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1 **Beech and hornbeam dominate oak 20 years after the creation of storm-**
2 **induced gaps**

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8

9 **Abstract**

10 Oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. grouped), European beech (*Fagus*
11 *sylvatica* L.) and hornbeam (*Carpinus betulus* L.) are three major species of western and central
12 European forests. When conditions are suitable for the three species, silvicultural management
13 often favours oak because of its greater economic interest. Forest managers know that beech
14 and hornbeam are strong competitors for oak during the regeneration phase, but the conditions
15 that influence the relative success of the regeneration of the three species growing in mixture
16 are still poorly characterised. The natural regeneration of the three species 20 years after canopy
17 openings was studied based on 108 study sites established in 2001 in French forests impacted
18 by the windstorms Lothar and Martin in 1999. In spring and summer 2018 and 2019, all saplings
19 over 0.1 m in height were counted, species were identified and diameter at breast height (DBH)
20 was measured for all saplings over 1.30 m. The height of the saplings with the highest and
21 median DBH in each plot was recorded for each species. Mixed models were used to analyse
22 the combined effects of former stand type, distance from the edge of the gap and soil conditions

23 on species presence, sapling abundance, DBH and height. The modelling approach highlighted
24 the preponderant role of the initial seed rain on the presence and sapling density of the three
25 species compared to interspecific competition or distance from the edge. The two latter factors
26 had a secondary effect on sapling DBH and height. Beech and hornbeam saplings were more
27 abundant than oak saplings regardless of soil conditions (on average, 3,097, 3,063 and 344
28 saplings ha⁻¹, respectively), suggesting a strong competitive ability of these two species. Oak
29 was present on 22% (43% for hornbeam and 68% for beech) of the studied plots, at a low
30 density but with a height and DBH similar to that of beech or hornbeam. This result highlights
31 the high dissemination capacity of beech and hornbeam, which prevents the establishment of a
32 stand dominated by oak. When seeking to obtain oak-dominated stands in the lowlands of
33 Europe, the abundance of beech and hornbeam can be a limiting factor that could lead to the
34 disappearance of oak from large areas if no silvicultural operations are performed to promote
35 it.

36 **1. Introduction**

37 Oak (*Quercus petraea* (Matt) Liebl. and *Quercus robur* L. grouped together), European
38 beech (*Fagus sylvatica* L.) and hornbeam (*Carpinus betulus* L.) are key European broadleaved
39 species with distribution areas that largely overlap (San-Miguel-Ayanz et al., 2016). In their
40 common area, forest managers usually aim to favour oak, which represents a greater economic
41 interest (Thomas et al., 2002; Annighöfer et al., 2015). In addition, actions to mitigate climate
42 change tend towards a more oak-oriented forestry. Since beech and hornbeam are more
43 sensitive to drought than oak (Bréda et al., 2006; Friedrichs et al., 2009), their future remains
44 uncertain in the context of more intense and/or more frequent spring and summer droughts
45 (Jump et al., 2006; Geßler et al., 2007). However, beech and hornbeam are strong competitors
46 for oak, especially during the regeneration stage (Ligot et al., 2013; Petritan et al., 2012; Van
47 Couwenberghe et al., 2013), and have strong negative impacts on the survival, height and

48 diameter growth of young oaks (Jensen and Löf, 2017; De Groote et al., 2018; Maleki et al.,
49 2020). In this context, it is crucial to identify which environmental and silvicultural conditions
50 would favour the regeneration of oak compared to that of hornbeam and beech in order to define
51 management options that would facilitate oak regeneration and eventually promote oak in
52 European forests in the next century.

53 Distance from seed source is a major determinant of regeneration success for all tree
54 species (Clark et al., 1999; Nathan & Muller-Landau, 2000), and was shown to predominate
55 over competition from tree seedlings or neighbouring vegetation in mixed forests in north-
56 eastern France ((Dassot and Collet, 2015)). Long distances from potential seed sources reduce
57 seedling density according to patterns that may differ among tree species (Clark et al., 1998;
58 Hewitt & Kellman, 2002; Rozman et al., 2015). The dissemination strategies of oak, beech and
59 hornbeam differ (Vittoz and Engler, 2007): beech and oak are barochorous, whereas hornbeam
60 is anemochorous and usually disseminates over longer distances (Vittoz and Engler, 2007).
61 Several studies have shown the impact of surrounding stand composition (Petritan et al., 2012;
62 Annighöfer et al., 2015; Manso et al., 2020) or of distance from the gap edge on the density of
63 oak and beech saplings in canopy gaps (Van Couwenberghe et al., 2010; Tinya et al., 2020). To
64 date, very few studies (Tinya et al., 2020) have quantified these patterns for hornbeam.

65 Light availability in the understory strongly influences the coexistence of tree species at
66 the early stage and, consequently, long-term forest composition and structure (Oliver and
67 Larson, 1996). Controlling the amount of light available for saplings is widely used as a
68 management tool to promote species. Beech is highly shade-tolerant (Ellenberg et al., 1992;
69 Modrý et al., 2004; Niinemets and Valladares, 2006) since it may germinate, survive and grow
70 under a wide range of light conditions, including dense canopy conditions (Watt, 1923; Emborg,
71 1998; Petritan et al., 2007). Hornbeam is relatively shade-tolerant, although less than beech.
72 Conversely, oak is shade-intolerant and needs much more light to establish itself and grow

73 (Ellenberg et al., 1992; Emborg, 1998; Ligot et al., 2013). Recent studies have shown that
74 during the regeneration stage, beech outcompetes oak along the entire gradient of light
75 availability that prevails in the understory of beech and oak stands (Ligot et al., 2013; Manso
76 et al., 2020; Van Couwenberghe et al., 2013). However, the differences in diameter and height
77 growth between beech and oak saplings are smaller under high than under low light conditions.
78 These studies suggest that creating canopy gaps may favour oak but may not be sufficient to
79 ensure its successful regeneration when growing in mixture with beech (Petritan et al., 2017;
80 Modrow et al., 2019; Jaloviar et al., 2020).

81 Finally, soil characteristics also influence regeneration success and species composition
82 (Bigelow & Canham, 2002; Finzi & Canham, 2000; Van Couwenberghe et al., 2010). Oak and
83 beech have a large amplitude in terms of soil fertility and acidity (Pinto & Gégout, 2005;
84 Walthert & Meier, 2017), especially oak, which is more tolerant to acid soils. Conversely,
85 hornbeam does not develop on acid soils and shows an optimum of presence for soil pH ranging
86 from 5 to 7 (Gégout et al., 2005). Contrary to oak and beech, hornbeam is also sensitive to soil
87 nitrogen availability, and several studies have shown a positive correlation between the
88 availability of nitrogen and the presence of hornbeam (Pinto & Gégout, 2005; Walthert &
89 Meier, 2017). A greater tolerance of oak to acid soils and low nitrogen availability compared
90 to beech and hornbeam may potentially promote its regeneration in such conditions.

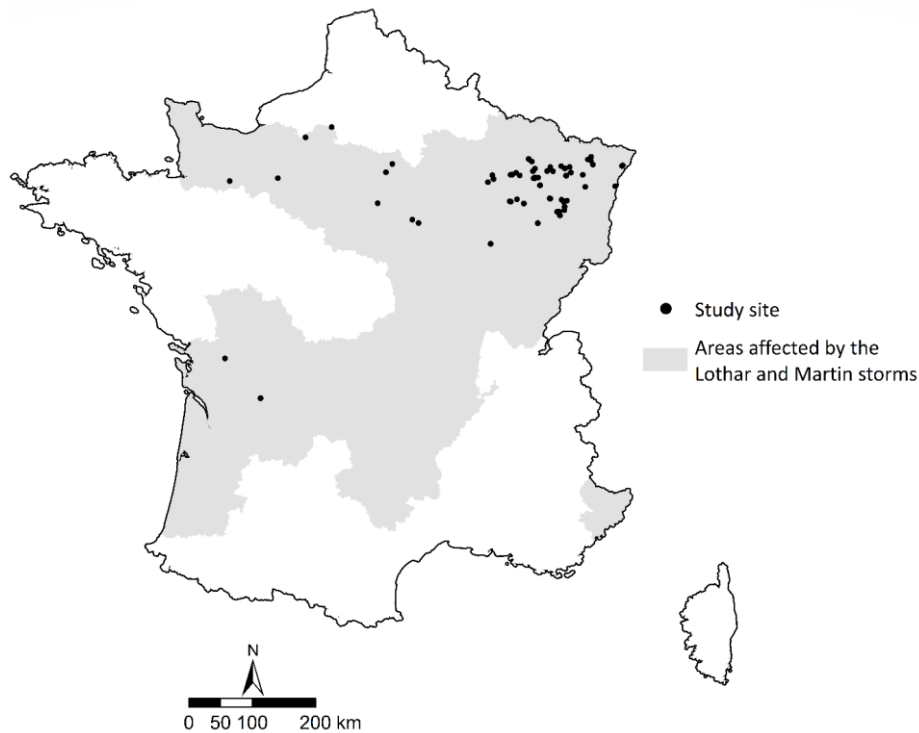
91 The aim of our study is to compare the natural regeneration of oak, beech and hornbeam in
92 small to large gaps according to soil characteristics and former stand characteristics in order to
93 identify the conditions the most favourable to oak regeneration and where oak could dominate
94 over its main competitors. We analysed the regeneration success (sapling presence, density,
95 height and diameter at breast height (DBH)) of each of the three species in storm-induced forest
96 gaps, 20 years after the storms, as a function of former stand composition, distance from gap
97 edge, interspecific sapling competition and soil conditions. We hypothesize that within forest

