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► To cite this version:

Julien Barrere, Linda Petersson, Vincent Boulanger, Catherine C. Collet, Annika Felton, et al.. Canopy openness and exclusion of wild ungulates act synergistically to improve oak natural regeneration. *Forest Ecology and Management*, 2021, 487 (11), pp.1-13. 10.1016/j.foreco.2021.118976 . hal-03926049

HAL Id: hal-03926049

<https://hal.science/hal-03926049>

Submitted on 22 Mar 2023

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1 **Canopy openness and exclusion of wild ungulates act**
2 **synergistically to improve oak natural regeneration.**

3

4 Julien Barrere^{a,d*}, Linda K. Petersson^b, Vincent Boulanger^c, Catherine Collet^a, Annika M.
5 Felton^b, Magnus Löf^b, Sonia Saïd^d

6

7 ^a Université de Lorraine, Agroparistech, INRAE, UMR SILVA, 54000 Nancy, France

8 ^b Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences,
9 Box 49, 230 53 Alnarp, Sweden

10 ^c Office National des Forêts, Département Recherche et Développement, Boulevard de
11 Constance, 77300 Fontainebleau, France

12 ^d Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique,
13 « Monfort », 01330 Birieux, France

14

15 *corresponding author:

16 julien.barrere@inrae.fr

17 <https://orcid.org/0000-0002-6686-726X>

18

19 **Abstract**

20 The recruitment of forest trees is driven by both bottom-up processes (the acquisition of
21 resources) and top-down processes (herbivory). To initiate stand regeneration, foresters
22 commonly reduce tree density to increase light levels for seedlings and enhance primary
23 productivity. These changes in vegetation dynamics, however, could also influence effects of
24 ungulate browsing, resulting in unintended consequences for forest management. Here, we
25 assessed how effects of ungulate exclusion and canopy opening interacted to affect the
26 regeneration of two oak species: *Quercus robur* and *Quercus petraea*. We monitored the
27 growth and survival of oak seedlings for two to three growth seasons in paired fenced and
28 unfenced plots under contrasting conditions of canopy openness (8% to 52%) at five sites in
29 southern Sweden and three sites in northeastern France. We scored browsing in the unfenced
30 plots by the four cervids occurring in these areas (*Alces alces*, *Capreolus capreolus*, *Cervus*
31 *elaphus* and *Dama dama*). Fencing increased the growth of (mostly taller) seedlings occurring
32 in Sweden and the survival of (mostly smaller) seedlings in France. Both effects increased as
33 canopies became more open. Browsing reduced oak seedling growth in both countries,
34 independently of canopy openness. Canopy openness increased browsing levels in Sweden.
35 Cervid densities did not appear to modify how fencing affected oak seedling growth and
36 survival. In both contrasting forest environments, creating gaps tended to enhance ungulate
37 damage on young forest stands as browsing frequency increased. We conclude that net forest
38 regeneration reflects a subtle equilibrium between enhancing resource availability, boosting
39 seedling growth, and limiting herbivory, which curtails seedling growth and survival.

40 **Key words**

41 Plant-herbivore interactions, red deer, roe deer, moose, fallow deer, herbivory

42

43 **1. Introduction**

44 The development of most living communities is driven by both bottom-up and top-down
45 processes. A bottom-up process is the regulation of communities by lower trophic levels – e.g.
46 limited nutrients for plants or prey for predators – while a top-down process is the impact of a
47 higher trophic level on lower levels – e.g. predation (Hairston et al., 1960; Power, 1992). For
48 decades, scientists have focused on the respective importance of these two types of
49 mechanisms to regulate populations (Dyer and Letourneau, 1999; Hairston et al., 1960), and
50 on the factors influencing resource acquisition (bottom-up) and predation (top-down) (Power,
51 1992). In recent years, there has been a growing interest in the interactions between bottom-
52 up and top-down processes, observed in a wide range of ecosystems (Churski et al., 2017;
53 Collar et al., 2017; Lynam et al., 2017; Wieters, 2005). For instance, both in marine
54 communities (Hillebrand, 2005) and in cultivated fields (Moran and Scheidler, 2002), it has
55 been shown that increasing resource availability does not necessarily benefit the organism
56 consuming the resource as it may also enhance the importance of predation. This type of
57 interaction may have major implications for ecosystem management, as it questions the
58 efficiency of an anthropogenic increase in resource availability to promote organisms of high
59 ecological or economic value such as, for instance, forest trees.

