improve moisture conditions and avoid

515 a detrimental impact of drought on the growth and survival of oak seedlings.

516 In this experiment, we unfortunately only had the opportunity to test the initial regeneration responses

517 of four ecological and economically important European oaks. It would be very interesting to include

518 a more ecologically and phylogenetically diverse set of oak species in further research. Furthermore,

519 performance of the four study 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 and 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 the differences within and between provenances and species.

Data availability statement

Upon acceptance data will be made available.

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