98 gaps: (1) the presence and density of beech and oak would decrease with increasing distance
99 from the gap edge, whereas the presence and density of hornbeam would be less influenced by
100 the distance from the edge due to its higher seed dispersal capacity; (2) sapling DBH and the
101 height of all species would increase with distance from the gap edge due to higher light
102 availability and lower stem density away from the edge; (3) the positive effect of the distance
103 from the gap edge on sapling density and size would be stronger for oak compared to beech and
104 hornbeam due to the higher light requirements of oak saplings; and (4) hornbeam would be less
105 present on acid soils than oak and beech. We used an observation network established in France
106 after the 1999 storms that took account of large gradients of soil conditions, former stand types
107 and gap sizes to investigate the regeneration of the three tree species and test our hypotheses.

108 **2. Material & Methods**

109 **2.1. Study sites**

110 The study was conducted in temperate forests in France (**Fig. 1**). In December 1999, 968,000
111 ha of French forests were affected by two windstorms, Lothar and Martin (Inventaire Forestier
112 National, 2003), which destroyed 8% of French forest resources (Pignard et al., 2009). In 2001,
113 108 study sites were established in forests impacted by the windstorms (**Fig. 1**).



114

115 **Fig. 1. Location of the 108 study sites and area affected by the 1999 windstorms in**
 116 **France.**

117 Study sites were mainly semi-natural hardwood stands dominated by oak, beech and hornbeam,
 118 located in lowland areas with an altitude below 600 m. Mean annual temperatures ranged
 119 between 7.9°C and 11.85°C, and annual precipitation ranged from 593 mm to 1505 mm. We
 120 investigated large gradients of disturbance intensity (damaged area ranged between 10% and
 121 90% of the forest surface area), soil conditions (pH and C/N of the organo-mineral A horizon
 122 ranged from 3.9 to 7.9 and 11 to 28, respectively) and previous stand type (corresponding to
 123 the stand present before the storm: oak-dominated, beech-dominated or mixed oak and beech).
 124 A total of 108 gaps were selected for the study, with an area ranging from 0.02 to 144 ha
 125 (**Appendix, Fig. A1**). No silvicultural operations were performed in the selected gaps after the
 126 storms. The absence of silvicultural operations allowed the study of the natural reconstitution
 127 of the stands. **Table 1** summarizes the different gradients (gap size, C/N, pH and number of
 128 saplings) for the three former stand types of the 108 gaps.

129

Former stand type (ST)	Gap size (ha)	C/N	pH	Sapling density (ha ⁻¹)
Oak (n=42)	6 (0.03 – 70)	13.6 (11 – 24)	5.3 (4.0 – 7.9)	11,988 (0 - 304,762)
Beech (n=50)	21 (0.02 – 144)	16.3 (11 – 27)	5.4 (4.0 – 7.9)	8,413 (0 -123,571)
Mixture (n=14)	17 (0.04 – 88)	16.1 (11 – 28)	5.6 (3.9 – 7.7)	11,111 (0 - 146,031)

130 **Table 2. Characteristics of the plots sampled in each of the three former stand types types:**
131 **mean value (min-max).**

132

133 2.2. Data collection

134 Gaps were classified according to their surface area, with a threshold of 1 ha to differentiate
135 small gaps (SG) from large gaps (LG). Two different sampling designs were used for
136 measurements in SG and LG (**Appendix, Fig. A2**). In SG, 2-m-radius circular plots (=12.6 m²)
137 were distributed every 12 m from the barycentre of the gap, along the north-south and east-west
138 axes of the gap. The axes extended outside the gap and one or two plots were placed under the
139 forest cover. The number of plots differed among gaps and ranged between 7 and 24 plots,
140 depending on gap size. In LG, the centre of the gap was approximately located, and four 10-m-
141 radius circles were established at 50 gr, 150 gr, 250 gr and 350 gr (0 gr indicating north) and
142 30 m with respect of the gap centre. In each circle, three 2-m-radius circular plots were
143 established at 0 gr, 133 gr and 266 gr, respectively, with respect to the circle centre. Thus, 12
144 plots were installed in each LG. A total of 1,153 plots of 12.6 m² (592 in small gaps, 561 in
145 large gaps) was established between 2001 and 2004 for the study.

146 In spring and summer 2018 and 2019, (i.e., 19 and 20 growing seasons after the windstorms
147 occurred), sapling regeneration was measured in each plot. All saplings with a height above 0.1
148 m were considered. Saplings with a DBH greater than 20 cm were considered as pre-existent to
149 the storms and were not considered. The species was recorded for each sapling. The DBH of
150 each sapling greater than 1.3 m in height was measured. Within each plot and each species, the
151 height was measured for the sapling with the largest DBH and the sapling with the median

152 DBH. A total of 19,445 saplings was recorded, 7,341 and 1,756 with a DBH and a height
 153 measurement, respectively (**Table 3**).

Species	Number of gaps	Number of plots	Number of saplings	Occurrence frequency	Sapling density (ha ⁻¹)	Mean maximum height (m)	Mean DBH (cm)
Oak	81	250	1,037	0.22	3,254	5.9	3.3
Beech	103	785	8,766	0.68	8,888	6.8	2.4
Hornbeam	81	498	9,642	0.43	15,317	6.3	3.1

154 **Table 3. Total number of gaps and plots where at least one sapling of the considered**
 155 **species was present, out of 1,153 measured plots; total number of saplings recorded over**
 156 **the 1,153 plots; species occurrence frequency from plot; mean sapling density (ha⁻¹)**
 157 **calculated over the plots where the species is present; mean maximum height (m) and**
 158 **mean diameter at breast height (DBH) (cm).** Height and DBH are average values computed
 159 over all plots, including plots where the three species are not necessarily mixed.

160

161 One soil sample per gap was collected in 2001 by taking a 0-5 cm layer of soil below the
 162 litter at the gap centre. Chemical analyses were carried out in the laboratory and pH-H₂O,
 163 organic carbon and nitrogen content were measured following the NF ISO 10390,
 164 NF ISO 10694 and NF ISO 13878 procedures, respectively.

165 Former stand type (ST) was evaluated by forest managers prior to plot installation using
 166 management plans. When possible, a control of the stumps was carried out during the
 167 installation of the plots in 2001 to identify the former stand type. Former stand type was
 168 classified into three classes: oak, beech and mixture, according to the dominance of oak or
 169 beech. In former "oak" stands, the basal area of oak was greater than the basal area of any other
 170 species; in former "beech" stands, the basal area of beech was greater than the basal area of any
 171 other species; and all other stands were considered as former "mixture" stands (**Appendix, Fig.**
 172 **A3**).

