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# Beech and hornbeam dominate oak 20 years after the creation of storm-induced gaps

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## Abstract

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

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

## 1. Introduction

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

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

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

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

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

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

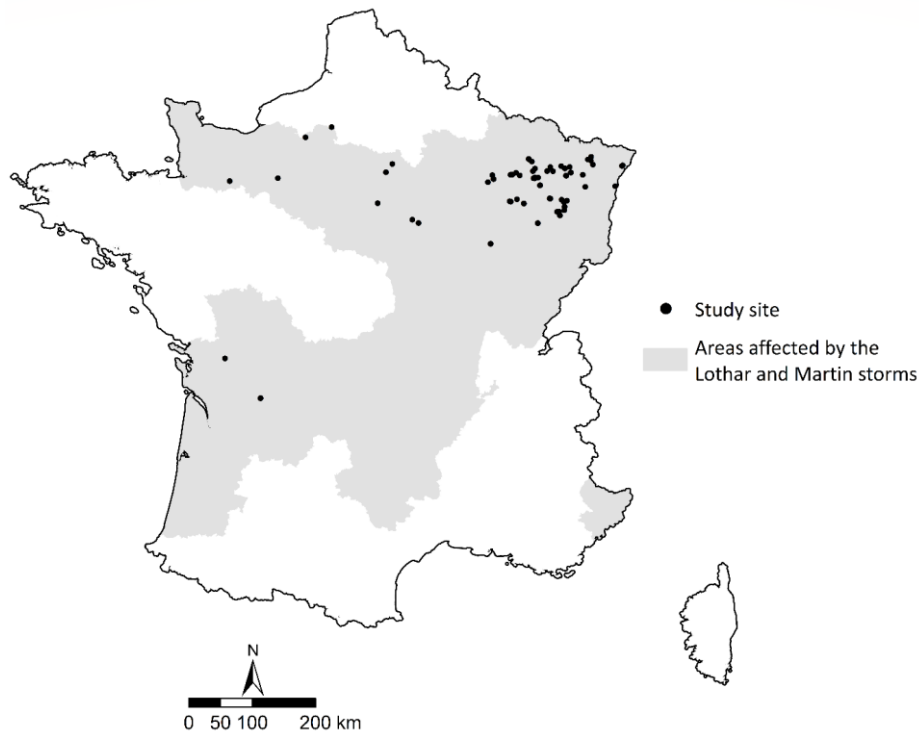
The aim of our study is to compare the natural regeneration of oak, beech and hornbeam in small to large gaps according to soil characteristics and former stand characteristics in order to identify the conditions the most favourable to oak regeneration and where oak could dominate over its main competitors.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

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

## **2. Material & Methods**

### **2.1. Study sites**

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



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

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

Former stand type (ST)	Gap size (ha)	C/N	pH	Sapling density (ha <sup>-1</sup> )
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)

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

## 2.2. Data collection

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

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



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

Species	Number of gaps	Number of plots	Number of saplings	Occurrence frequency	Sapling density (ha <sup>-1</sup> )	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

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

One soil sample per gap was collected in 2001 by taking a 0-5 cm layer of soil below the litter at the gap centre. Chemical analyses were carried out in the laboratory and pH-H<sub>2</sub>O, organic carbon and nitrogen content were measured following the NF ISO 10390, NF ISO 10694 and NF ISO 13878 procedures, respectively.

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

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

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

### **2.3. Data analysis**

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

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

#### **2.3.1. Species presence**

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

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

$$\begin{aligned} \text{Eq. 1. } \text{logit}(p_{ij}) &= \log\left(\frac{p_{ij}}{1 - p_{ij}}\right) \\ &= \beta_0 + \beta_1 D_{ij} + \beta_2 \frac{C}{N_i} + \beta_3 IC_{ij} + \beta_4 ST_i + \beta_5 IC_{ij} * ST_i + \text{Gap}_i \end{aligned}$$

where  $\text{Gap}_i$  is the random effect sampled from a normal distribution  $N(0, \sigma^2)$  and  $\beta_s$  are the unknown coefficients to be determined. Centred and scaled explanatory variables were used to solve convergence issues.