60 Light is a crucial resource for plants as it provides them the energy required to assimilate
61 carbon and grow, defend and store nutrients (Ericsson et al., 1996; Giertych et al., 2015)
62 while ungulate browsing is a major top-down force regulating the production of plant biomass
63 (Martin et al., 2010). In forest ecosystems, because the canopy of mature trees intercepts most
64 of the solar irradiance, tree seedlings often need an opening of the canopy to be recruited into
65 adult trees (Watt, 1947; Yamamoto, 2000). The natural formation of gaps through the
66 senescence and decay of old trees or natural disturbances such as fire or storms can take a
67 very long time. In forestry, the harvesting of adult trees at their economic optimum hastens

68 canopy opening and initiates the process of forest natural regeneration. Though many studies
69 acknowledge that the creation of canopy gaps enhances seedling growth and biomass
70 production (Cannell et al., 1988; Lu et al., 2018), surprisingly little is known about how this
71 sudden increase in resource availability influences top-down processes such as ungulate
72 browsing.

73 A high degree of canopy openness often leads to an increase in ground cover (Willms et al.,
74 2017) and species richness (Alexander and Mack, 2017) in the forest understory. An increase
75 in canopy openness may also, however, increase browsing pressure in forest gaps by
76 providing a higher quantity and diversity of forages (Kuijper et al., 2009; Mangas and
77 Rodríguez-Estival, 2010). Other studies have documented that plants growing under canopy
78 gaps may have a different chemical composition than plants growing in the shade (Agrell et
79 al., 2000; Giertych et al., 2015), and hence a different palatability for ungulates (Tucker et al.,
80 1976). For instance, light-demanding species are believed to be more palatable than shade-
81 tolerant species due to a higher nutrient content and fewer chemical defenses (e.g. phenolic
82 compounds) (Giertych et al., 2015; Kitajima et al., 2012). Lastly, canopy openness may
83 influence the ability of individual seedlings to recover and/or respond to browsing in terms of
84 growth, morphology or chemistry. No common response across tree species has been found,
85 however: light availability may improve or worsen seedling growth response to deer browsing
86 in field conditions, depending on tree species (Baraza et al., 2010; Kupferschmid et al., 2014).
87 Petersson et al. (2019) showed that the accelerating decline in pedunculate (*Quercus robur* L.)
88 and sessile oak (*Quercus petraea* (Matt.) Liebl.) regeneration observed in Sweden over the
89 last 60 years was due to the increased abundance of wild ungulates, but also to changes in
90 forestry practice that led to denser forests and insufficient light availability for seedlings (Von
91 Lüpke, 1998). This increase in ungulate populations follows a global trend observed in the
92 Northern Hemisphere (Beguin et al., 2016; Côté et al., 2004). In most temperate European

93 forests, pedunculate and sessile oak (hereinafter referred to as oak) are classified as highly
94 palatable species (Bergqvist et al., 2018; Kullberg and Bergström, 2010). Browsing by wild
95 ungulates may therefore be an important limiting factor for growth during the first stages of
96 oak regeneration (Braithwaite and Mayhead, 1996; Harmer, 2001). Browsing may also reduce
97 oak seedling survival, though to a lower extent than growth, due to the high sprouting ability
98 of oak seedlings (Drexhage and Colin, 2003). Several field studies in Europe have confirmed
99 that fencing to exclude wild ungulates could greatly benefit oak natural regeneration by
100 protecting the seedlings from browsing (Leonardsson et al., 2015; Petersson et al., 2020). Oak
101 is also particularly shade-intolerant at the beginning of the regeneration phase and cannot
102 survive low light availability (Von Lüpke, 1998). In forest environments, opening the canopy
103 is often necessary to achieve the successful regeneration of these oak species (Ligot et al.,
104 2013; Petersson et al., 2020).