173 In SG, the gap edge was defined using the edge trees. Each edge tree was geo-located using
 174 azimuth and distance from the centre of the gap, and gaps were delimited using ArcGis mapping
 175 software (version 10.4.1; ESRI Inc., Redlands, CA, USA). In LG, the entire stand was destroyed

176 and the edge was located in another stand. The gap edge was defined using Landsat-5 images
177 (U.S. Geological Survey) by comparing images taken before and after 1999. In all gaps, each
178 sampled plot was geo-located, and the distance from the edge (D , m) was estimated by
179 calculating the smallest distance from the gap edge. Distance from the gap edge ranged between
180 -15.2 m (plots located in the understory outside the gap, in SG) and 234 m (in LG).

181 **2.3. Data analysis**

182 Mixed models were used to analyse the combined effects of distance from the edge (D),
183 former stand type (ST), interspecific competition (IC), pH (pH) and nitrogen availability (C/N)
184 on four variables that characterise sapling regeneration for each species: species presence,
185 sapling abundance (number of saplings per hectare), sapling DBH (cm) and sapling height (m).
186 IC represents the number of stems on the plot, excluding the species studied (oak, beech, or
187 hornbeam).

188 Models were fitted for each of the three species separately. Final models contained fixed and
189 random effects (see below), but variable selection was carried out on models including only
190 fixed effects (Zuur et al., 2009). We used a backward elimination procedure based on AIC to
191 select variables. All variables that were significant for at least one species were kept in the final
192 models. All first-order interactions were tested and interactions that were significant for at least
193 two of the three species were kept in the models. Pearson residuals of the models were evaluated
194 to check the absence of a visible pattern. The final models used for each regeneration variable
195 are presented below.

196 **2.3.1. Species presence**

197 The presence of each species was evaluated over the 1,153 inventoried plots. The presence
198 of species in a plot is a binary variable (0 or 1) that follows a binomial law. For each species,
199 generalised linear mixed models were fitted using the R package 'lme4' (Bates et al., 2015),

200 where species presence is expressed as a function of D, ST, IC and C/N, the interaction between
 201 ST and IC as fixed effects, and gap identity as a random effect. Let Y_{ij} be the binary outcome
 202 (absence/presence of the studied species for plot j in gap i). Knowing the gap-specific effect b_i ,
 203 ($Y_{ij} | b_i$), the presence was denoted by $p_{ij} = P(Y_{ij} = 1 | b_i)$. The following logistic model was used:

204 **Eq. 1.**
$$\text{logit}(p_{ij}) = \log\left(\frac{p_{ij}}{1 - p_{ij}}\right)$$

$$= \beta_0 + \beta_1 D_{ij} + \beta_2 \frac{C}{N_i} + \beta_3 IC_{ij} + \beta_4 ST_i + \beta_5 IC_{ij} * ST_i + \text{Gap}_i$$

205

206 where Gap_i is the random effect sampled from a normal distribution $N(0, \sigma^2)$ and β_s are the
 207 unknown coefficients to be determined. Centred and scaled explanatory variables were used to
 208 solve convergence issues.

209 **2.3.2. Species-specific sapling abundance**

210 The abundance model of each species was established using the gaps where the species
 211 was present in at least one plot, i.e., gaps where the species was absent were removed from the
 212 dataset used for the species model. In total, 81 gaps and 857 plots were selected for oak, 103
 213 gaps and 1,098 plots for beech, and 81 gaps and 870 plots for hornbeam. In these plots, a total
 214 of 989, 8,751 and 8,139 saplings were recorded for oak, beech and hornbeam, respectively.

215 Due to the high number of zeros in the dataset (oak, beech and hornbeam were absent from
 216 71%, 28% and 43%, respectively, of the plots used in the analysis), we used a zero-inflated
 217 distribution. In order to fit a zero-inflated negative binomial (ZINB) model (Zeileis et al., 2008)
 218 using the R package ‘pscl’ (Zeileis et al., 2008), the overdispersion coefficient was estimated
 219 to be less than 1.5 for each of the three species, which is an acceptable threshold (Zuur et al.,
 220 2009). To take the random effects into account, we fitted a mixed ZINB model using the R
 221 package ‘glmmTMB’ (Brooks et al., 2017), where D, C/N, log(IC), ST, the interaction
 222 log(IC):ST and D:ST were fixed effects, and Gap was a random effect. Let μ_{ij} be the number

223 of saplings of the studied species for plot j in gap i . The following model was fitted for each
 224 species:

225 **Eq. 2.** $Y_{ij} \sim \text{ZINB}(\pi_{ij}, \mu_{ij})$

226 $\text{logit}(\pi_{ij}) = \gamma$

227 $\log(\mu_{ij}) = \beta_0 + \beta_1 D_{ij} + \beta_2 \frac{C}{N_i} + \beta_3 \log(IC_{ij}) + \beta_4 \log(IC)_{ij} * ST_i + \beta_5 D_{ij} * ST_i + \text{Gap}_i$

228 where π_{ij} is the probability of false 0, μ_{ij} the expected value for the count process, Gap_i the
 229 random effect sampled from a normal distribution $N(0, \sigma^2)$ and β_s the unknown coefficients. π_{ij}
 230 was modelled to ensure that the logistic part of the model contained only an intercept γ .

231 **2.3.3. Species-specific sapling DBH**

232 Sapling DBH was evaluated over all saplings with a height greater than 1.3 m, representing
 233 a total of 237, 4,910 and 2,206 saplings for oak, beech and hornbeam, respectively. Mixed linear
 234 models were used to predict DBH, which was log-transformed to satisfy the assumptions of
 235 linearity and normality of the residuals. The selected variables were: D, pH, IC, ST, D:pH,
 236 pH:IC as fixed effects, and Gap as a random effect. Let Y_{ij} be the DBH for the studied species
 237 on plot j in gap i . The following model was used:

238 **Eq. 3.** $\log(Y_{ij})$

239 $= \beta_0 + \beta_1 D_{ij} + \beta_2 \text{pH}_i + \beta_3 \text{IC}_{ij} + \beta_4 \text{ST}_i + \beta_5 D_{ij} * \text{pH}_i + \beta_6 \text{pH}_i * \text{IC}_{ij}$

240 $+ \text{Gap}_i + \varepsilon_{ij}$

241 where Gap_i is the random effect of gap i sampled from a normal distribution $N(0, \sigma^2)$, β_s the
 242 unknown coefficients, and ε_{ij} the normally distributed model error.

243 2.3.4. Species-specific sapling height

244 For each species, the height of the sapling with the largest diameter and the sapling with
245 the median diameter were measured on each plot. This represents a measurement of two heights
246 per species and per plot, and a total of 107, 1,139 and 518 saplings, respectively, for oak, beech
247 and hornbeam. Mixed linear models were used to predict height, which was log-transformed to
248 satisfy the assumptions of linearity and normality of the residuals. The selected variables were:
249 D, C/N, pH, log(IC) as fixed effects, and Gap as a random effect.

250 Let Y_{ij} be the height for the studied species on plot j in gap i . The following model was used:

251 **Eq. 4.**
$$\log(Y_{ij}) = \beta_0 + \beta_1 D_{ij} + \beta_2 \frac{C}{N_i} + \beta_3 \text{pH}_i + \beta_4 \log(\text{IC})_{ij} + \text{Gap}_i + \varepsilon_{ij}$$

