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Camille Meeussen, Karen de Pauw, Pieter Sanczuk, Jörg Brunet, Sara A.O. Cousins, Cristina Gasperini, Per-Ola Hedwall, Giovanni Iacopetti, Jonathan Roger Michel Henri Lenoir, Jan Plue, et al.

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**Initial oak regeneration responses to experimental warming  
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# 1 Initial oak regeneration responses to 2 experimental warming along 3 microclimatic and macroclimatic 4 gradients

5 Running title: Oak regeneration along climatic gradients.

6

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22 Keywords

23 Climate change, Edge influence, Forest structure, Temperate deciduous forests, Transplant  
24 experiment, *Quercus*

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## 25 Abstract

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

## 48 Introduction

49 Oaks (*Quercus* spp.) are one of the largest tree genera worldwide with over 450 different species  
50 across the Northern hemisphere (Jones, 1974; Nixon, 2006; Gil-Pelegrín et al., 2017). They are one  
51 of the most important tree genera both in forests and agricultural landscapes across Europe (Eaton et  
52 al., 2016; Mitchell et al., 2019). Oaks are not only one of the most abundant tree species in many  
53 temperate deciduous forests, they also contribute to numerous ecosystem services such as wood  
54 production, are key species for biodiversity conservation and are of high cultural value (Eaton et al.,  
55 2016; Mitchell et al., 2019; Mölder et al., 2019).

56 Both the economic (Hanewinkel et al., 2013) as well as the ecological and cultural value associated  
57 with oak forests are under pressure due to climate change and other forest disturbances, such as pests  
58 and pathogens (Thomas et al., 2002; Mitchell et al., 2019). For instance, defoliation of *Quercus robur*  
59 and *Q. petraea* has been shown to significantly increase over time, predominantly as a result of  
60 drought impacts (Sousa-Silva et al., 2018) sometimes followed by pathogen outbreaks such as the  
61 processionary moth or vice versa (Tomlinson et al., 2015; Godefroid et al., 2019). The combined  
62 impact of both abiotic (i.e. extreme weather conditions) and biotic (e.g. insect defoliators) stressors  
63 have subsequently triggered increasing incidences of oak decline across Europe (Thomas et al., 2002).  
64 Moreover, the long-term persistence of these keystone species remains uncertain as also natural  
65 regeneration is impacted. Already more than 100 years ago, Watt (1919) wrote on the causes of failure  
66 of natural regeneration of oak and since then alarming signals have been noticed across Europe (e.g.  
67 Palmer et al., 2004; Petritan et al., 2013). Neither open nor shaded habitats such as closed forests are  
68 optimal for oak regeneration (Bobiec et al., 2018). Besides issues with pathogens, predators, browsers  
69 and insects, successful oak regeneration depends on a specific set of abiotic conditions (Annighöfer  
70 et al., 2015; Kamler et al., 2016). Due to management changes many of the traditional semi-open  
71 wooded landscapes have disappeared (Vera, 2000). Oak seedlings are generally more abundant in  
72 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 local microclimate (i.e. local climatic conditions shaped by the  
84 surrounding vegetation and topography; Geiger et al., 2009). Local microclimatic gradients can, for  
85 instance, occur near forest edges, where temperature decreases and humidity increases towards the  
86 forest core (Schmidt et al., 2019; Meeussen et al., 2021). Likewise, forest management interventions  
87 that lead to reductions in canopy cover such as thinning can create an increase in light and temperature  
88 at the forest floor (Kovács et al., 2017; Zellweger et al., 2019; Meeussen et al., 2021). Via the  
89 temperature buffering effect of the canopy, microclimatic conditions near the forest floor are  
90 stabilized (De Frenne et al., 2013), which might facilitate regeneration of oaks and protect seedlings  
91 against extreme temperatures and drought. To better understand natural oak regeneration, more  
92 research is necessary to figure out how local and large-scale climatic gradients interact and determine  
93 the regeneration success of different oak species in a warming world. Also, warming experiments in  
94 the field can be very useful to test oak recruitment under future temperature scenarios in alternative  
95 macroclimatic and microclimatic contexts. However, no single experiment to date performed such an  
96 in-situ warming experiment of oaks in different forest types and along edge-to-core gradients across  
97 Europe.

98 Knowledge on the preferred set of abiotic conditions might, however, not be enough to enhance  
99 natural regeneration of oaks in a warming world. Many tree species might not be able to adapt or

100 migrate as fast as the shifting environmental conditions (Svenning and Skov, 2004; Lenoir et al.,  
101 2008), leading to time-lag dynamics and therefore putting pressure on future forest resilience,  
102 biodiversity and ecosystem services (Iverson et al., 2004; Bertrand et al., 2011). Besides providing  
103 management guidelines regarding the preservation of local microclimatic conditions, a potential  
104 solution could thus be to translocate species to climatically more suitable locations to help them track  
105 the shifting isotherms (i.e. assisted migration, Leech et al., 2011). Both in-situ warming experiments  
106 as well as translocation experiments beyond the actual range margins, which are both currently  
107 lacking for many tree species (Saxe et al., 2001), can get us valuable insights on how species perform  
108 outside their natural range and help conserve important species and forest functions threatened by  
109 climate change (Gaston, 2003; Lee-Yaw et al., 2016).

110 Here we investigated the germination, survival and seedling performance (the latter quantified as  
111 aboveground biomass, height, root collar diameter and specific leaf area) of four economically and  
112 ecologically important oak species: *Q. cerris*, *Q. ilex*, *Q. petraea* and *Q. robur*. In total, 1024 acorns  
113 were sown, distributed across five sites along a c. 2000 km broad latitudinal gradient from Italy to  
114 Sweden. Along the latitudinal gradient with varying macroclimate, seedlings were subject to varying  
115 microclimatic conditions determined by more local factors including forest management and distance  
116 to the forest edge. We finally also experimentally manipulated microclimates by means of a warming  
117 treatment to test how experimental warming affected the initial stages of natural regeneration of the  
118 different species. We hypothesized to find different germination, survival and performance signals of  
119 the four species along our macro- and microclimatic gradients; we expected that the southern species  
120 *Q. ilex* and *Q. cerris* performed better in warmer environments (both micro- and macroclimates),  
121 whereas the northern species *Q. robur* and *Q. petraea* benefitted from locally buffered (cooler)  
122 microclimatic conditions, especially in the more southern regions, such as can be found in the forest  
123 interior or in complex forests.