105 Because its regeneration is highly influenced by both ungulates browsing and canopy
106 openness (Leonardsson et al., 2015; Petersson et al., 2020; Tinya et al., 2020; Von Lüpke,
107 1998), a case study of oak is relevant when investigating the interactive effects of these two
108 factors on the first stages of natural regeneration – i.e. seedling development and survival.
109 Although many studies investigated the effects of canopy openness and browsing on oak
110 regeneration, the interactive effect of these two factors and the mechanisms driving this
111 interaction are poorly understood. In this paper, we used the data from two comparable
112 studies, conducted over similar periods in forests in southern Sweden and northeastern
113 France. Both studies monitored the growth and survival of oak seedlings in pairs of fenced
114 and unfenced plots located under different levels of canopy openness ranging from 8% to
115 52%. We tested for the existence of common patterns in the contrasted environments (e.g. in
116 terms of ungulate species, soil or climate) considering the following predictions:

117 P1: Both ungulate exclusion and canopy openness increase oak seedling height growth (P1.a)
118 and survival (P1.b).

119 P2: Oak seedlings growing under an open canopy are more likely to be browsed by ungulates
120 than seedlings growing under closed canopy.

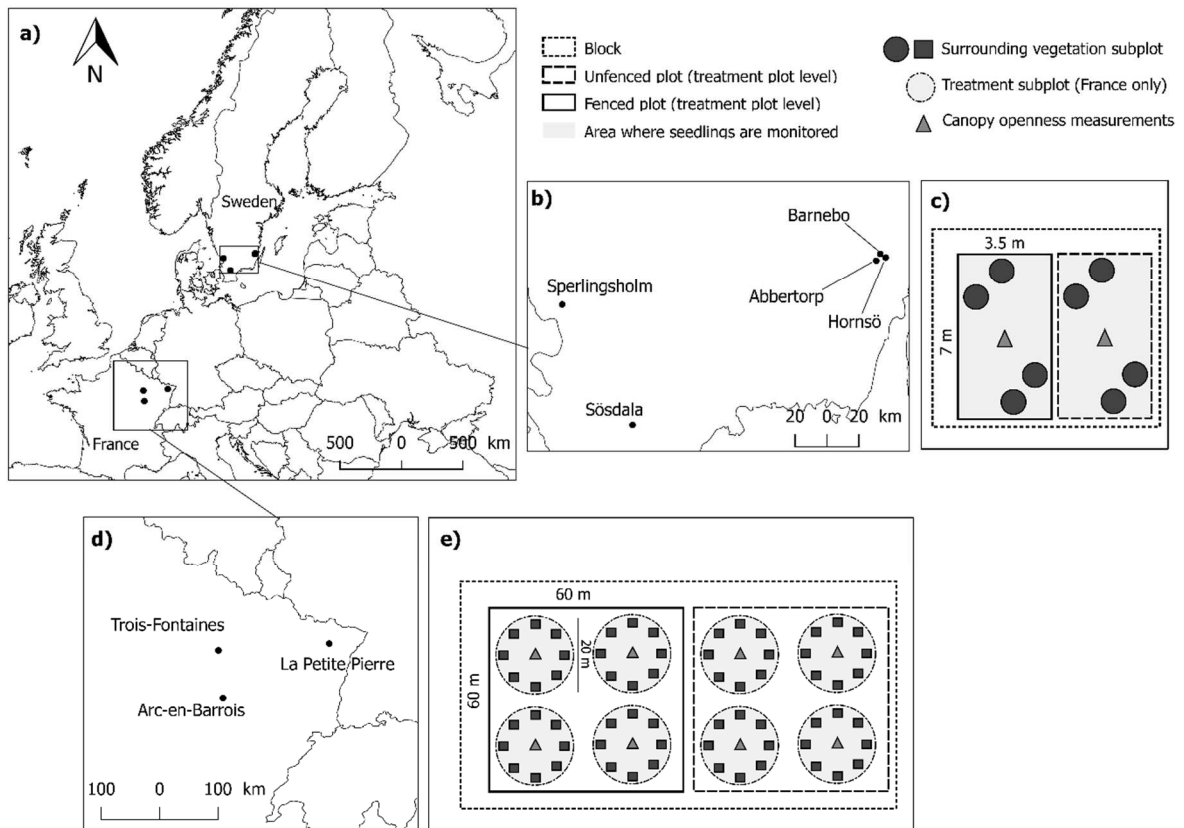
121 P3: Annual height growth is reduced less by browsing for oak seedlings growing under an
122 open canopy than for seedlings under a closed canopy.