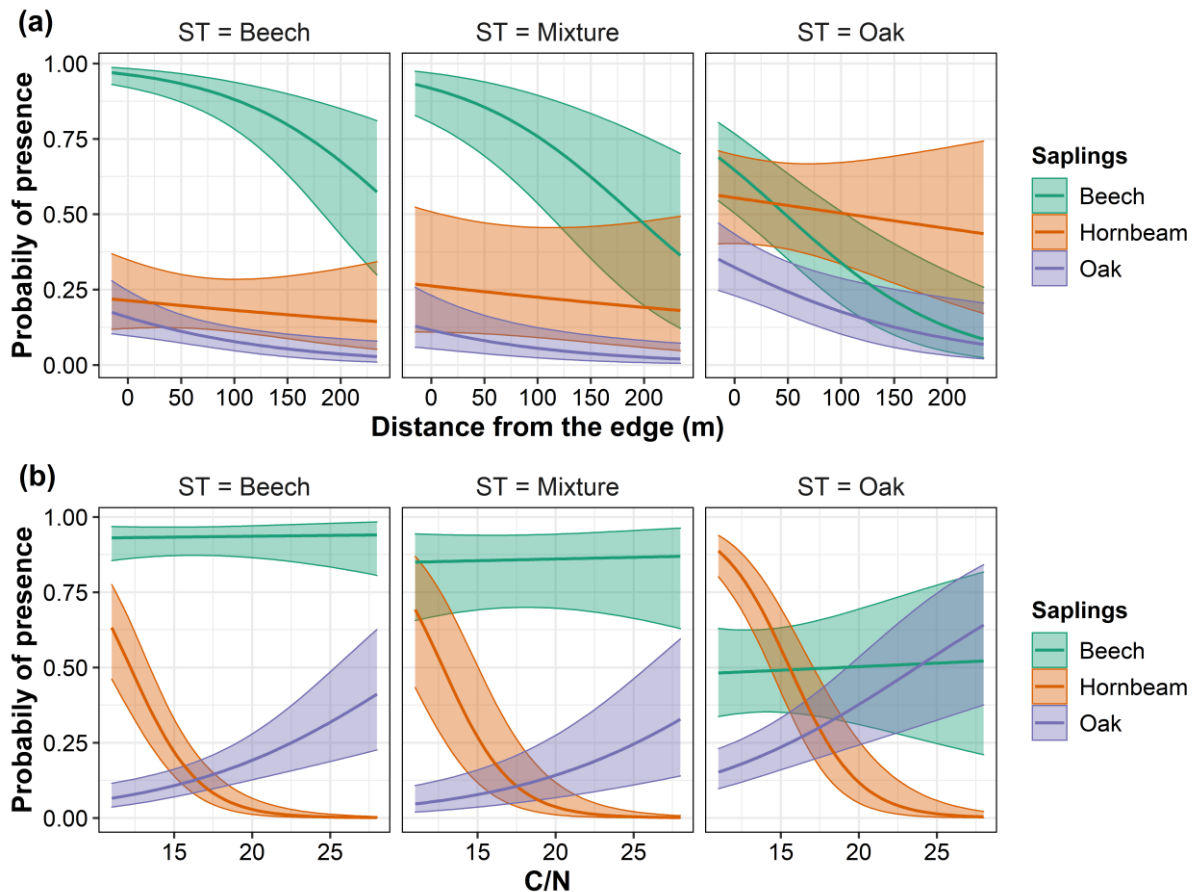
252 where Gap_i is the random effect of gap i sampled from a normal distribution $N(0, \sigma^2)$, β s the
253 unknown coefficients, and ε_{ij} the normally distributed model error.

254 3. Results

255 3.1. Species presence

256 The observed frequencies of occurrence of the species at the plot scale are 0.22, 0.43 and
257 0.68 for oak, hornbeam and beech, respectively. For each of the three species, the probability
258 of presence decreased when the distance from the forest edge increased (**Fig. 2**), but the effect
259 was statistically significant only for oak and beech (p-value < 0.01) (**Table 4**). Former stand
260 type significantly influenced the presence of all species. The presence of oak and hornbeam
261 were the highest when the former stand was dominated by oak, and the presence of beech was
262 the highest when the former stand was dominated by beech or in former mixed stands (**Fig. 2**;
263 **Appendix, Table A1**). However, regardless of the former stand type and the distance from the
264 forest edge, oak always had a lower presence than beech and hornbeam. Nitrogen availability
265 significantly influenced the presence of oak and hornbeam, but not beech (**Table 4; Appendix,**

266 **Table A1).** When nitrogen availability decreased (C/N increased), the presence of oak
 267 increased, whereas it decreased for hornbeam, reaching 0 for $C/N > 20$ in all former stand types
 268 (**Fig. 2**). The interspecific competition index showed a positive correlation with the presence of
 269 oak and hornbeam (**Table 4; Appendix, Table A1**).



270 **Fig. 2. Predicted probability of the presence of oak, beech and hornbeam saplings for each**
 271 **former stand type (ST=Beech, Mixture or Oak), according to (a) the distance from the**
 272 **forest edge, and (b) soil C/N.** Probabilities of presence were calculated using Equation 1
 273 adjusted for each species. The 95% pointwise confidence interval of the predictor is
 274 represented.
 275

276

MODEL	PREDICTORS	OAK	BEECH	HORNBEAM
		p-value	p-value	p-value
Presence: Equation 1				
	D	<0.01	<0.001	0.50
	C/N	<0.001	0.84	<0.001
	IC	<0.001	0.92	0.08
	ST	<0.01	<0.001	<0.001
	IC:ST	0.15	<0.01	0.03
Density: Equation 2				
	D	0.01	<0.001	0.49
	C/N	<0.01	0.42	<0.001
	log(IC)	<0.001	0.10	<0.01
	ST	<0.01	<0.001	<0.001
	D:ST	<0.01	<0.01	0.25
DBH: Equation 3				
	D	0.13	<0.001	0.07
	pH	0.15	0.71	0.01
	IC	<0.001	<0.001	0.33
	ST	0.91	0.86	<0.001
	D:IC	<0.01	<0.001	<0.001
	IC:pH	0.49	<0.01	<0.001
Height: Equation 4				
	D	0.11	<0.001	<0.001
	pH	0.03	0.02	0.38
	C/N	0.55	0.12	0.03
	log(IC)	<0.01	<0.001	<0.001

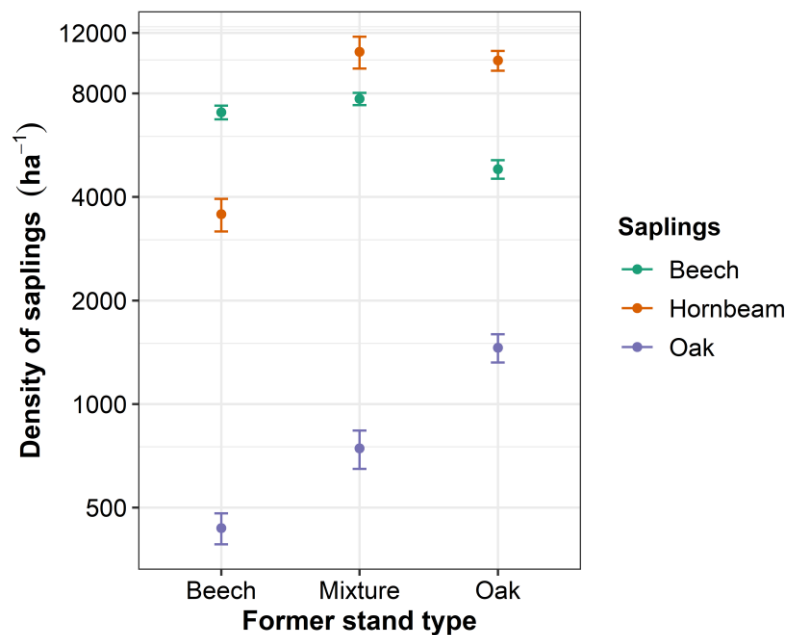
278 **Table 4. Significance of each model parameter used to predict probability of presence,**
279 **density, DBH and height for oak, beech and hornbeam saplings.** D: distance from the forest edge;
280 C/N: nitrogen availability; IC: total number of saplings on the plot excluding the studied species; ST: former stand
281 type.

282

283 3.2. Sapling abundance

284 Across the study area, the average density of oak, beech and hornbeam saplings was 344,
285 3,097 and 3,063 saplings ha⁻¹, respectively. Abundance strongly depended on former stand type
286 (**Fig. 3; Table 4**). In former oak stands, oak had a density of 1,251 saplings ha⁻¹ on average,
287 compared to 289 saplings ha⁻¹ in former beech stands. Likewise, beech had a higher density in
288 former beech stands than in former oak stands, 7,052 and 4,280 saplings ha⁻¹, respectively. The
289 effect of the former stand type is stronger for oak than for beech. For oak, there are four times

290 more saplings in former oak stands, whereas for beech, there are only 60% more saplings when
291 the former stand is beech.