124



## 125 Material and Methods

### 126 Study species

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

### 146 Study design

147 We included both macroclimatic and microclimatic gradients, as well as experimental warming  
148 replicated along each of the macroclimatic and microclimatic gradients, in our study. To be able to  
149 study the effect of macroclimatic variation on initial oak regeneration, we planted acorns of the four  
150 studied species along a 1,800 km wide latitudinal gradient (i.e. temperature difference of 8.2°C,

151 CHELSA, Karger et al., 2017, **Table S1**) crossing the temperate forest biome in Europe. Along this  
152 south-north gradient, five experimental sites were selected in deciduous forests: Florence in Central  
153 Italy, Amiens in Northern France, Ghent in Belgium, Halmstad in Southern Sweden and Stockholm  
154 in Central Sweden (**Figure 1a**). The tree layer in most experimental sites was dominated by *Q. robur*  
155 or *Q. petraea*, but with diverse species co-occurring in the different sites (**Table S1**).

156 In all five sites, four experimental locations were established: we included variation in forest  
157 structure and distance to the forest edge to be able to study the effect of the local microclimate  
158 (i.e. sub-canopy gradients in light, humidity and temperature) on the initial regeneration stages  
159 of oak (**Figure 1b**). Two forest stands were selected with a different forest structure as  
160 differences in vegetation structure will affect the forest microclimate (Frey et al., 2016;  
161 Kovács et al., 2017; Meeussen et al., 2021). The first stand, hereafter referred to as ‘complex  
162 forest’, was always a vertically dense and multi-layered forest stand with a well-developed  
163 shrub layer in the understorey (i.e. at least more than 15%) and a closed upper canopy layer  
164 (canopy cover above 90%). A second stand type represented a ‘simple forest’ which was  
165 composed only of a single tree layer, had a higher canopy openness (canopy cover below  
166 70%) and no or few shrubs in the understorey (i.e. a maximum shrub cover of 45%).  
167 Moreover, in each of these stands, two plots were established (n = 20 plots across the five  
168 sites), forming a second microclimatic gradient determined by distance to the edge (Meeussen  
169 et al., 2021). The centre of the first plot was located at a distance of roughly 2-5 m from the  
170 edge whereas the second plot lied at least 50-100 m towards the core of the forest patch. The  
171 studied edges were all bordered by a matrix of agricultural land and were approximately  
172 south-oriented, as edge orientation due to the impact of direct radiation, is known to affect the  
173 microclimate and edge width (Chen et al., 1995; Matlack, 1993). Further details on the study  
174 design, forest structure and site selection are available in De Pauw et al. (2021) and in **Table**  
175 **S1**.

176 In three sites, i.e. Southern Sweden, Belgium and Central Italy, an experimental warming treatment  
177 was installed (for feasibility reasons, this was not possible at the other two sites). We therefore  
178 doubled the number of plots present at those three locations. This led to a total of 32 plots (i.e. five  
179 sites with four plots per site, among which three sites had an additional set of four plots with  
180 experimental warming: 20 plots for control vs. 12 plots for warming treatment). The warming  
181 treatment was applied both day and night during the growing seasons of 2019 (from installation in  
182 May to the 30<sup>th</sup> of September) and 2020 (from the 1<sup>st</sup> week of February to the 1<sup>st</sup> week of September)  
183 making use of two infrared heater arrays of 100 W per experimental plot (Elstein - Werk M Steinmetz  
184 GmbH & Co KG, Northeim, Germany) located approximately 85 cm above the ground (see Nijs et  
185 al., 1996; Kimball, 2005; Kimball et al., 2008; for a discussion on the advantages and drawbacks of  
186 infrared heaters in climate change experiments). To quantify the amount of warming and the  
187 temperature differences along microclimatic and macroclimatic gradients, soil temperature  
188 measurements occurred hourly, from September 2019 until September 2020, with lascar temperature  
189 loggers (EasyLog EL-USB-1, accuracy at -35 to +80 °C:  $\pm 0.5$  °C). The loggers were buried in each  
190 plot immediately next to the oaks in the soil in a protective plastic tube at a depth of 5 cm. A linear-  
191 mixed effect model with all design variables (i.e. site, forest structure, distance to the edge and  
192 treatment) as fixed effects and with sensor ID as random effect, showed that the soil temperature in  
193 the warming treatment was significantly elevated by  $0.89 \pm 0.16$  °C parameter estimate and S.D.,  $p <$   
194  $0.001$ ) compared to the control treatment. Moreover, on average, the air temperature in the  
195 experimental locations was  $0.62$ °C higher in simply structured forests in comparison to complex  
196 forests, also near the edge the air temperature slightly increased although not significant but the soil  
197 water content was significantly lower in edge plots compared to core plots (on average a decrease of  
198 8%) (De Pauw et al., 2021).

199 Acorns were bought from the tree nursery Sylva-Van Hulle® (Belgium; [www.sylva.be](http://www.sylva.be)) and stratified  
200 in a cold environment (i.e. fridge  $\pm 4$  °C) until the day of sowing. Right before sowing, the acorns  
201 were hydrated in a bucket of water for two hours. Floating and damaged (e.g. visible weevil exit

202 holes) acorns were discarded. Subsequently, the acorns were weighed, placed in a container (7 cm by  
203 7 cm and 15 cm deep) and covered by a thin layer of potting soil. To avoid an effect of soil conditions  
204 on oak germination and growth, all acorns were sown in containers filled with the same potting soil,  
205 consisting of 85% peat and 15% coconut fibre with a pH-KCl of 5-6.5. Per plot 32 containers were  
206 installed, divided across two rows (**Figure S1**). Each row thus contained four acorns of the four  
207 selected oak species randomly distributed along the row. In total, 1024 acorns (32 plots  $\times$  32 acorns  
208 per plot) were planted for the experiment. The containers were placed in closed cages (meshes 6.4  
209 mm by 6.4 mm) (see **Figure S1**) to protect the acorns against rodents. Acorns of *Q. robur* and *Q. ilex*  
210 were sown in the spring of 2019, whereas acorns of *Q. cerris* and *Q. petraea* were sown one year  
211 later in the spring of 2020 because of germination failure for *Q. petraea* in 2019 and because no  
212 acorns of *Q. cerris* were commercially available in 2019 in many European countries. The oak species  
213 differed in provenance, similar to their original distribution area. *Quercus cerris* and *Q. ilex* came  
214 respectively from Hungary and Spain whereas acorns of *Q. petraea* came from England and finally,  
215 those of *Q. robur* had a Belgian origin. Per species, we kept the provenance uniform as it was not our  
216 intention to study the effect of tree provenance on germination and seedling performance. While we  
217 are aware that provenance effects can exist in trees, including more provenances was simply not  
218 feasible given our study extent.

219

#### 220 Data collection

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

224 To quantify germination and survival, for each container (n = 1024), we determined if a seedling was  
225 present (no measurement periods in 2019 and 2 measurement periods in 2020 for *Q. cerris* and *Q.*  
226 *petraea* and 2 measurements in 2019 and 2 in 2020 for *Q. robur* and *Q. ilex*). If seedlings were present  
227 during the course of the experiment, the acorn was considered as germinated (germination = 1),

228 regardless of the period and of future survival. For those acorns that germinated during the  
229 experiment, we subsequently also checked seedling survival at the end of the experiment  
230 (August/September 2020) (survival = 1).