123 The development of understory vegetation – e.g. shrubs, forbs, vines – is also highly
124 conditioned by canopy openness (Gaudio et al., 2008) and may influence seedling growth
125 (Jensen and Löf, 2017), or browsing probability (Harmer et al., 2010; Jensen et al., 2012).
126 Therefore, we also tested whether understory competition influenced oak growth, and
127 browsing probability. Lastly, as we conducted the study at different study sites characterized
128 by different ungulate densities, we tested whether the effect of fencing on oak seedling growth
129 and survival increased with ungulate density.

130

131 **2. Materials and methods**

132 *2.1. Study area*



133

134 **Figure 1:** a) Location of the eight study sites in Europe, b) location of the 5 study sites in
 135 southern Sweden, c) experimental design in Sweden, d) location of the three study sites in
 136 northeastern France and e) experimental design in France.

137

138 Five study sites were located in southern Sweden and three in northeastern France (Fig. 1).

139 All eight sites were located at low elevations (45 to 400m above sea level) in forests where

140 both pedunculate and sessile oak were abundant. Because the two species occurred in

141 sympatry at every site and present very similar morphological characteristics during the

142 regeneration phase (Bacilieri et al., 1995) we made no distinction between the two species,

143 hereinafter referred to as oak (i.e. *Quercus sp*). Due to the strong overlap in the distribution of

144 these species in Europe, this simplification is relatively common in studies on oak

145 regeneration (Annighöfer et al., 2015; Petersson et al., 2020). Oak, Scots pine (*Pinus*

146 *sylvestris*) and Norway spruce (*Picea abies*) were dominant in the Swedish sites (Table 1). In

147 France, most of the study sites were dominated by oak, beech (*Fagus sylvatica*) and hornbeam

148 (*Carpinus betulus*) (Table 1). Although moose (*Alces alces*) and roe deer (*Capreolus*
149 *capreolus*) were most abundant in southern Sweden, red deer (*Cervus elaphus*) and fallow
150 deer (*Dama dama*) were also present (Table 1). Roe deer occurred at all three French sites and
151 red deer was present at two of the sites. Wild boar (*Sus scrofa*) was abundant in both
152 countries. We did not apply any herbicide neither in the French, nor in the Swedish sites. We
153 did not observe the occurrence of fire in any of the stands included in the experiment
154 throughout the study. A snow cover reaching 10 to 30 cm depth occasionally persisted up to
155 30 consecutive days in some of the Swedish sites, while snow accumulation was negligible in
156 the French sites.

157

158 2.2. Experimental design and site preparation

159 At each Swedish site, there were two pairs of fenced (without browsing) and unfenced (with
160 browsing) plots (i.e. total of 10 pairs in Sweden). Hereinafter, a pair of fenced-unfenced plots
161 will be referred to as a block and a treatment plot will designate either a fenced or an
162 unfenced plot (thus making two treatment plots per block) (Fig. 1.c). We erected a 2-m-high
163 steel wire fence (mesh size: 5 x 5 cm) around one treatment plot per block to protect the
164 seedlings from ungulates and hares, but not from rodents. In one block per site, we cut out a
165 circular canopy gap of around 400 m². Each site therefore contained two blocks associated
166 with two different levels of canopy openness. The treatment plots were 24.5 m² (3.5 x 7m)
167 (Fig. 1.c). At each site, we set up the blocks in April 2016 and monitored the seedlings every
168 year from 2016 to 2018 (Table 1).