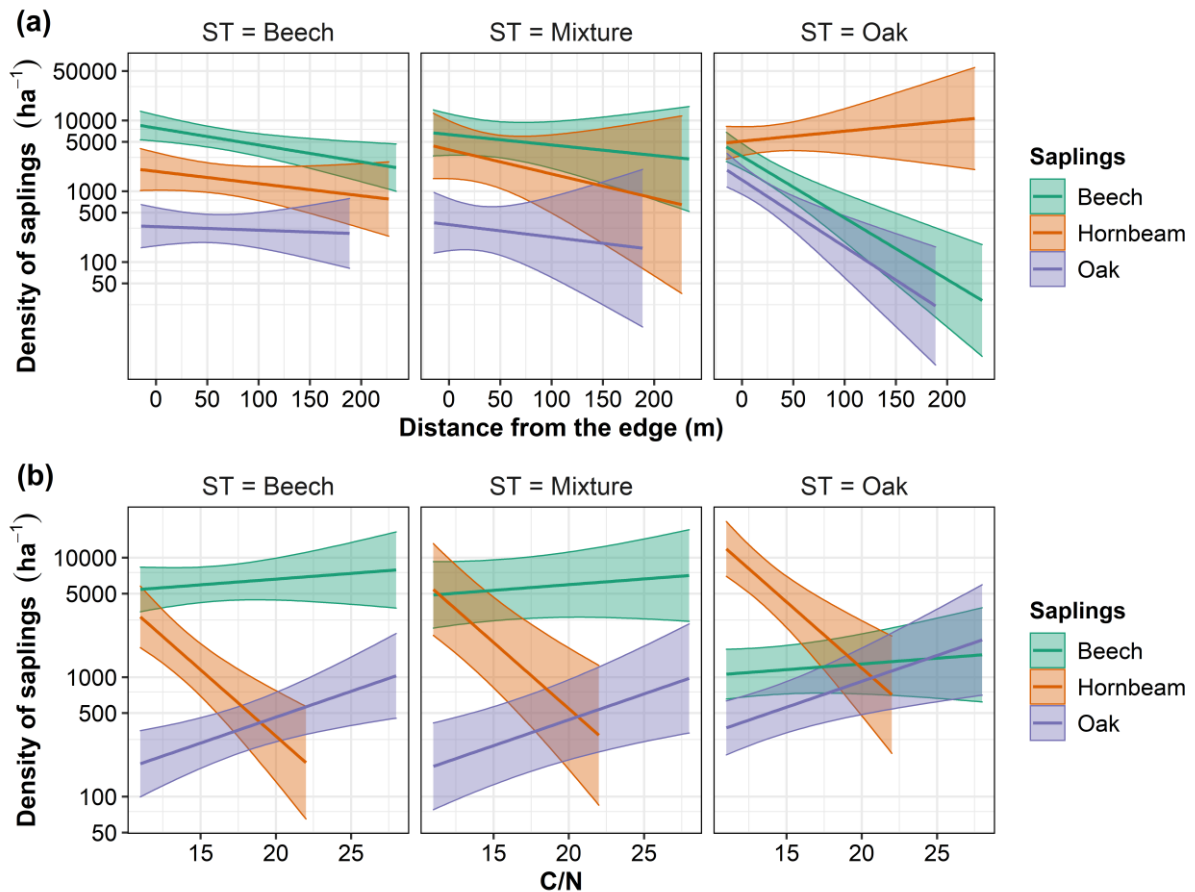


292

293 **Fig. 3. Sapling density (mean \pm standard deviation of the mean) of oak, beech and**
294 **hornbeam according to former stand type. Note the logarithmic scale on the vertical axis.**

295

296 The distance from the edge, in interaction with former stand type, strongly influenced the
297 abundance of oak and beech (**Fig. 4**). The abundance of the two species decreased with
298 increasing distance from the forest edge. Oak was dominated by hornbeam and beech in former
299 beech or mixed stands. In former oak stands, oak and beech showed similar abundance with
300 distance from the edge. The abundance of hornbeam was strongly influenced by C/N, and was
301 the highest in former oak stands and when C/N was close to 10 (**Table 4; Fig. 4**).



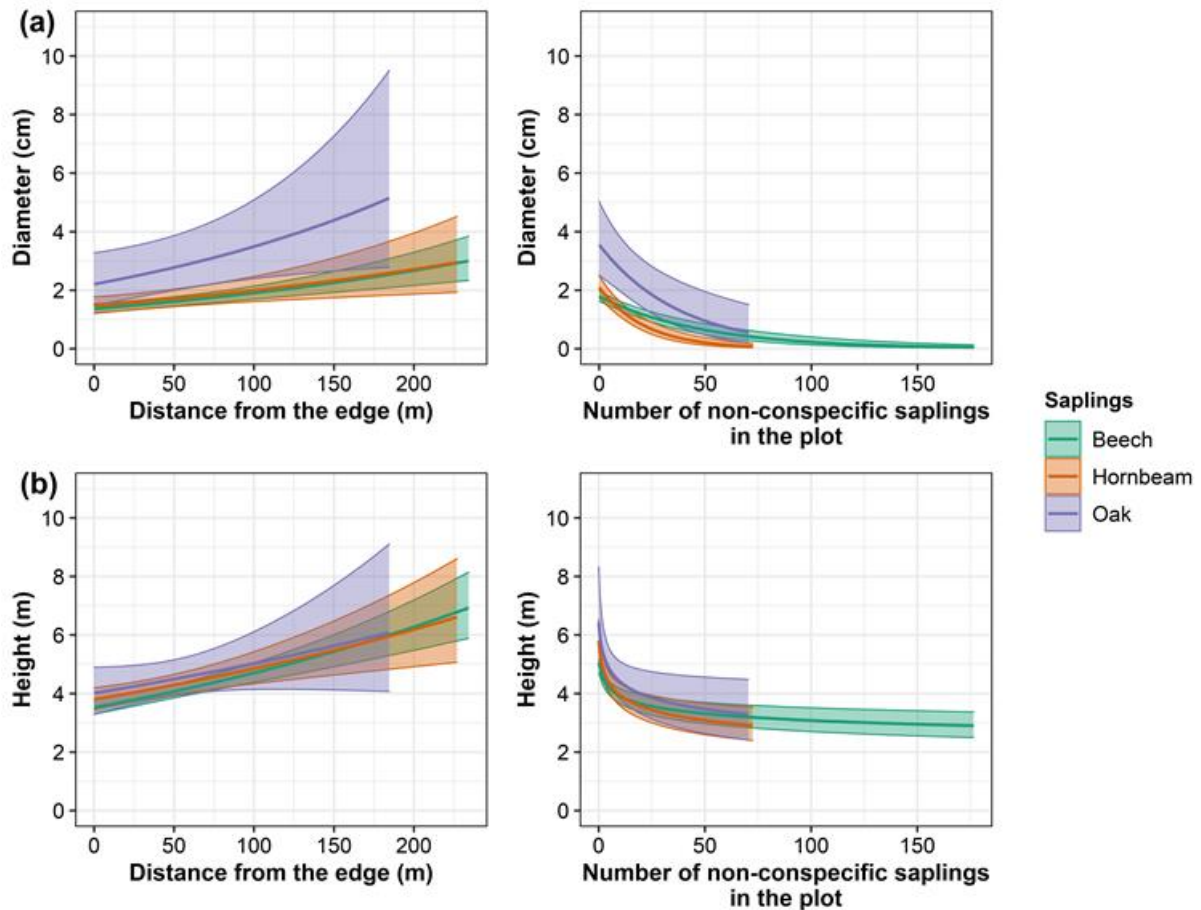
302

303 **Fig. 4. Predicted density of oak, beech, and hornbeam saplings for each former stand type**
 304 **(ST=Beech, Mixture or Oak), according to (a) the distance from the edge, and (b) soil C/N.**
 305 Density values were calculated using Equation 2 adjusted for each species. The 95% pointwise
 306 confidence interval of the predictor is represented. Note the logarithmic scale on the vertical
 307 axis.

308

309 3.3. Sapling DBH

310 The average DBH of oak, beech, and hornbeam stems over 1.3 m tall was 3.3
 311 (significant: **a**), 2.4 (**b**) and 3.1 cm (**a**), respectively. The distance from the edge had a positive
 312 effect on sapling DBH for the three species (**Fig. 5a**). Interspecific competition had a negative
 313 effect on the DBH of all three species (**Fig. 5a; Appendix, Table A3**). For an IC of more than
 314 50 saplings per plot, DBH was less than 1 cm for the three species. Unlike species presence and
 315 sapling density, when considering sapling DBH, oak showed better performance than beech
 316 and hornbeam. Hornbeam DBH was negatively correlated with pH, whereas pH had no
 317 influence on oak or beech DBH. DBH was not correlated with C/N for any species.