### 2.3.2. Species-specific sapling abundance

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

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

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

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

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

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

where  $\pi_{ij}$  is the probability of false 0,  $\mu_{ij}$  the expected value for the count process,  $\text{Gap}_i$  the random effect sampled from a normal distribution  $N(0, \sigma^2)$  and  $\beta$ s the unknown coefficients.  $\pi_{ij}$  was modelled to ensure that the logistic part of the model contained only an intercept  $\gamma$ .

### 2.3.3. Species-specific sapling DBH

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

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

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

where  $\text{Gap}_i$  is the random effect of gap  $i$  sampled from a normal distribution  $N(0, \sigma^2)$ ,  $\beta$ s the unknown coefficients, and  $\varepsilon_{ij}$  the normally distributed model error.

### 2.3.4. Species-specific sapling height

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

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

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

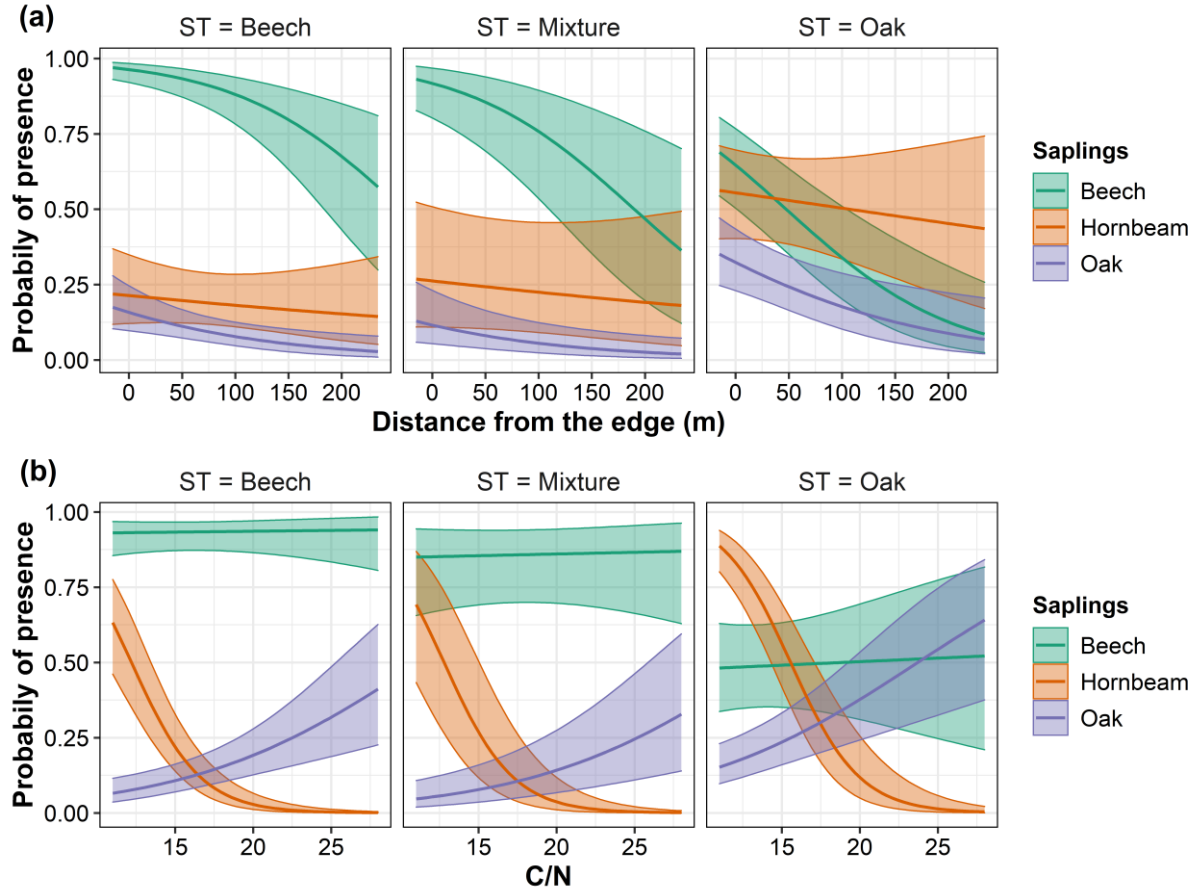
where  $\text{Gap}_i$  is the random effect of gap  $i$  sampled from a normal distribution  $N(0, \sigma^2)$ ,  $\beta$ s the unknown coefficients, and  $\varepsilon_{ij}$  the normally distributed model error.