169 In France, there were between four and nine pairs of fenced-unfenced plots – i.e. blocks – at
170 each site (total of 19 pairs in France). We erected a 2-m-high steel wire fence around one
171 treatment plot per block (mesh size: 10 x 10cm) to protect the vegetation from ungulates, but

172 not from hares or rodents. The same year, we performed partial cutting in each treatment plot,
173 which resulted in contrasted canopy openness conditions both between and within blocks. We
174 also removed all shrubs, seedlings and saplings – except oak – on each treatment plot. The
175 treatment plots were 3600 m² (60 x 60m or 30 x 120m depending on the position of the seed
176 trees) and were divided into four circular treatment subplots with a 10m radius (*i.e.* 314 m²)
177 (Fig. 1.e). Table 1 presents the dates the blocks were set up, the seedling monitoring period
178 and the number of blocks at each site.

179 *2.3. Monitoring the oak seedlings*

180 In Sweden, at the beginning of the study, we marked all the available seedlings in each
181 treatment plot. If the number of available seedlings was higher than 100 in a given treatment
182 plot, a random subset of at least 50 seedlings was selected for measurements (*i.e.* no selection
183 criteria based on the seedling characteristics were applied). An available seedling was defined
184 as any oak individual less than 3m in height since moose can browse trees up to 3m high
185 (Nichols et al., 2015). The year following the beginning of the study, we did not select any
186 additional seedling to compensate for dead or missing seedlings.

187 **Table 1:** Date of treatment installation, monitoring period (first and last year), main canopy tree and main cervid species, range of canopy
 188 openness (%) and understory cover index (%) and understory height index (cm) for the eight study sites in Sweden and France. In La Petite
 189 Pierre, though the experiment was set up earlier (2012), we restricted the analysis to the 2016-2019 period to ensure uniformity between the
 190 French sites. For description of the indices, see text.

Site	Date of treatment installation	Monitoring period	Tree species	Cervid species	Number of blocks	Canopy openness (%)		Understory cover index (%)	Understory height index (cm)
						Min	Max		
Abbetorp	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	18.1	23.4	59%	18cm
Barnebo	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	17.3	22.9	43%	20cm
Hornsö	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	15.4	25.7	44%	20cm
Sperlingsholm	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	12.7	25.5	68%	25cm
Sösdala	2016	2016-2018	Oak, Scots pine, Norway spruce	Red deer, roe deer, fallow deer, moose	2	10.6	30.9	38%	18cm
Arc-en-Barrois	2014-2015	2016-2019	Oak, beech, hornbeam	Red deer, roe deer	9	8.8	52.4	15%	33cm
Trois Fontaines	2015	2016-2019	Oak, beech, hornbeam	Roe deer	4	8.1	41.9	15%	17cm
La Petite Pierre	2012	2016-2019	Oak, beech, silver fir, Norway spruce	Red deer, roe deer	6	7.8	39.5	4%	8cm

191 In France, we selected seedlings less than 2 m in height – i.e. maximum browsing for red deer
192 (Nichols et al., 2015). At the beginning of the study, we selected ten oak seedlings per
193 treatment subplot (*i.e.* 40 per treatment plot), or fewer when the number of oak seedlings in
194 the treatment subplot was less than ten. In later measurements, if a seedling was found dead or
195 missing, we selected a new seedling in the treatment subplot to maintain the number of
196 seedlings monitored constant. As far as possible, we targeted one-year-old seedlings when
197 selecting new individuals.

198 For our final analysis, we removed all seedlings higher than 2 m from the dataset to ensure
199 compatibility between the two countries. We selected a total of 1163 seedlings in Sweden and
200 2761 in France (the number of selected seedlings in France is higher because we selected
201 additional seedlings throughout the experiment to replace dead or missing ones). We
202 measured the height of each selected seedling once a year, after the growing season in
203 Sweden (August) and before the growing season in France (March). We also noted whether
204 the current year shoots presented marks of browsing by ungulates (binary data, with no
205 distinction between winter and summer browsing). Marks of ungulate browsing were
206 identified using the same criteria as Kullberg and Bergström (2001). From the height
207 measurements, we computed the annual growth rate of a seedling i in year y_1 (GR_{i,y_1}) as:

$$208 \quad GR_{i,y_1} = \frac{H_{i,y_2} - H_{i,y_1}}{y_2 - y_1} \quad \text{(Eq. 1)}$$