318
 319 **Fig. 5. (a) Predicted sapling DBH and (b) predicted sapling height of oak, beech and**
 320 **hornbeam along the distance from the edge and the number of non-conspecific saplings**
 321 **in the plot.** DBH and height were computed using Equations 3 and 4, respectively, adjusted for
 322 each species. The 95% pointwise confidence interval of the predictor is represented.

323

324 3.4. Sapling height

325 The average height for oak, beech and hornbeam saplings was 5.6, 5.2 and 5.6 m,
 326 respectively. Differences among the three species were very slight along gradients of distances
 327 from the edge or interspecific competition (**Fig. 5b**). Sapling height increased with the distance
 328 from the edge and decreased with increasing interspecific competition. Nitrogen availability
 329 had a positive effect on hornbeam height but not on beech or oak. On the contrary, pH had a
 330 positive effect on beech and oak height but not on hornbeam height.

331 **4. Discussion**

332 Our study compared the natural regeneration of oak, beech, and hornbeam, three major
333 species of European forests, 20 years after storm disturbance. The analysis was carried out using
334 a set of explained variables (species presence, sapling abundance, DBH and height) that may
335 be used to characterise the performance of the regeneration and that responded differently to
336 soil and stand factors. The results highlighted the overall dominance of beech and hornbeam
337 saplings over oak saplings, irrespective of the distance from the edge, former stand type,
338 interspecific competition, soil acidity and nitrogen availability. Oak presence was two to three
339 times lower than that of hornbeam or beech, and oak had an average density 10 times lower
340 than the average density of hornbeam or beech. We showed that oak had a higher density in
341 stands formerly composed of oak and near the forest edges, which is in line with Hypothesis 1
342 regarding the low dispersal ability of the species. However, increasing the distance from the
343 forest edge did not have a stronger negative effect on the density of beech compared to oak,
344 which partially invalidates Hypothesis 3. DBH for the three species increased with increasing
345 canopy opening (reflected by the distance from the gap edge), and oak DBH was larger than
346 beech or hornbeam DBH, which validates Hypothesis 2 and partially validates Hypothesis 3.
347 Finally, oak density was higher on soils with low nitrogen availability, which also corresponded
348 to sites where hornbeam was absent, in agreement with Hypothesis 4.

349 **4.1. Initial seed rain has a predominant effect over interspecific** 350 **competition and canopy opening**

351 Modelling sapling density and species presence highlighted the effects of former stand
352 composition and distance from the forest edge, especially for oak and beech. Saplings of the
353 two species were more present and denser where they dominated the former stand and close to
354 the forest edge. Species composition of former stands and distance to potential seed trees are
355 known to be correlated with seed availability and, eventually, species presence and density

356 (Amm et al., 2012; Clark et al., 1999; Nathan & Muller-Landau, 2000). Former stand type
357 determined the seed source before and after the disturbance occurred, and the distance from the
358 forest edge represents the distance from the seed source after the disturbance. These effects are
359 expected to be stronger for barochorous species with short seed dispersal distances, such as
360 beech and oak (Sagnard et al., 2007; Vittoz and Engler, 2007; Battaglia et al., 2008). An
361 important secondary disperser is the European jay, but Gómez (2003) observed that it avoids
362 large open areas. Our results emphasize the effect of the initial seed rain over the effect of
363 interspecific competition or canopy opening on the abundance of the species. Distance to gap
364 edge reflects simultaneous variations in proximity to seed trees, light availability and inter-
365 sapling competition. Among these three factors, proximity to seed trees is the only factor that
366 leads to a positive correlation between distance to gap edge and sapling abundance or sapling
367 presence, which was observed in our study, indicating the predominant effect of the proximity
368 to seed trees over the two other factors. This result is in agreement with previous studies that
369 show that the presence of oak in the overstory promotes its regeneration (Petritan et al., 2012;
370 Annighöfer et al., 2015; Manso et al., 2020) and that, conversely, a high proportion of beech in
371 the overstory reduces oak regeneration (Hein and Dhôte, 2006). Our study went further and
372 showed the predominant effect of initial seed availability on the abundance of oak, 20 years
373 after the gap creation.

374 **4.2. Canopy opening and interspecific competition modulate the** 375 **primary effect of initial seed availability**

376 Average oak sapling DBH was equivalent or greater than average beech and hornbeam
377 DBH. Models highlighted the major role of the distance from the forest edge on the DBH and
378 height of the three species: greater distance from the edge implies a higher level of irradiance
379 in openings and, consequently, a greater sapling DBH and height. Unlike Ligot et al., (2013),
380 Van Couwenberghe et al. (2013) or Tinya et al. (2020), we did not observe a dominance of

381 beech or hornbeam over oak DBH or height, showing that oak saplings were not overtopped 20
382 years after opening. However, the positive effect of canopy opening on sapling DBH and height
383 was strongly modulated by interspecific competition for the three species. When competition
384 increased, the effect of the distance from the edge was reduced for the three species. As previous
385 studies showed, interspecific competition has a major impact on oak growth (De Groote et al.,
386 2018; Toïgo et al., 2018; Mölder et al., 2019b) and on beech growth (Collet et al., 2014). In
387 complement to these studies, our results showed similar negative impacts of interspecific
388 competition on the growth of hornbeam saplings. Thus, canopy opening and interspecific
389 competition modulated the initial effect of former stand type through seed production and
390 dispersal and, although all species were more abundant at the gap edge, the saplings reached a
391 greater DBH and height in the gap centre.

392 **4.3. Soil nutrients influence regeneration mainly through the effects** 393 **on species distribution in the mature stands**

394 Soil nitrogen availability strongly influenced the regeneration of the three species (presence
395 and density), especially for hornbeam, which was absent in oligotrophic soils with C/N higher
396 than 20, in agreement with Pinto & Gégout (2005), and Walthert & Meier (2017). The trophic
397 niche of saplings we observed here is similar to that of adult trees reported in the literature for
398 the three species. Complementing previous studies, our study provides information about the
399 stem density response of the three species to soil characteristics. At the regeneration stage,
400 hornbeam is very competitive towards the other species on rich soils, with a higher density than
401 oak for C/N values below 15, and higher than beech in former oak stands. In former oak stands
402 on rich soils, hornbeam is the main competitor for oak.

403 **4.4. Abundance and DBH are needed to characterize the**
404 **regeneration strategy of the three species**

405 Our study emphasized the need to use more than one variable to qualify regeneration
406 success. Our models revealed different responses of the four explanatory variables (sapling
407 presence, density, DBH and height). Nevertheless, not all four variables were necessary to reach
408 our final conclusions. Sapling DBH and height had similar responses to explanatory factors and
409 seemed redundant. Considering that sapling DBH is easier to measure than sapling height, DBH
410 could therefore be favoured over height in experiments similar to our study. Similarly, presence
411 and abundance provided correlated results. Presence is quicker to record in the field than
412 abundance, but abundance is more informative since it also provides an estimate of stem
413 density, a useful variable for the forest manager. The choice between recording presence or
414 abundance depends on the objectives of the inventory and recording sapling abundance and
415 DBH seems relevant to characterise species regeneration strategies.

416 **4.5. Management perspectives**

417 This study was conducted in forest plots without any silvicultural treatment, which is
418 considered to represent unfavourable conditions for oak regeneration in mixed stands (Mölder
419 et al., 2019a). However, 20 years after the storm, at the end of the regeneration phase, oak was
420 still present and oak saplings were not overtopped by competing species. Since the absence of
421 silvicultural operations does not lead to the total disappearance of oak, it may be a silvicultural
422 option as long as the area to be regenerated is large enough to allow some oak saplings to
423 regenerate. Nonetheless, after the regeneration phase, as the canopy progressively closes,
424 shade-tolerant species are expected to become more and more dominant at the expense of oak.
425 When the saplings enter the exclusion phase, competition from shade-tolerant species should
426 probably be controlled by regular silvicultural operations if the objective is to maintain oak in
427 the future stand.