## 3. Results

### 3.1. Species presence

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

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



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

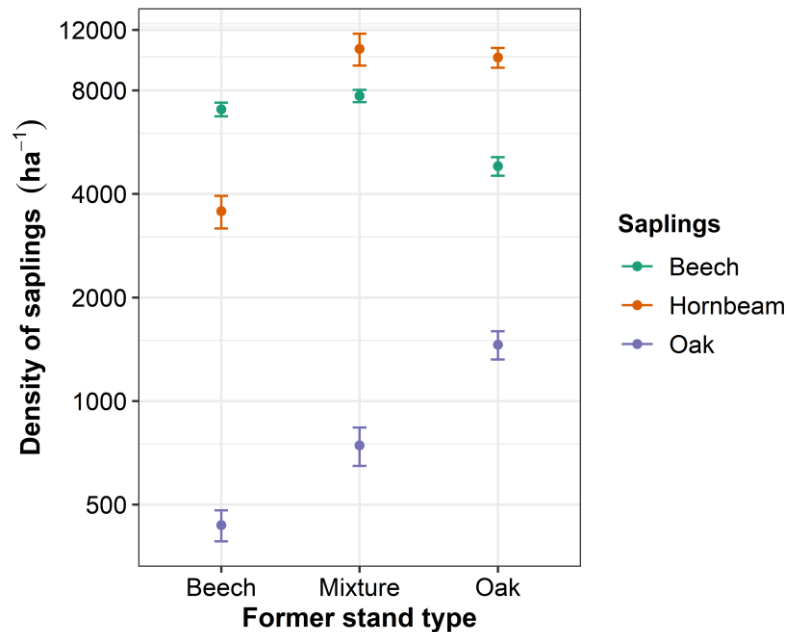
MODEL	PREDICTORS	OAK	BEECH	HORNBEAM
		p-value	p-value	p-value
Presence: Equation 1				
	D	<0.01	<0.001	0.50
	C/N	<0.001	0.84	<0.001
	IC	<0.001	0.92	0.08
	ST	<0.01	<0.001	<0.001
	IC:ST	0.15	<0.01	0.03
Density: Equation 2				
	D	0.01	<0.001	0.49
	C/N	<0.01	0.42	<0.001
	log(IC)	<0.001	0.10	<0.01
	ST	<0.01	<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