231 Moreover, at each survey, we measured plant height (cm) of the germinated individuals using a  
232 foldable ruler. The height was defined as the shortest distance between the upper boundary of the  
233 main photosynthetic tissues (youngest fully expanded or expanding leaf) of the oak and the ground  
234 level (Pérez-Harguindeguy et al., 2013) without stretching the plants axis. Besides the height, we also  
235 measured the diameter at root collar (DRC, mm), as close to the ground as possible, using a digital  
236 caliper. At the end of the experiment, we collected the largest healthy-looking leaf of each individual,  
237 avoiding leaves with obvious symptoms of pathogen or herbivore attack. These leaves were dried for  
238 48 hours at 40 °C and subsequently, their dry weight was determined. All leaves were also scanned  
239 with a LI-3000C Portable Area Meter in combination with a LI-3050C Transparent Belt Conveyor  
240 Accessory (LI-COR Environmental, Nebraska, USA) to measure their one-sided area. The ratio of  
241 total leaf area to total leaf dry mass or specific leaf area (SLA, mm<sup>2</sup> mg<sup>-1</sup>) was calculated as a response  
242 variable. Finally, in August 2020 at the end of the experiment, we also cut the whole seedling directly  
243 above the soil and dried it for 48 hours at 65 °C to determine the total aboveground biomass of each  
244 individual (mg).

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

#### 248 Data analysis

249 The effect of macroclimatic and microclimatic gradients, including the warming treatment, on the  
250 initial regeneration stages of the four studied oak species was modelled in R (R core Team 2020).  
251 Due to the hierarchical structure of the data, we used (generalized) linear mixed-effect models and  
252 the ‘*glmer*’ function from the package ‘*lme4*’ (Bates et al., 2015). The response variables  
253 ‘germination’ and ‘survival’ were modelled with a binomial distribution while DRC, SLA, plant

254 height and biomass were modelled with a Gaussian distribution. To determine the optimal model  
255 structure both for random as well as fixed effects, the protocol described by Zuur et al. (2009) was  
256 followed. Firstly, the optimal random structure was determined (i.e. the beyond optimal model). The  
257 selected random structure was a combination of (1) a single variable that combined the site, forest  
258 structure and distance to the edge of the experimental plot, and (2) individual ID (i.e. the specific  
259 container/acorn individual) for the repeated measurements (i.e. DRC and plant height) both as random  
260 intercepts. This random structure was used for all models as it reflected the optimal structure for all  
261 but one model. For germination, the optimal structure was one without random effects, but for the  
262 sake of simplicity and since AIC-values did differ only 6 units, we decided to select the same random  
263 structure for all models.

264 For each response variable two models were constructed. In a first model, latitude (as a continuous  
265 predictor for site), forest stand structure (a factor variable with two levels: complex vs. simple stands),  
266 distance to the edge (a factor variable with two levels: forest edge vs. core) and species (a factor  
267 variable with four levels: *Q. ilex*, *Q. petraea*, *Q. robur* or *Q. cerris*) were included as fixed effects. In  
268 a second model, we used a subset of the data containing only information of the sites with an  
269 experimental warming treatment (i.e. Central Italy, Belgium and Southern Sweden) and in this model,  
270 we also added experimental warming (a factor variable with two levels: control vs. warming) to the  
271 model as an additional fixed effect. Two-way interaction terms were included between all the fixed  
272 effects. Moreover, the initial weight of the acorn was added as covariate to each model, as acorn size  
273 is known to affect germination and growth (e.g. Tilki, 2010; Kormanik et al., 2011). Continuous  
274 predictor variables like latitude and acorn weight were standardized to allow for a comparison of  
275 model coefficients. The response variable biomass was log-transformed prior to the analyses as it  
276 showed a strong right-skewed distribution. Subsequently, via a manual backward model selection  
277 non-significant interactions and main effects were removed from the model. Finally, restricted  
278 maximum likelihood was employed to assess the parameters and the model fit was determined as the

279 variance explained by the fixed effects (i.e. marginal  $R^2$ ) and the combination of random and fixed  
280 effects (i.e. conditional  $R^2$ ) (Nakagawa and Schielzeth, 2013).

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## 281 Results

### 282 Germination and survival

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

289 Germination rates of heavier acorns were higher, whereas we found no effect of acorn weight on  
290 survival (**Table 2**). We found significant interaction effects between latitude and species for both  
291 germination and survival (**Table 2**). These interactions showed, firstly, that germination success  
292 increased for *Q. cerris* and *Q. petraea* towards the north, whereas it decreased towards the north for  
293 *Q. ilex* and *Q. robur*. Moreover, for survival, besides a latitude-species interaction, additional  
294 interactions between both stand structure and species as well as between stand structure and latitude  
295 were found (**Figure 2, Table 2**). These indicated that complex forests in comparison to open forests  
296 favoured the survival of seedlings in warmer regions. In simply structured stands survival strongly  
297 increased towards colder regions for *Q. cerris*, *Q. petraea* and *Q. robur* whereas there was only a  
298 weak increase for *Q. ilex*. In complex stands, however, the increase in survival for *Q. robur* towards  
299 northern regions was weaker and we even found a decrease in survival of *Q. ilex* seedlings towards  
300 northern regions (**Figure 2, Table 2**). We did not find an additional impact or interaction effect of  
301 the warming treatment on the survival rate of the seedlings, and neither on the germination success  
302 of the acorns. Acorn germination was however higher in the forest core (**Figure S2, Table 2**).

### 303 Seedling performance

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



307 interaction between stand structure and latitude on the biomass and there was a type-species  
308 interaction; in general biomass was higher in simple forests, except for *Q. petraea*, but in southern  
309 regions seedling biomass was higher in complex forest stands, whereas in northern regions seedling  
310 biomass was higher in simple forest stands (**Table 2, Figure 3**).

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

317 Seedlings of *Q. ilex* had the lowest SLA. Though, again species reacted differently along the  
318 latitudinal gradient. For most species, we found an increase in SLA towards higher latitudes, except  
319 for *Q. petraea* seedlings which decreased their SLA towards the north. Moreover, for all species the  
320 SLA was lower in simply structured forests (**Figure 4b, Table 2**).

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

## 326 Discussion

327 We found that macroclimate (i.e. latitude) and species identity had a strong interactive effect on the  
328 germination success, survival rate and performance level of oak seedlings. However, also  
329 microclimatic conditions and light availability had an important impact on the initial stages of oak  
330 regeneration with the direction of the effect often depending on the studied species. In general,  
331 experimental warming did not significantly alter oak recruitment, except for a positive effect on plant  
332 height and biomass for *Q. ilex* and *Q. cerris* and a negative effect on plant height and biomass for *Q.*  
333 *robur*.