428 Many studies have focused on the balance between oak and beech (Kohler et al., 2020)
429 since these two species represent a great economic interest. However, the balance between
430 hornbeam and oak is equally important, especially at the regeneration stage when hornbeam
431 can strongly compete with oak (Sikkema et al., 2016). We have demonstrated that creating
432 canopy openings favours hornbeam regeneration in nutrient-rich soils. Hornbeam is a pivotal
433 component of regeneration in many European oak and beech forests since it forms dense
434 regeneration and presents height growth rates similar to oak and beech. Up until now, hornbeam
435 was largely overlooked in research studies that analysed oak regeneration, probably because
436 hornbeam is usually dominated by oak and beech when it reaches the adult stage (San-Miguel-
437 Ayanz et al., 2016). It seems necessary to gain better knowledge about the impact of hornbeam
438 on oak regeneration in order to be able to deliver practical recommendations to successfully
439 regenerate oak in all forest contexts where hornbeam is abundant.

440 Our study raises questions about the future of European forests in a changing climate
441 context where it is predicted that storms will become more severe and/or more frequent. We
442 demonstrated that the creation of forest gaps favours the development of beech, which is
443 generally classified as a species more sensitive to drought than oak. In this context, forest
444 management plays an essential role in the composition of future stands since it may prevent the
445 development of monospecific regeneration of a species that is potentially fragile in the face of
446 climate change.

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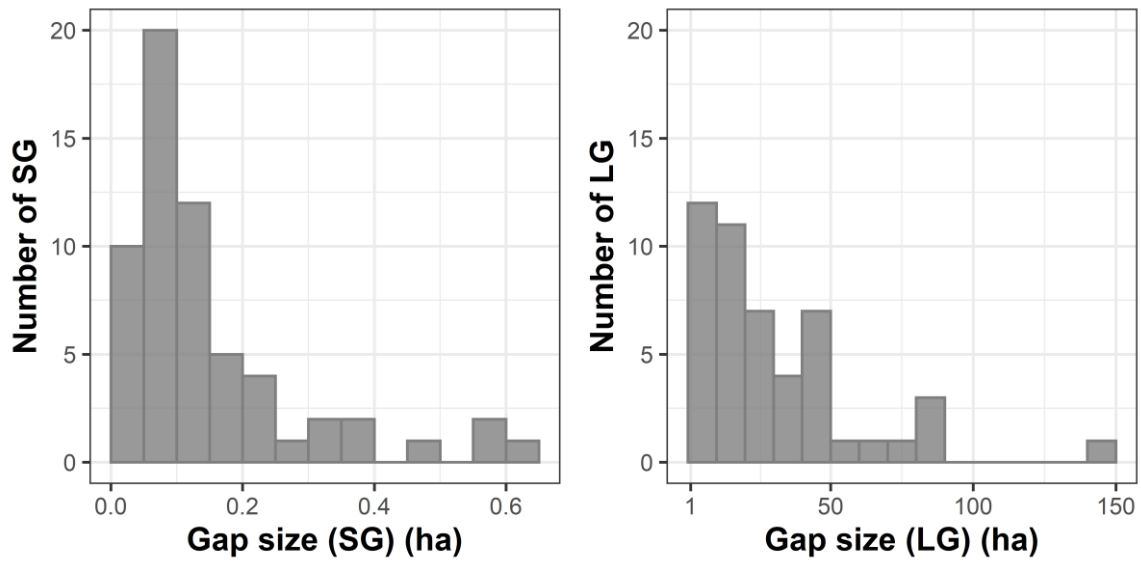
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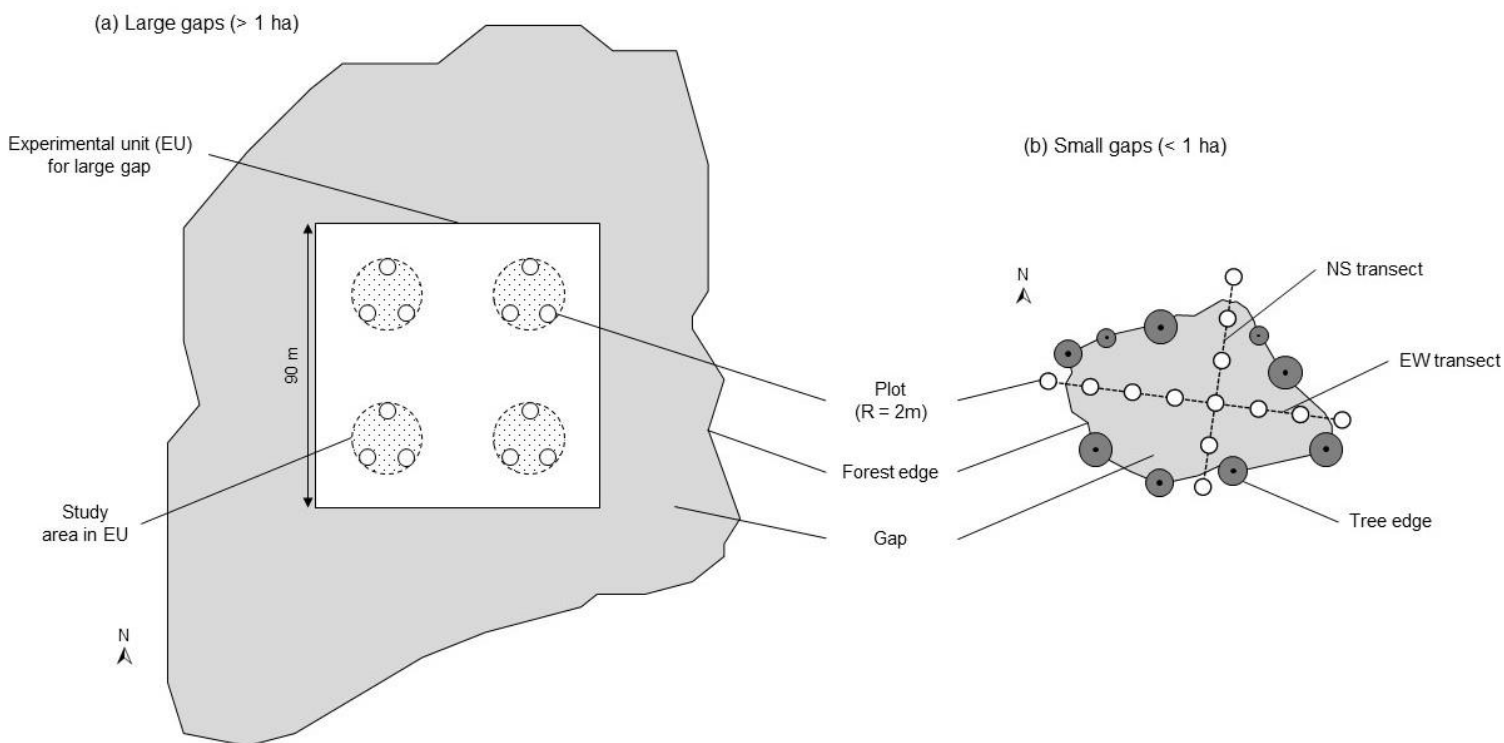
634 **5. Appendices**



635

636 **Fig. A1. Gap size distribution for (a) small gaps (SG); (b) large gaps (LG).**

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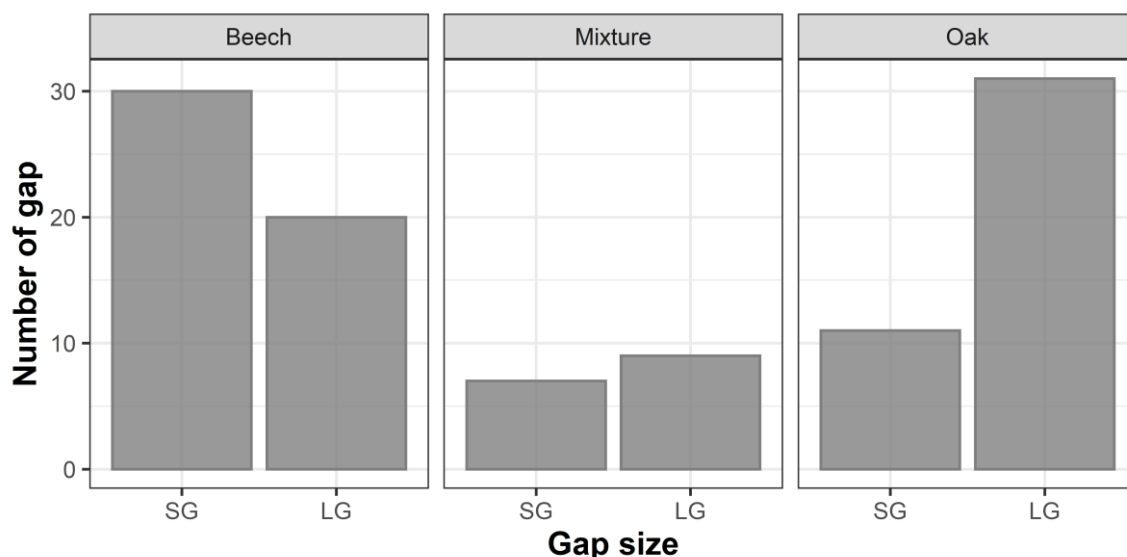