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

### 3.2. Sapling abundance

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

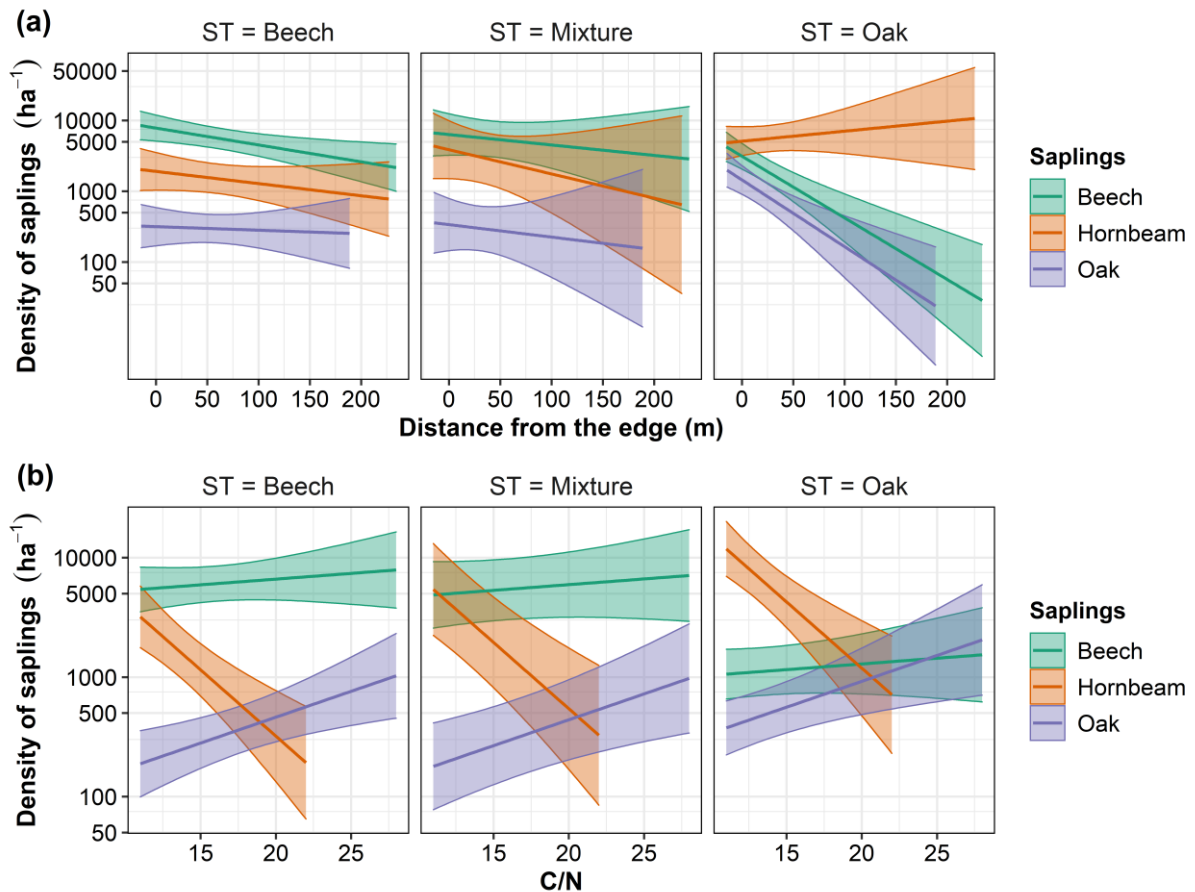
more saplings in former oak stands, whereas for beech, there are only 60% more saplings when the former stand is beech.