209 where H_{i,y_1} and H_{i,y_2} are the height of seedling i measured in year y_1 and y_2 respectively. We
210 used the growth rate instead of the relative growth rate (*i.e.* growth rate divided by the initial
211 height) because initial height had to be included in the statistical analyses anyway to account
212 for possible interactions with other explanatory variables. The relative growth rate also
213 assumes a linear relationship between the growth rate and initial height, which is not always

214 true for oak (Ligot et al., 2013). Years y_1 and y_2 were always two consecutive years, except in
215 the case of a data gap – i.e. a seedling was first lost, then found alive one or two years later.

216 *2.4. Understory competition*

217 In Sweden, we monitored understory competition in four circular 2m^2 vegetation subplots
218 randomly placed inside each treatment plot (Fig. 1.c). Once a year in August, we estimated
219 the cover (percentage of the soil surface occupied by the vertical projection of the leaves \pm
220 10%) and mean height (\pm 1cm) of the different understory species – i.e. shrubs, forbs and
221 vines – in each vegetation subplot.

222 In France, we monitored understory competition in eight vegetation subplots of 1m^2 (1 x 1m)
223 arranged in a circle (5m radius) around the center of each treatment subplot (Fig. 1.e). In each
224 vegetation subplot and each year, in spring, we estimated the cover class (0-5%, 5-25%, 25-
225 50%, 50-75% and 75-100%) of every understory species per vegetation layer (three
226 vegetation layers: below 50cm, 50-130cm and 130-300cm). To ensure that the data were
227 comparable between the two countries, we first converted the cover classes into a percentage
228 using median values (e.g. if a species was in the 25-50% cover class, its median cover was
229 37.5%). We combined the median cover values of the three layers to obtain the total cover for
230 each understory species per vegetation subplot (values ranged between 0 and 100%)
231 following the method proposed by Fischer (2015). We computed the cover ($Cover_{i,k}$) of
232 understory species i in vegetation subplot k as:

$$233 \quad Cover_{i,k} = 1 - \prod_{l=1}^3 (1 - c_{i,l,k}) \quad (\mathbf{Eq. 2})$$

234 where $c_{i,l,k}$ is the median cover of understory species i in layer l of vegetation subplot k .

235 Similarly, we computed the mean height $H_{i,k}$ of understory species i in vegetation subplot k as
236 the mean of the median heights (e.g. the median height of the vegetation layer 0-50cm was
237 25cm) weighted by the cover values of the species in each vegetation layer:

238
$$H_{i,k} = \frac{\sum_{l=1}^3 (C_{i,l,k} * h_l)}{\sum_{l=1}^3 C_{i,l,k}} \quad (\text{Eq. 3})$$

239 where h_l is the median height for vegetation layer l .

240 From the mean height and cover of each understory species, we computed an understory
 241 height index (UHI_k) and an understory cover index (UCI_k) in both countries, specific to each
 242 vegetation subplot k , as follows:

243
$$UHI_k = \frac{\sum_{i=1}^{n_k} (C_{i,k} * H_{i,k})}{\sum_{i=1}^{n_k} C_{i,k}} \quad (\text{Eq. 4})$$

244
$$UCI_k = 1 - \prod_{i=1}^{n_k} (1 - C_{i,k}) \quad (\text{Eq. 5})$$

245 where n_k is the number of understory species in vegetation subplot k . We averaged the values
 246 of the understory height index and understory cover index to obtain an index at the treatment-
 247 plot scale in Sweden, and at the treatment-subplot scale in France. The main understory
 248 species were bilberry (*Vaccinium myrtillus*) in Sweden and bramble (*Rubus fruticosus*) and
 249 raspberry (*Rubus idaeus*) in France.

250

251 2.5. Canopy openness

252 In Sweden, we measured canopy openness in the summer of every sampling year by taking
 253 one hemispherical photograph (Canon Coolpix 8800VR, fisheye lens LC-ER2) in the middle
 254 of each treatment plot (Fig. 1.c) during an overcast day. We took the photograph at a height of
 255 160 cm above ground level, with the lens perpendicular to the forest floor. The north was
 256 automatically referenced in the image. We thresholded the images in the blue color plane, and
 257 computed the percentage of canopy openness with the Gap Light Analyzer software (Frazer et
 258 al., 1999).