### 334 Germination and survival

335 Seedling germination was higher in the forest interior in comparison to the edge and this was valid  
336 across the whole latitudinal gradient as well as to all species we studied. Forest edges are  
337 characterized by a different structure (i.e. higher stem density; Meeussen et al., 2020), altered  
338 microclimatic conditions (i.e. warmer and drier; Chen et al., 1995; Davies-Colley et al., 2000;  
339 Meeussen et al., 2021), higher nutrient depositions (De Schrijver et al., 2007; Wuyts et al., 2008) and  
340 a different understorey plant, animal and soil microbiota community composition (e.g. De Smedt et  
341 al., 2019; Govaert et al., 2020) which can all affect the regeneration and establishment of tree species  
342 (Meiners et al., 2002). However, an improved germination rate in the forest core contrasts with studies  
343 finding a higher germination rate at forest edges or in open forests and landscapes (Wales, 1972;  
344 Meiners et al., 2002; Götmark, 2007; Bobiec et al., 2018). A reduced emergence in the forest interior  
345 could be related to a stronger shading by canopy trees and therefore especially shade-intolerant  
346 species could have a higher emergence near forest edges (Wales, 1972; Meiners et al., 2002). Oaks  
347 are shade-intolerant but on the other hand they have large seeds rich in nutrients which give them a  
348 kick start for growth. This is also shown by the significant positive effect of acorn weight on  
349 germination rate and might thus explain the high germination rate in the forest interior as well.  
350 Moreover, after already a few dry years, the spring and/or summer of 2019 and 2020 were very dry  
351 as well in all regions (Barbosa et al., 2020) and since our forest edges were characterized by a lower

352 soil moisture content (De Pauw et al., 2021), these drought effects might cause a higher germination  
353 in the forest interior.

354 Also, the latitude-species interaction found for germination, whereby *Q. ilex* and *Q. robur* germinate  
355 better in the south while *Q. cerris* and *Q. petraea* germinate better in the north is rather  
356 counterintuitive for *Q. robur* and *Q. cerris*. We speculate that these patterns are related to the fact that  
357 the latter two species were planted in 2020, whereas the first two oak species were planted in 2019.  
358 The trends thus, although not conclusive, might reflect annual variation in weather conditions rather  
359 than species-specific germination trends. Moreover, germination and growth during the first year, as  
360 discussed above, might be strongly impacted by the nutrients present in the acorn.

361 For survival, we found an increased probability to persist towards colder macroclimates, except for  
362 *Q. ilex* in complex forests. A lower survival rate in warm regions might be related to drought stress  
363 and this especially for *Q. robur* and *Q. petraea* as our most southern region was approximately located  
364 at the warm range margin of these species (Urli et al., 2014; Eaton et al., 2016). Moreover, the survival  
365 rate of *Q. ilex*, a species with a high tolerance to drought (Lobo et al., 2018), was not lower in southern  
366 regions and even increased towards the south in complex forest stands. In general, the survival in  
367 southern regions was also higher in complex forests, whereas in the north we found higher survival  
368 rates in simply structured forests. This might reflect the importance of the buffering effect of dense  
369 forests in warm environments, creating less environmental stress due to more humid and cooler  
370 conditions in complex forests (De Frenne et al., 2019; Zellweger et al., 2019; Meeussen et al., 2021),  
371 and thus protecting young seedlings from withering (Aussenac, 2000; Badano et al., 2015). Whereas  
372 in cold environments, simply structured forests provide a warmer and brighter environment, as was  
373 also the case in our experiment (see also De Pauw et al., 2021). Finally, the overall high mortality  
374 rates of *Q. robur* might be related to its susceptibility to oak powdery mildew (Marçais and Desprez-  
375 Loustau, 2014) which we also observed in our study.

376 Performance

377 Towards colder macroclimates, both plant height and diameter at root collar (DRC) increased, except  
378 for *Q. ilex* which performed better in warmer macroclimates. We suggest that this species-latitude  
379 interaction might be caused by the temperature and drought tolerance of the different oak seedlings  
380 along the gradient. Under dry circumstances, temperate species are more likely to invest in their root  
381 biomass instead of aboveground biomass (i.e. expressed here as plant height and stem diameter) (Van  
382 Hees, 1997). Indeed, along the latitudinal gradient, we also detected an interaction between species  
383 identity and macroclimate for aboveground biomass; seedlings from the two Mediterranean oak  
384 species had a higher biomass in southern regions. Though, along the macroclimatic gradient, also the  
385 forest structure interactively affected the biomass: a simple forest structure led to a higher biomass  
386 for oak seedlings. But this was especially the case for northern regions, as in the south we found a  
387 higher biomass in complex stands in comparison to simple stands (except for *Q. petraea*). Also, DRC  
388 was affected by the vegetation structure with a higher DRC in simple stands (except for *Q. petraea*)  
389 and near edges (except for *Q. cerris*). These trends are all probably related to enhanced microclimatic  
390 growing conditions (i.e. trade of between water availability and warmth) and light availability in open  
391 forest patches or near edges. Previous studies already found a higher growth, biomass and height near  
392 forest edges or under increased light intensities (Meiners et al., 2002; Lhotka and Stringer, 2013;  
393 Sevillano et al., 2016). Microclimatic conditions and light availability in simply structured forests or  
394 near forest edges might also be more representative of those of traditional management practices  
395 leading to semi-open woody landscapes, which are known to have enhanced *Quercus* reproduction  
396 in the past over more shade-tolerant species (Watt, 1919; Bobiec et al., 2018). Moreover, the positive  
397 effect of a low canopy cover might also favour the survival and growth of oaks affected by mildew,  
398 which was the case for many seedlings in our experiment. The fungus tends to reduce the shade and  
399 drought-tolerance of seedlings and therefore has the potential to reduce the regeneration capacity of  
400 oaks in forest environments (Lonsdale, 2015; Bobiec et al., 2018; Demeter et al., 2021).

401 Finally, SLA values were lower in simply structured forests and at low latitudes (except for *Q. petraea*  
402 for which the SLA slightly decreased towards the north). Also, significantly lower SLA values for *Q.*

403 *ilex* were expected since this species is adapted to dry Mediterranean climates and characterized by  
404 small, thick and coriaceous leaves, allowing the tree to reduce its transpiration rate (de Rigo and  
405 Caudullo, 2016). Traits such as SLA, besides resembling a different ecological strategy, are not only  
406 influenced by global but also by local environmental factors (Wright et al., 2004; De Pauw et al.,  
407 2021, Govaert et al., 2021). So, higher SLA values in complex forests might be a reaction to lower  
408 light intensity as plants growing in shade need to have larger leaves to capture sufficient light for their  
409 photosynthesis (Sevillano et al., 2016; Buajan et al., 2017). Besides, a lower SLA value in southern  
410 regions might be a mechanism to reduce water stress as a response to a higher vapor pressure deficit.