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640 **Fig. A2. Diagram of the two experimental devices according to gap size.**

641



642

643 **Fig. A3. Gap distribution for small gaps (SG) and large gaps (LG) according to species**
 644 **composition of the former stand type.**

645

SPECIES	PREDICTORS	ESTIMATE	STD.ERROR	Z.VALUE	P-VALUE
OAK	(Intercept)	-1.14	0.25	-4.60	<0.001
	D	-0.48	0.17	-2.85	<0.01
	C/N	0.58	0.15	3.85	<0.001
	IC	1.01	0.23	4.46	<0.001
	ST mixture	-1.30	0.48	-2.71	<0.01
	ST beech	-0.94	0.35	-2.67	<0.01
	IC:ST mixture	-0.58	0.31	-1.83	0.06
	IC:ST beech	-0.47	0.32	-1.46	0.14
BEECH	(Intercept)	-0.03	0.30	-0.11	0.91
	D	-0.75	0.17	-4.36	<0.001
	C/N	0.04	0.20	0.21	0.84
	IC	-0.03	0.10	-0.30	0.76
	ST mixture	1.81	0.58	3.10	<0.01
	ST beech	2.67	0.48	5.55	<0.001
	IC:ST mixture	-0.09	0.31	-0.29	0.77
	IC:ST beech	2.75	0.90	3.07	<0.01
HORNBEAM	(Intercept)	0.12	0.30	0.38	0.70
	D	-0.12	0.18	-0.67	0.50
	C/N	-1.95	0.27	-7.16	<0.001
	IC	-0.16	0.18	-0.87	0.38
	ST mixture	-1.25	0.59	-2.12	0.03
	ST beech	-1.52	0.41	-3.67	<0.001
	IC:ST mixture	0.51	0.34	1.52	0.13
	IC:ST beech	0.66	0.25	2.61	<0.01

646 **Table A1. Generalized Linear Mixed Model for presence analysis: effect of distance from**
 647 **edge (D), nitrogen availability (C/N), number of stems (IC,) and former stand type (ST).**
 648 For each species, all seedlings > 0.1 m were recorded in a plot of 12.6 m². Coefficient
 649 parameters of the fixed effects (D, C/N, IC and ST for the former stand type with oak as the
 650 reference) and their associated p-values (Z test).
 651

652

SPECIES	PREDICTORS	COND.ESTIMATE	COND.STD.ERROR	COND.Z.VALUE	COND.P-VALUE
OAK	(Intercept)	-1.78	0.58	-3.06	<0.01
	D	-0.02	0.005	-3.92	<0.001
	C/N	0.10	0.03	2.94	<0.01
	log(IC)	0.33	0.09	3.53	<0.001
	ST mixture	-1.45	0.49	-2.97	<0.01
	ST beech	-1.52	0.41	-3.66	<0.001
	D:ST mixture	0.02	0.009	1.85	0.06
	D:ST beech	0.02	0.007	3.02	<0.01
BEECH	(Intercept)	0.86	0.45	1.92	0.05
	D	-0.02	0.004	-4.80	<0.001
	C/N	0.02	0.03	0.80	0.42
	log(IC)	0.08	0.05	1.62	0.10
	ST mixture	0.71	0.40	1.75	0.08
	ST beech	0.92	0.30	3.02	<0.01
	D:ST mixture	0.02	0.01	2.79	<0.01
	D:ST beech	0.01	0.005	3.13	<0.01
HORNBEAM	(Intercept)	4.84	0.84	5.76	<0.001
	D	0.00	0.00	0.82	0.41
	C/N	-0.25	0.06	-4.15	<0.001
	log(IC)	0.23	0.08	2.88	<0.01
	ST mixture	-0.28	0.53	-0.53	0.60
	ST beech	-0.98	0.39	-2.52	0.01
	D:ST mixture	-0.01	0.01	-1.37	0.17
	D:ST beech	-0.01	0.01	-1.40	0.16

653 **Table A2. Zero Inflated Negative Binomial Mixed Model for density analysis: effect of**
654 **distance from edge (D), nitrogen availability (C/N), number of stems (IC), and former**
655 **stand type (ST).** For each species, all seedlings > 0.1 m were recorded in a plot of 12.6 m².
656 Coefficient parameters of the fixed effects (D, C/N, IC and ST for the former stand type with
657 oak as the reference) and their associated p-values (Z test).
658

SPECIES	PREDICTORS	ESTIMATE	STD.ERROR	T.VALUE	P-VALUE
OAK	(Intercept)	2.52	1.28	1.96	0.05
	D	0.008	0.003	3.21	<0.01
	pH	-0.34	0.27	-1.28	0.20
	IC	-0.11	0.15	-0.75	0.45
	ST mixture	-0.07	0.49	-0.14	0.89
	ST beech	-0.11	0.25	-0.43	0.67
	D: IC	-0.0004	0.0001	-3.15	<0.01
	IC:pH	0.02	0.03	0.69	0.49
BEECH	(Intercept)	0.45	0.27	1.70	0.09
	D	0.004	0.0007	6.78	<0.001
	pH	-0.02	0.05	-0.47	0.64
	IC	-0.04	0.01	-3.52	<0.001
	ST mixture	-0.06	0.16	-0.39	0.70
	ST beech	0.02	0.12	0.15	0.88
	D:IC	0.0003	0.00005	-5.04	<0.001
	pH:IC	0.006	0.002	3.04	<0.01
HORNBEAM	(Intercept)	2.34	0.50	4.65	<0.001
	D	0.005	0.001	4.63	<0.001
	pH	-0.38	0.09	-4.23	<0.001
	IC	-0.15	0.03	-5.28	<0.001
	ST mixture	1.08	0.26	4.12	<0.001
	ST beech	0.59	0.18	3.21	<0.01
	D: IC	0.0006	0.0001	-6.20	<0.001
	pH: IC	0.02	0.004	5.51	<0.001

659 **Table A3. Linear Mixed Effect Model for diameter analysis: effect of distance from edge**
660 **(D), soil pH (pH), number of stems (IC) and former stand type (ST).** For each species, all
661 seedlings > 1.3 m were recorded in a plot of 12.6 m². Coefficient parameters of the fixed effects
662 (D, pH, IC and ST for the former stand type with oak as the reference) and their associated p-
663 values (Z test).
664

SPECIES	PREDICTORS	ESTIMATE	STD.ERROR	T.VALUE	P-VALUE
OAK	(Intercept)	2.86	0.71	4.01	<0.001
	D	0.0002	0.001	1.58	0.12
	pH	-0.18	0.09	-2.12	0.04
	C/N	-0.01	0.02	-0.60	0.55
	log(IC)	-0.16	0.06	-2.64	<0.01
BEECH	(Intercept)	0.91	0.24	3.74	<0.001
	D	0.003	0.0004	6.92	<0.001
	pH	0.06	0.03	2.29	0.02
	C/N	0.01	0.008	1.55	0.12
	log(IC)	-0.11	0.02	-5.82	<0.001
HORNBEAM	(Intercept)	1.33	0.37	3.54	<0.001
	D	0.002	0.007	3.51	<0.001
	pH	-0.04	0.04	-0.87	0.38
	C/N	0.04	0.02	2.19	0.03
	log(IC)	-0.16	0.03	-5.00	<0.001

665 **Table A4. Linear Mixed Effect Model for diameter analysis: effect of distance from edge**
666 **(D), soil pH (pH), nitrogen availability (C/N) and the number of stems (IC).** For each
667 species, two stems (larger and median diameter) were recorded in a plot of 12.6 m². Coefficient
668 parameters of the fixed effects (D, pH, C/N and IC) and their associated p-values (Z test).