259 In France, in the summer of 2019, we measured canopy openness at the center of each
260 treatment subplot (i.e. four measurements per treatment plot) (Fig. 1.e) at a height of
261 approximately 130 cm above the ground with a spherical convex densiometer following the
262 protocol of Baudry et al. (2014). We assumed that canopy openness was constant throughout
263 the different sampling years. Baudry et al. (2014) includes a regression analysis of the
264 relationship between canopy openness percentage measured with hemispherical photographs
265 (*CO_f*) and with a densiometer (*CO_d*) ($R^2 = 0.60$), as follows:

$$266 \quad CO_d = -6.75 + 1.77 * CO_f \iff CO_f = 3.81 + 0.57 * CO_d \quad (\text{Eq. } 6)$$

268 We used this regression equation to convert the French measurements, originally expressed in
269 *CO_d*, to *CO_f* to ensure that the data were comparable between the two countries. Hereinafter,
270 this percentage is referred to as “canopy openness” for both countries.

271 In this study, canopy openness never exceeded 60%. Indeed, during the first stages of oak
272 natural regeneration, it is common practice to maintain adult trees in the stand to ensure a
273 minimal flow of seeds in case the regeneration fails. Foresters harvest these remaining trees
274 (i.e. final cut) only when there is a sufficient density of saplings above 3m high, which was
275 not the case yet in neither of the two protocols (France and Sweden).

276

277 *2.6. Cervid density*

278 In Sweden, we computed a moose density index and a deer density index (red deer, roe deer
279 and fallow deer were all included in the same index, but roe deer was by far the most common
280 deer species) for each site based on data from dung pellet counts. This count is performed on
281 an intermediate landscape scale and is designed to assess the average density of ungulates
282 frequenting that landscape wintertime (Bergström et al., 2011). We collected pellet-count data

283 in 20 circular sample plots located every 200 m along the side of a 1x1 km square transect (= 284 4 km transect) laid out in the landscape around each site, following protocol described in 285 Månsson et al. (2011). Moose sample plots were 100 m² and deer sample plots were 10 m². 286 Every year from 2016 to 2018, the sample plots were cleaned in autumn (all fecal pellets were 287 removed) and surveyed the following spring. We only took into account pellet groups with at 288 least 20 single moose and 10 single deer pellets, with the majority of the pellets located within 289 the boundaries of the plots. The density index $DI_{i,j}$ for species i (deer or moose), and year j 290 was computed as:

$$291 \quad DI_{i,j} = \frac{PG_{i,j} * k_i}{NP * D_i * T_j} \quad (\text{Eq. 7})$$

292 where $PG_{i,j}$ is the number of pellet groups found for species i during year j , k_i is an area 293 scaling factor per species ($k_{deer} = 100000$, $k_{moose} = 10000$). NP is the number of surveyed 294 sample plots (20 excluding exceptions). D_i is an index correlated to the defecation rate of each 295 species ($D_{deer} = 22$, $D_{moose} = 17$) and T_j is the number of days between the previous autumn 296 clearing and the spring survey during year j . In addition to the deer and moose indices, we 297 also computed a cervid density index, the sum of moose density index and of deer density 298 index for each site. For the rest of the analysis, we averaged each of the three indices over the 299 three years to obtain a mean density index per species (deer, moose) and for all cervids for 300 each site.

301 In France, we computed abundance indices for red deer and roe deer at each site 302 (Supplementary material, Appendix A, Table A.1). However, because of the limited number 303 of sites in France, and the difficulty to compare these indices among sites, we only used the 304 Swedish data for the analysis.

305

306 *2.7. Statistical analysis*

307 In a first approach, we analyzed the data from the two countries in a single model. However,
308 the country effect interacted with all the other variables and, in order to obtain model
309 equations that are easy to interpret, we fitted the data separately for the two countries, using
310 the same explanatory variables.