411 Experimental warming and transplant experiment beyond range limits

412 In warm and dry climates, the Mediterranean species *Q. ilex* and *Q. cerris* clearly performed better  
413 with a higher biomass and height, and higher survival rates. Moreover, even when being transplanted  
414 beyond their coldest range limits, both species still performed well and their survival rates remained  
415 high (especially for *Q. ilex*). *Quercus ilex* was able to maintain the highest biomass and DRC, even  
416 in our Swedish plots. However, one must keep in mind that *Q. cerris* and *Q. petraea* were only  
417 monitored for one growing season and were not exposed to winter conditions along the gradient. Frost  
418 is known to affect seedling performance and survival, and might limit species distribution at the  
419 northern range margin (Bianchi et al., 2019; Hofmann et al., 2014). Survival and performance results  
420 of those latter two species could thus be strongly altered if we would have studied them during two  
421 consecutive growing seasons. Besides frost, latitudinal patterns might also be caused by other species-  
422 specific drivers such as phenological differences, the light quality and quantity, drought or herbivory  
423 patterns along the gradients (Ducousso et al., 1996; Collet et al., 1998; Sevillano et al., 2016; Moreira  
424 et al., 2021).

425 Rather unexpectedly, we only found a limited impact of our experimental warming treatment on the  
426 germination, survival and performance of our four studied oak species. More specifically, we found  
427 a negative effect on plant height and biomass for *Q. robur*, whereas this effect was positive for both  
428 *Q. cerris* and *Q. ilex*. *Quercus robur* is generally known as less shade tolerant than *Q. cerris* and *Q.*

429 *petraea* (Leuschner and Meier, 2018) and might thus better regenerate in open conditions, as it was  
430 demonstrated in previous research (Demeter et al., 2021). Consistently, in the northern regions, we  
431 found a strong increase in the survival rate of *Q. robur* in simple and relatively more open forests in  
432 comparison with more complex and darker forests. This species thus requires sufficient light to grow  
433 but might also be more sensitive to heat and drought compared to the other tree species. The  
434 Mediterranean species, on the other hand, are better adapted to heat and drought (such as via their  
435 leaf characteristics or their provenance; de Rigo and Caudullo, 2016; Bert et al., 2020) and therefore  
436 could benefit from the additional warmth, especially at locations beyond their northern edge.  
437 Moreover, stronger effects might be expected if the degree of warming would be higher and for long-  
438 term warming experiments since the seedlings could also experience time-lags in response to the  
439 warming treatment (Bertrand et al., 2011; De Pauw et al., 2021). Therefore, in our rather short-term  
440 experiment, other drivers such as the nutrient available in the acorn and the microclimate, could have  
441 had a stronger impact on the observed patterns than the warming treatment. Differences in  
442 microclimate due to vegetation characteristics were on average approximately of the same magnitude  
443 than the observed temperature increase under the warming treatment (De Pauw et al., 2021).

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

#### 450 Potential management implications

451 Successful natural oak regeneration is complex and largely context dependent. Both species identity  
452 and macroclimate determine the outcome, while microclimate conditions and management  
453 interventions may locally alter these influences on initial oak regeneration. Moreover, conditions  
454 enhancing or limiting acorn germination, differ from those for survival, growth or biomass

455 accumulation. And these conditions might differ in turn from the growth requirements in later  
456 growing stages or those of adult trees (Morin et al., 2007; Annighöfer et al., 2015; Leuschner and  
457 Meier, 2018). Therefore, successful regeneration requires constant as well as species and location  
458 specific monitoring and forehanded management interventions to control the local climate and light  
459 availability and herewith the initial regeneration success.

460 We show that light is key for the initial stages of regeneration and establishment of oaks (see also e.g.  
461 Théry, 2001; Sevillano et al., 2016). Previous studies showed that neither fully exposed sites or light  
462 limited sites led to a successful regeneration for oaks (Puerta-Piñero et al., 2007; Bobiec et al., 2018).  
463 Simply structured forests, forest edges or natural and human-induced canopy gaps, might provide an  
464 important regeneration niche for oak species thanks to warmer microclimate conditions and more  
465 light availability in the understorey (Canham et al., 1990; Aussenac, 2000; Davies-Colley et al., 2000;  
466 Meeussen et al., 2021). However, optimal light conditions for oak regeneration will depend on the  
467 focal species and will require management interventions as the forest-floor microclimate will be  
468 influenced by both the macroclimate and the local forest structure (Aussenac, 2000; De Frenne et al.,  
469 2019; Meeussen et al., 2021). The detected macroclimate-forest structure interactions, as found for  
470 biomass and survival, showed that such trade-offs in microclimatic requirements exist along the  
471 studied latitudinal gradient. An increased light availability (and subsequently forest-floor  
472 temperature) might benefit the initial regeneration stages and seedling performance in northern  
473 regions whereas in southern regions managers might want to keep forest stands dense and closed to  
474 improve moisture conditions and avoid a detrimental impact of drought on the growth and survival  
475 of oak seedlings.

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## 485 Data availability statement

486 Upon acceptance data will be made available.

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## 794 Figure captions

795 **Figure 1:** (a) Distribution maps of the four species. The red and blue circles represent the different regions involved in  
796 the experiment. Red circles are the regions equipped with experimental warming and control plots. Blue circles are the  
797 regions equipped with control plots. Distribution maps are from: <http://www.euforgen.org/species/> (b) Pictures of the  
798 microclimatic gradients (here in Stockholm): two forest edges and two forest core plots were selected of which each time  
799 one was located in a “simple” (or more open) forest (bottom) and one in a more “complex” (or dense) forest (top). In  
800 regions represented by a red dot, additional plots with experimental warming were established at the four locations.

801 **Figure 2:** Predicted probabilities of survival for the four studied oak species (species are shown in different colours) as a  
802 function of latitude ( $^{\circ}\text{N}$ ) for two forest types (left: complex forests; right: simply structured forest). The dots represent the  
803 raw data points with 0 = no survival and 100 = survival. A small amount of jittering was added to the raw data points  
804 along the x and y-axis to improve clarity.

805 **Figure 3:** Predicted biomass (log-transformed) of the oaks (species shown in different colours) as a function of latitude  
806 ( $^{\circ}\text{N}$ ) for the two forest types (left: complex forests; right: simply structured forests). The dots represent the raw data  
807 points.