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

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

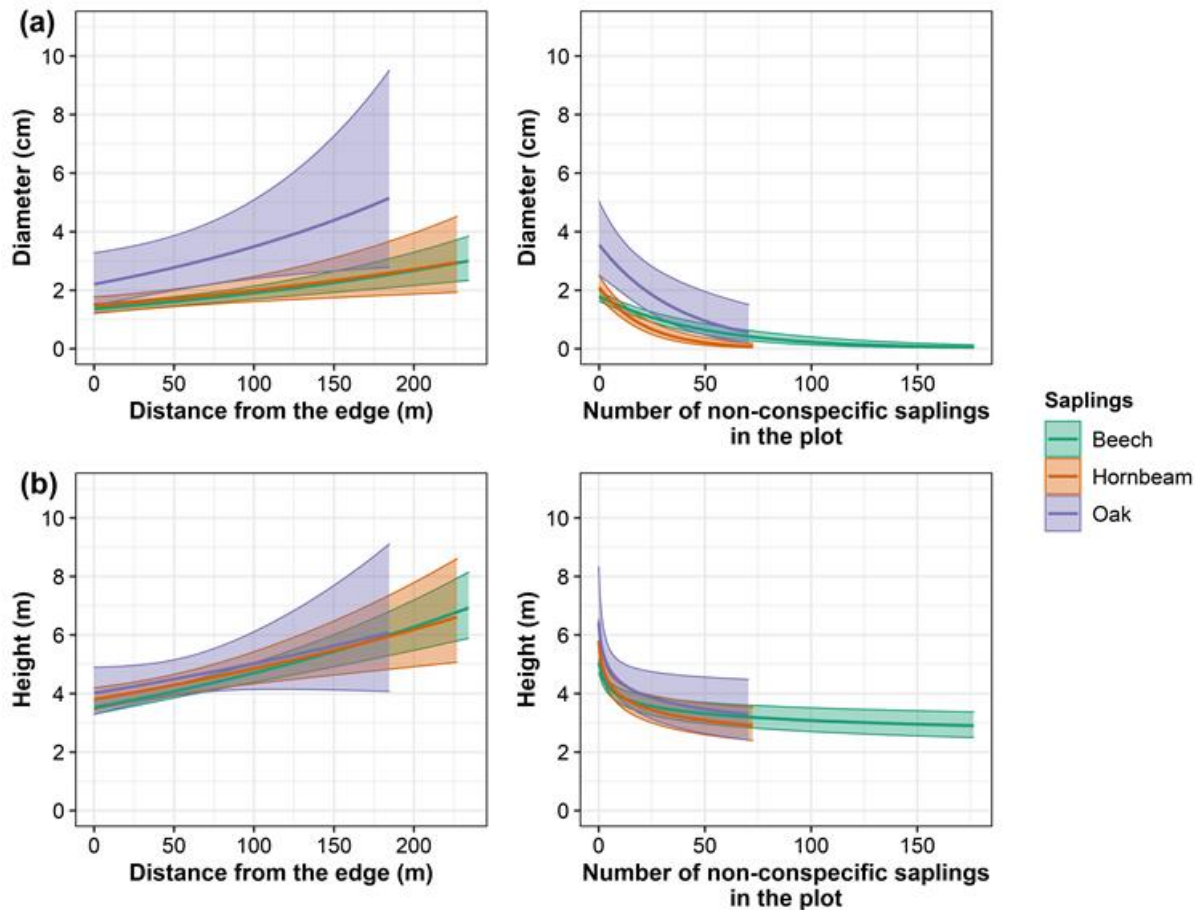




**Fig. 4. Predicted density of oak, beech, and hornbeam saplings for each former stand type (ST=Beech, Mixture or Oak), according to (a) the distance from the edge, and (b) soil C/N.** Density values were calculated using Equation 2 adjusted for each species. The 95% pointwise confidence interval of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