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

## Tables

**Table 1:** Average seedling characteristics of the oak species at the end of the experiment (August 2020) across 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 $\pm$ sd)	Plant height (cm) (Mean $\pm$ sd)	Diameter at root collar (mm) (Mean $\pm$ sd)	Specific leaf area (mm <sup>2</sup> mg <sup>-1</sup> ) (Mean $\pm$ sd)
<i>Q. cerris</i> *	134	115	466.22 $\pm$ 276.23	18.6 $\pm$ 6.9	2.40 $\pm$ 0.60	23.95 $\pm$ 5.73
<i>Q. ilex</i>	234	199	1056.02 $\pm$ 964.23	23.1 $\pm$ 9.4	2.66 $\pm$ 0.91	13.99 $\pm$ 3.86
<i>Q. petraea</i> *	170	123	227.23 $\pm$ 163.55	13.6 $\pm$ 5.5	1.93 $\pm$ 0.49	22.96 $\pm$ 6.15
<i>Q. robur</i>	203	83	358.73 $\pm$ 491.01	20.6 $\pm$ 8.4	2.21 $\pm$ 0.82	25.08 $\pm$ 4.75

\**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:** 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 (mm <sup>2</sup> mg <sup>-1</sup> )
Latitude ( $^{\circ}$ 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

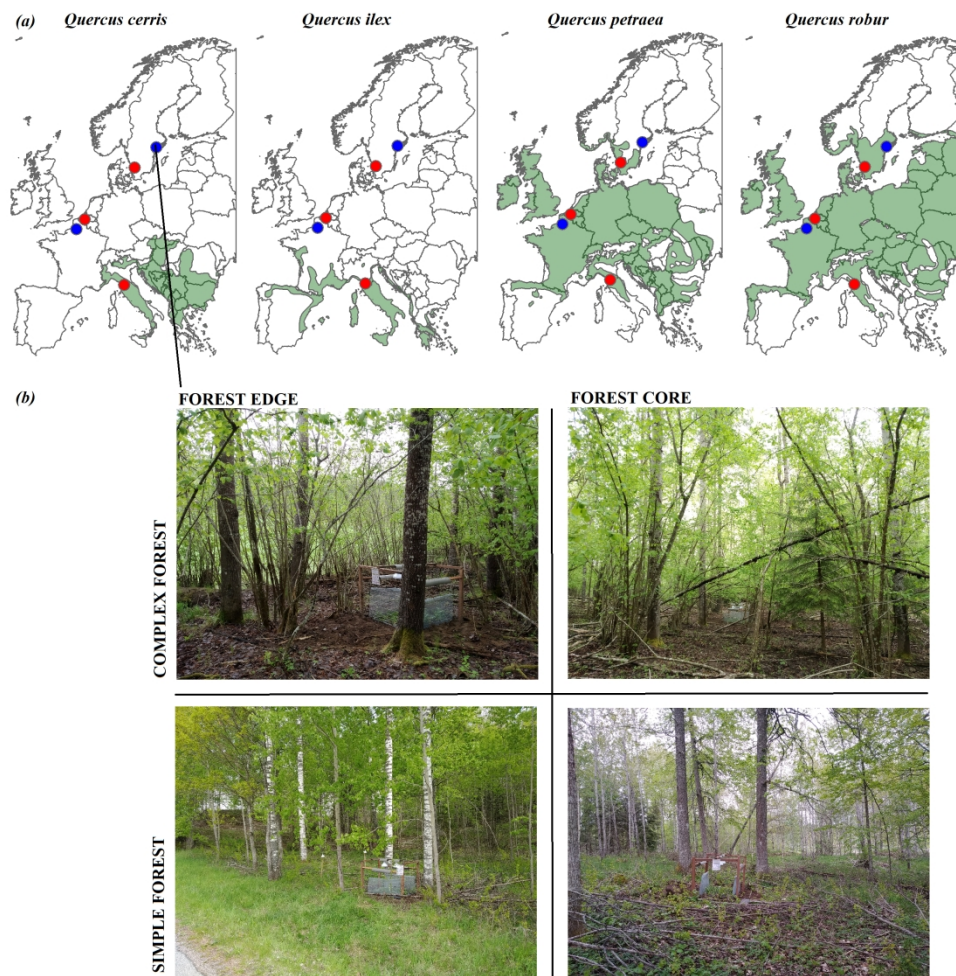


Figure 1: (a) Distribution maps of the four species. The red and blue circles represent the different regions involved in the experiment. Red circles are the regions equipped with experimental warming and control plots. Blue circles are the regions equipped with control plots. Distribution maps are from: <http://www.euforgen.org/species/> (b) Pictures of the microclimatic gradients (here in Stockholm): two forest edges and two forest core plots were selected of which each time one was located in a "simple" (or more open) forest (bottom) and one 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.

1494x1514mm (47 x 47 DPI)



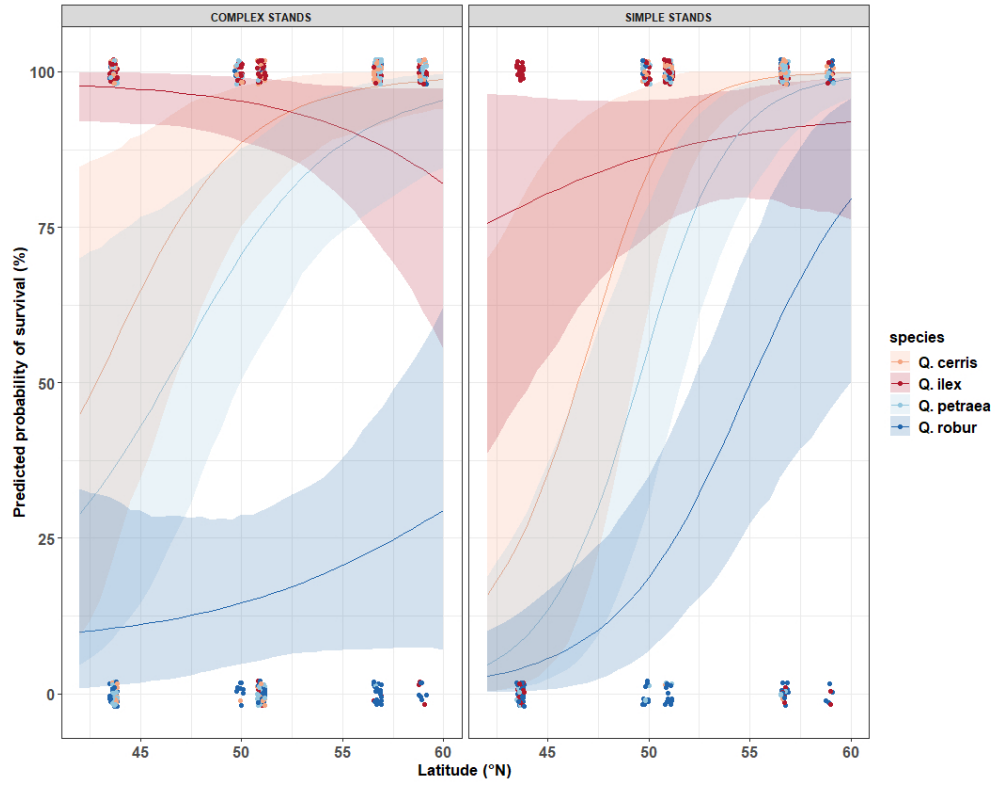


Figure 2: Predicted probabilities of survival for the four studied oak species (species are shown in different colours) as a function of latitude (°N) for two forest types (left: complex forests; right: simply structured forest). The dots represent the raw data points with 0 = no survival and 100 = survival.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