### 3.3. Sapling DBH

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



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

### 3.4. Sapling height

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

## 4. Discussion

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

### 4.1. Initial seed rain has a predominant effect over interspecific competition and canopy opening

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

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

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

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

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

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

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

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

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

#### **4.5. Management perspectives**

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

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

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

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5. Appendices

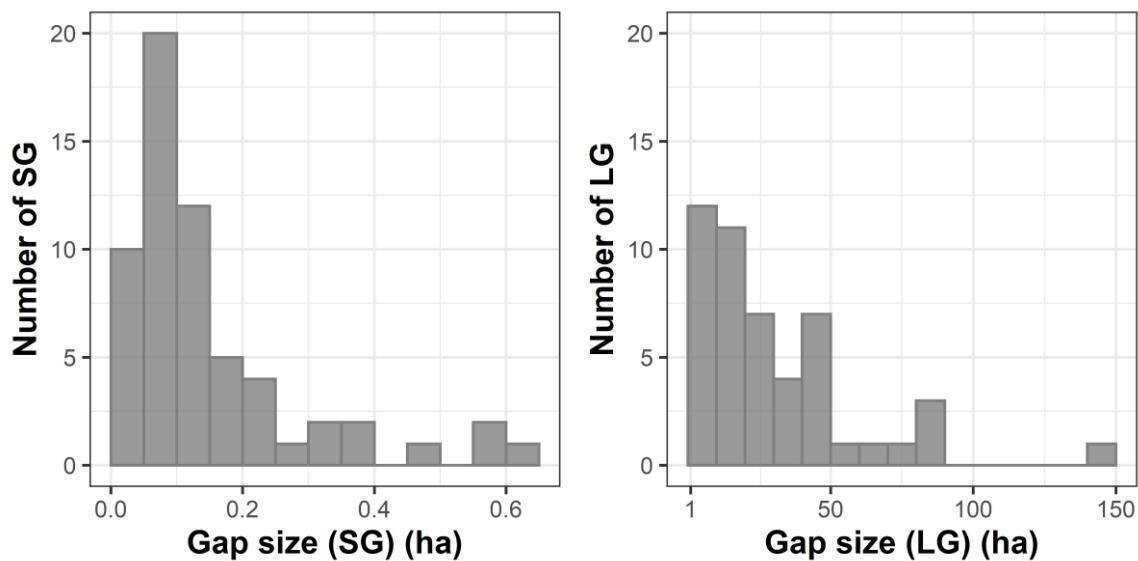


Fig. A1. Gap size distribution for (a) small gaps (SG); (b) large gaps (LG).

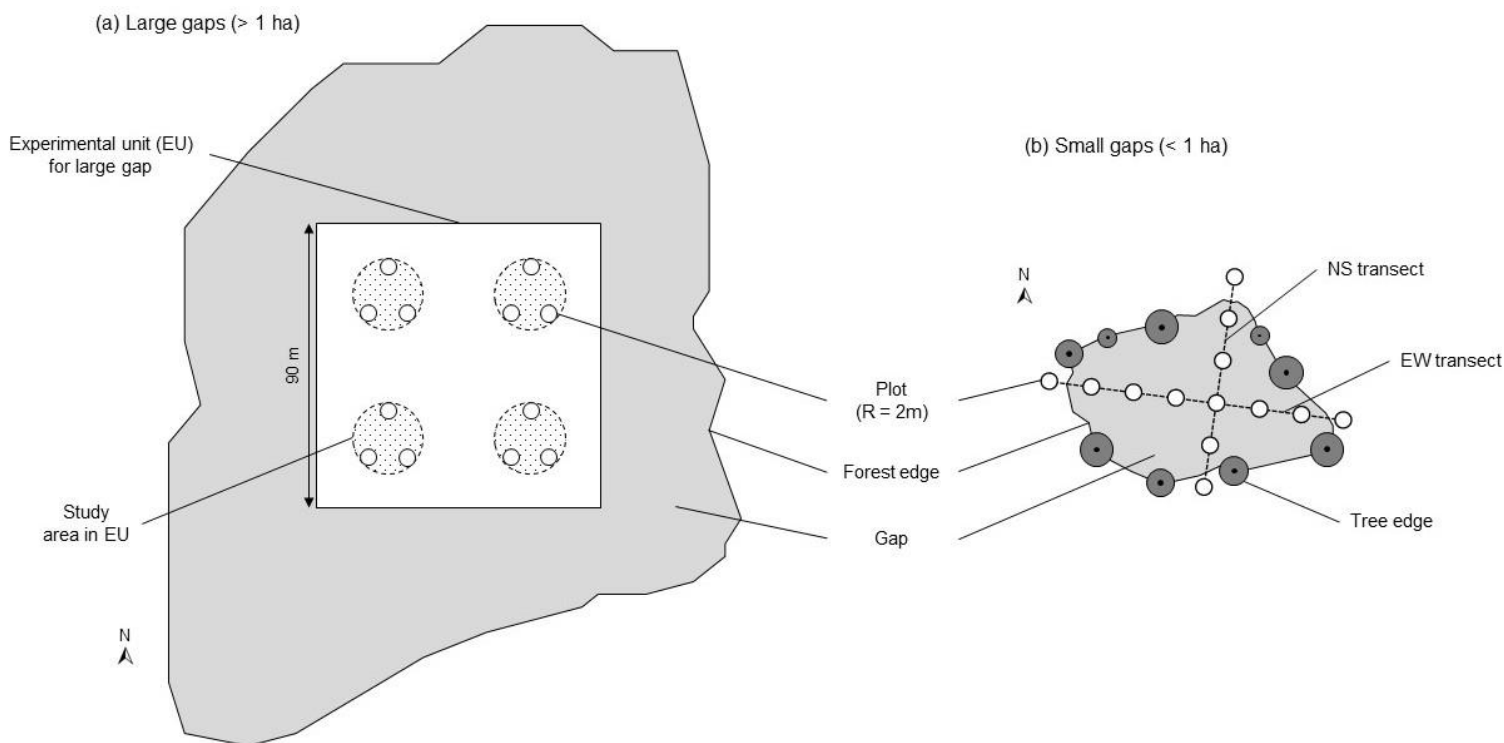
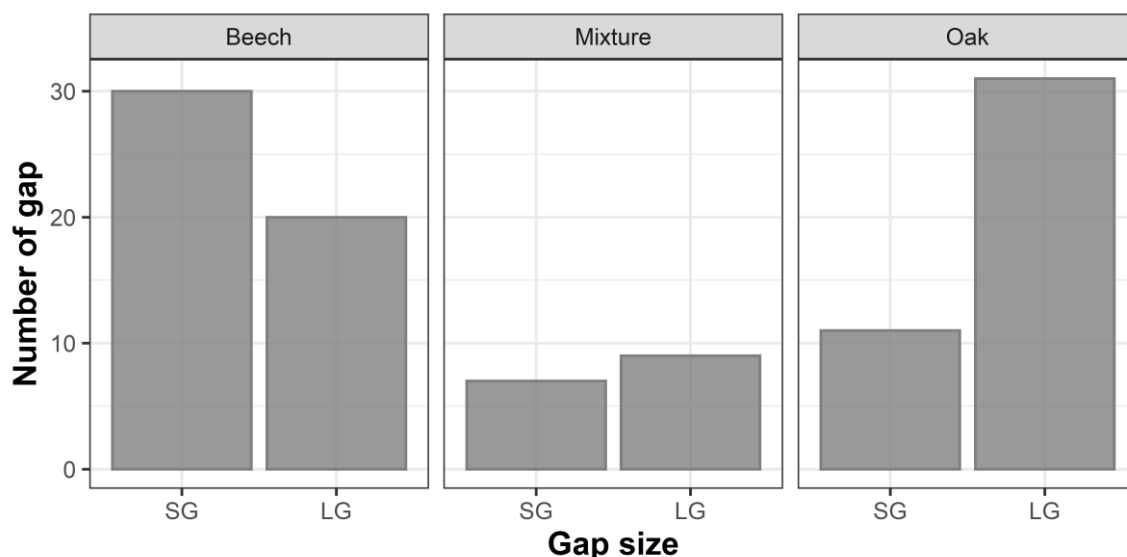


Fig. A2. Diagram of the two experimental devices according to gap size.



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

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

**Table A1. Generalized Linear Mixed Model for presence analysis: effect of distance from edge (D), nitrogen availability (C/N), number of stems (IC,) and former stand type (ST).** For each species, all seedlings > 0.1 m were recorded in a plot of 12.6 m<sup>2</sup>. Coefficient parameters of the fixed effects (D, C/N, IC and ST for the former stand type with oak as the reference) and their associated p-values (Z test).

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

**Table A2. Zero Inflated Negative Binomial Mixed Model for density analysis: effect of distance from edge (D), nitrogen availability (C/N), number of stems (IC), and former stand type (ST).** For each species, all seedlings > 0.1 m were recorded in a plot of 12.6 m<sup>2</sup>. Coefficient parameters of the fixed effects (D, C/N, IC and ST for the former stand type with oak as the reference) and their associated p-values (Z test).

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

**Table A3. Linear Mixed Effect Model for diameter analysis: effect of distance from edge (D), soil pH (pH), number of stems (IC) and former stand type (ST).** For each species, all seedlings > 1.3 m were recorded in a plot of 12.6 m<sup>2</sup>. Coefficient parameters of the fixed effects (D, pH, IC and ST for the former stand type with oak as the reference) and their associated p-values (Z test).

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

**Table A4. Linear Mixed Effect Model for diameter analysis: effect of distance from edge (D), soil pH (pH), nitrogen availability (C/N) and the number of stems (IC).** For each species, two stems (larger and median diameter) were recorded in a plot of 12.6 m<sup>2</sup>. Coefficient parameters of the fixed effects (D, pH, C/N and IC) and their associated p-values (Z test).