711x558mm (38 x 38 DPI)

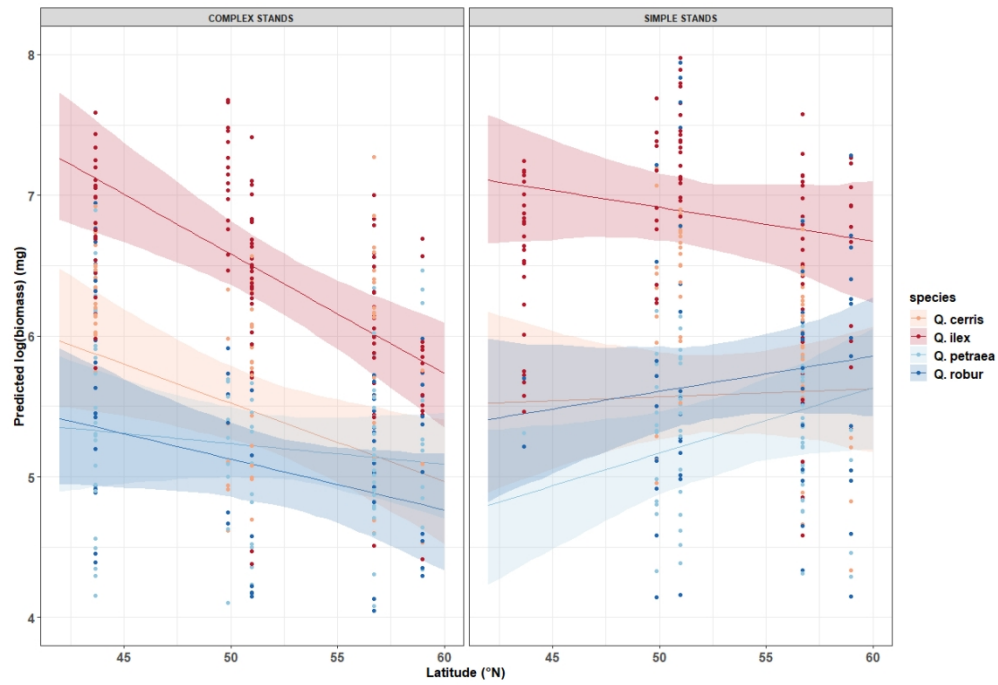


Figure 3: Predicted biomass (log-transformed) of the oaks (species shown in different colours) as a function of latitude (°N) for the two forest types (left: complex forests; right: simply structured forests). The dots represent the raw data points.

842x575mm (38 x 38 DPI)

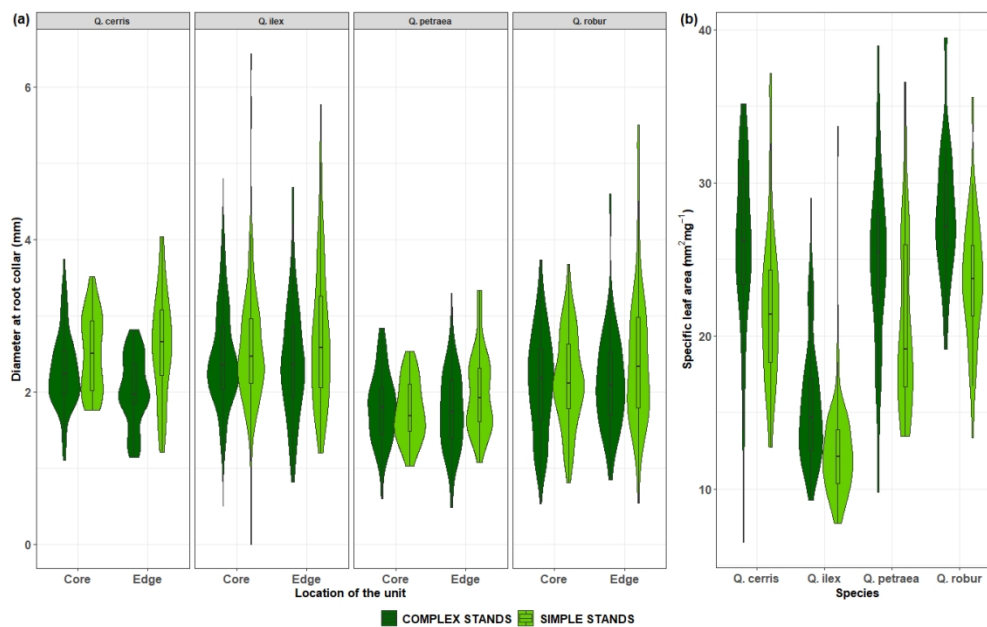


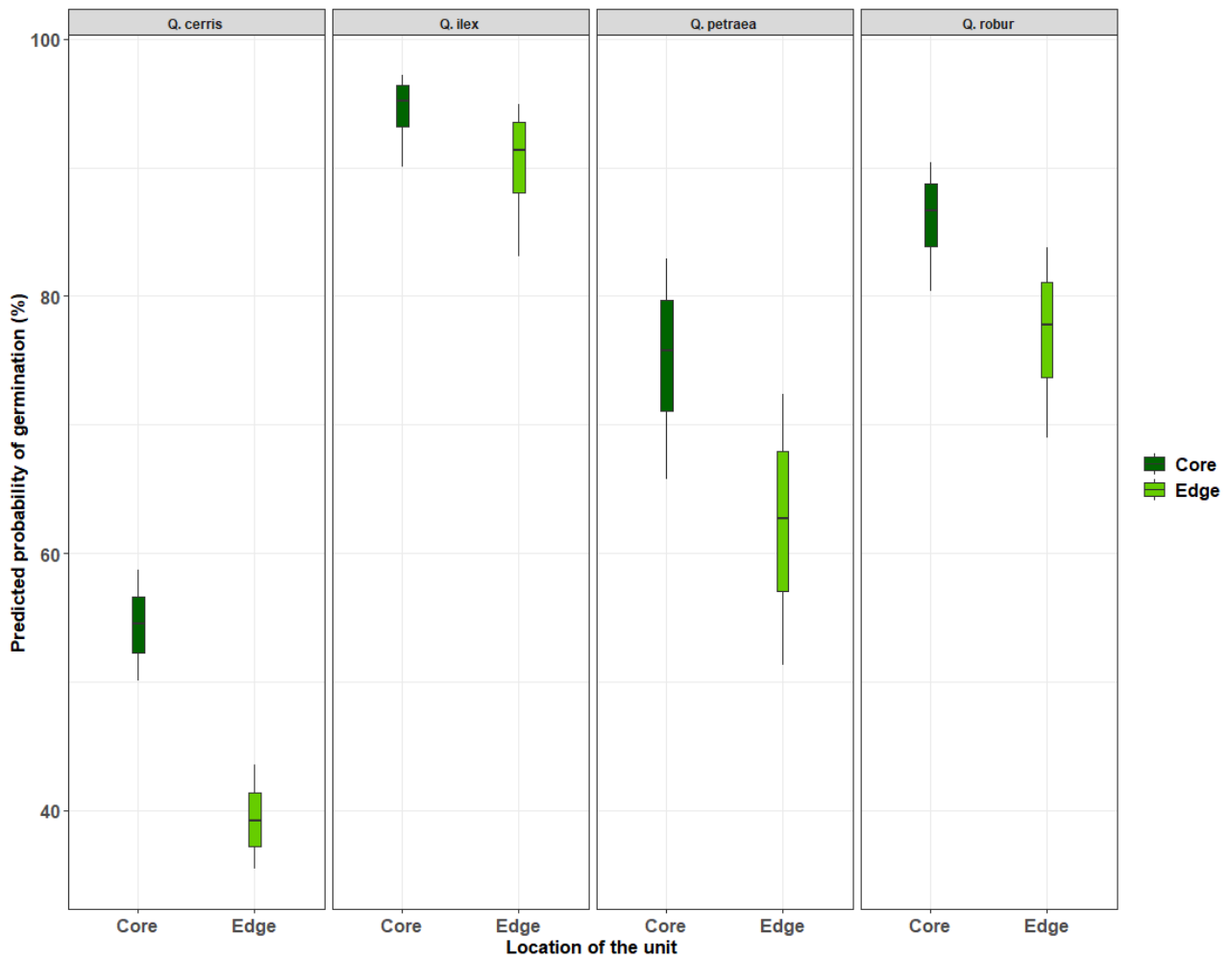
Figure 4: (a) Violin plots of the root collar diameter (mm) of the different oak species (shown in the subpanels) across the microclimatic gradients formed by stand structure (complex vs. simple forest stands, visualized by dark and light green colours, respectively) and the distance to the edge of the 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<sup>2</sup> mg<sup>-1</sup>) for the oak species.

920x575mm (38 x 38 DPI)

- 1 Supplementary information for the manuscript: Initial oak regeneration responses to  
2 experimental warming along microclimatic and macroclimatic gradients



- 3  
4 **Figure S1:** Left: overview of an experimental plot (without warming treatment) with two rows of 16 oak seedling  
5 containers protected by a cage. Right: row with acorns right before planting (top) and a germinating *Q. ilex* (bottom).



6

7 **Figure S2:** Predicted probabilities of germination (%) of the acorns (the four selected oak species are all shown in a  
8 different subpanel) in function of the distance to the edge of the plot (at the edge or in the core of the forest).

9 **Table S1:** Overview and characteristics of the 20 experimental locations. Mean annual temperature (MAT) and mean annual precipitation (MAP) were derived from CHELSA  
 10 (version 1.2, average climatic conditions over the period 1979-2013 at a spatial resolution of 30 arc sec, equivalent to approximately a 0.5 km<sup>2</sup> resolution at 50 °N) (Karger et al.,  
 11 2017).

Regions	MAT (°C)	MAP (mm/year)	Structure	Edge or core position	Tree cover (%)	Shrub cover (%)	Dominant tree species
Central Italy	14.9	761	Simple	Edge	75	30	Quercus pubescens, Quercus cerris, Fraxinus ornus
				Core	60	43	
			Complex	Edge	68	35	Quercus pubescens, Quercus cerris, Fraxinus ornus
				Core	70	40	
Northern France	10.8	693	Simple	Edge	/	60	Prunus avium, Fagus sylvatica, Populus alba, Fraxinus excelsior
				Core	70	30	
			Complex	Edge	65	50	Prunus avium, Fagus sylvatica, Populus alba, Acer pseudoplatanus
				Core	75	27	
Belgium	10.5	809	Simple	Edge	35	15	Quercus robur, Castanea sativa, Fraxinus excelsior, Ulmus glabra
				Core	60	10	
			Complex	Edge	90	30	Quercus robur, Acer pseudoplatanus, Fraxinus excelsior, Fagus sylvatica
				Core	95	80	
Southern Sweden	7.2	1010	Simple	Edge	98	8	Quercus petraea, Fagus sylvatica, Betula pendula
				Core	75	5	
			Complex	Edge	98	15	Fagus sylvatica, Quercus petraea
				Core	92	50	
Central Sweden (Stockholm)	6.7	547	Simple	Edge	60	/	Quercus robur, Betula pendula
				Core	60	/	
			Complex	Edge	65	80	Populus tremula, Betula pendula
				Core	70	80	

13 **Table S2:** The impact of macroclimate (i.e. latitude °N), microclimate (i.e. forest structure and distance to the edge),  
 14 experimental warming, species and their interaction effects, as well as the impact of acorn weight, on the biomass and  
 15 natural height of oak seedlings. Complex forests, forests cores, the control treatment and *Q. ilex* were used as the reference  
 16 forest structure, reference distance to the edge, reference treatment and reference species. For these models only a subset  
 17 of the data with regions Italy, Belgium and Southern Sweden was used, as in France and Stockholm no experimental  
 18 warming was present. The direction of the effect is given and the significance of the effect is indicated with asterisks (\*  
 19 =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ ). Non-significant interactions and terms were removed from the model. For  
 20 germination, survival, root collar diameter and specific leaf area index we could not find an impact of the warming  
 21 treatment and therefore results aren't shown.

	Aboveground biomass (mg, log- transformed)	Plant height (cm)
Latitude (°N)	↓	↓
Edge-to-core gradient (edge plot compared to interior)	↑	↑
<i>Q. cerris</i> (compared to <i>Q. ilex</i> )	↓***	↓***
<i>Q. petraea</i> (compared to <i>Q. ilex</i> )	↓***	↓***
<i>Q. robur</i> (compared to <i>Q. ilex</i> )	↓***	↑
Experimental warming	↑	↑*
Acorn weight (mg)	↑***	↑***
Lat : <i>Q. cerris</i>	↑	↑***
Lat : <i>Q. petraea</i>	↑*	↑***
Lat : <i>Q. robur</i>	↑	↑*
Edge plot : <i>Q. cerris</i>	↓***	↓*
Edge plot : <i>Q. petraea</i>	↓	↓*
Edge plot : <i>Q. robur</i>	↓	↓
<i>Q. cerris</i> : warming	↑	↑
<i>Q. petraea</i> : warming	↓	↓
<i>Q. robur</i> : warming	↓*	↓**
Marginal $R^2$	0.48	0.20
Conditional $R^2$	0.61	0.42

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