311 To study the effect of fencing and canopy openness on oak seedling growth (P1.a), we
312 explained the growth rate of individual seedlings using a linear mixed model with three fixed
313 effects: initial seedling height ($H_{i,y,t}$ in eq. 1, added as a control variable), canopy openness
314 and fencing. To account for the hierarchical structure of the experimental design, and the fact
315 that there were several measurements per individual (one per growing season), we included a
316 nested random effect (Site/Block/Individual). To study the effect of fencing and canopy
317 openness on survival (P1.b), we used as a response variable the survival of the oak seedlings
318 after two years (binary variable: 1= alive, 0 = dead), in order to have comparable data
319 between the two countries. We analyzed this variable using a generalized linear mixed model
320 with a binomial error distribution and a logit link function. We included three fixed effects:
321 initial seedling height (*i.e.* height of the seedling the year of its selection), canopy openness
322 and fencing, and a nested random effect (Site/Block).

323 We analyzed browsing occurrence (binary data, measured for each individual seedling once a
324 year) using unfenced plot data only. We studied the effect of canopy openness on browsing
325 occurrence (P2) through a generalized linear mixed model with a binomial error distribution
326 and a logit link function. In addition to canopy openness, we included a previous browsing
327 factor (with two modalities: previously browsed or not) and seedling height as fixed effects as
328 these variables may influence browsing occurrence (Mathisen et al., 2017; Moore et al., 2000)
329 and must be controlled for to assess the effect of canopy openness. To account for repeated
330 measurements on the same sample, we used a “Site/Block/Year” random effect that allowed
331 us to compare all the individuals within a block for a given year, which is closer to the

332 experimental design of feeding trials, and thus more appropriate for studying browsing
333 likelihood.

334 To test the effect of canopy openness on the growth response following browsing (P3), we
335 analyzed individual seedlings' growth rate with a linear mixed model with three fixed effects:
336 initial seedling height ($H_{i,y}$ in eq. 1, added as a control variable), canopy openness and
337 browsing (factor with two modalities, "browsed" or "unbrowsed"), and a nested random
338 effect (Site/Block/Individual).

339 We proceeded to the same model selection process for the test of each prediction in both
340 countries. We first included all possible interactions between the fixed effects in the model,
341 then non-significant interactions were removed one by one to select the most parsimonious
342 model (i.e. with the lowest number of terms). To take into account understory competition, we
343 tested whether adding understory cover index and/or shrub height index as additional fixed
344 effects improved the model, based on the Akaike's Information Criterion (AIC) values. For all
345 the selected models (presented in Table 2), we visually checked that the histogram of the
346 model residuals was consistent with the error distribution assumed in the model. We verified
347 the assumption of homogeneity of variance by plotting the residuals against the predictors and
348 the predicted values.

349 We computed two indices centered in zero that represented the magnitude of the "deer effect"
350 on oak growth and survival at each study site in Sweden. The complete calculation of these
351 indices is presented in the supplementary material, Appendix D. We fitted simple linear
352 regressions to study the relationship between the impact of deer on growth or survival and the
353 average values over the three years of the three density indices (deer, moose and cervid).

354 We conducted all the data analyses with the statistical software R version 3.6.3 (R Core Team
355 2019). We fitted mixed models with the 'lme4' package (Bates et al., 2014) and tested the

356 significance of the fixed effects by performing post-analyses of deviance (Wald χ^2 , type II)
 357 with the ‘Anova’ function of the ‘car’ package (Fox et al., 2012). We bootstrapped each
 358 selected generalized linear mixed model 500 times with the ‘bootMer’ function of the ‘lme4’
 359 package (Bates et al., 2014) to obtain a 95% confidence interval around the model prediction.

360

361 3. Results

362 **Table 2:** Selected model for each prediction in France and in Sweden. The complete model
 363 selection and the statistics of the selected models are included in the supplementary material,
 364 Appendix B and D respectively. The factors included are canopy openness (Ca), initial height
 365 (Hi), fencing (Fen), browsing (Br), understory cover index (UCI), understory height index
 366 (UHI) and previous browsing (PreB).

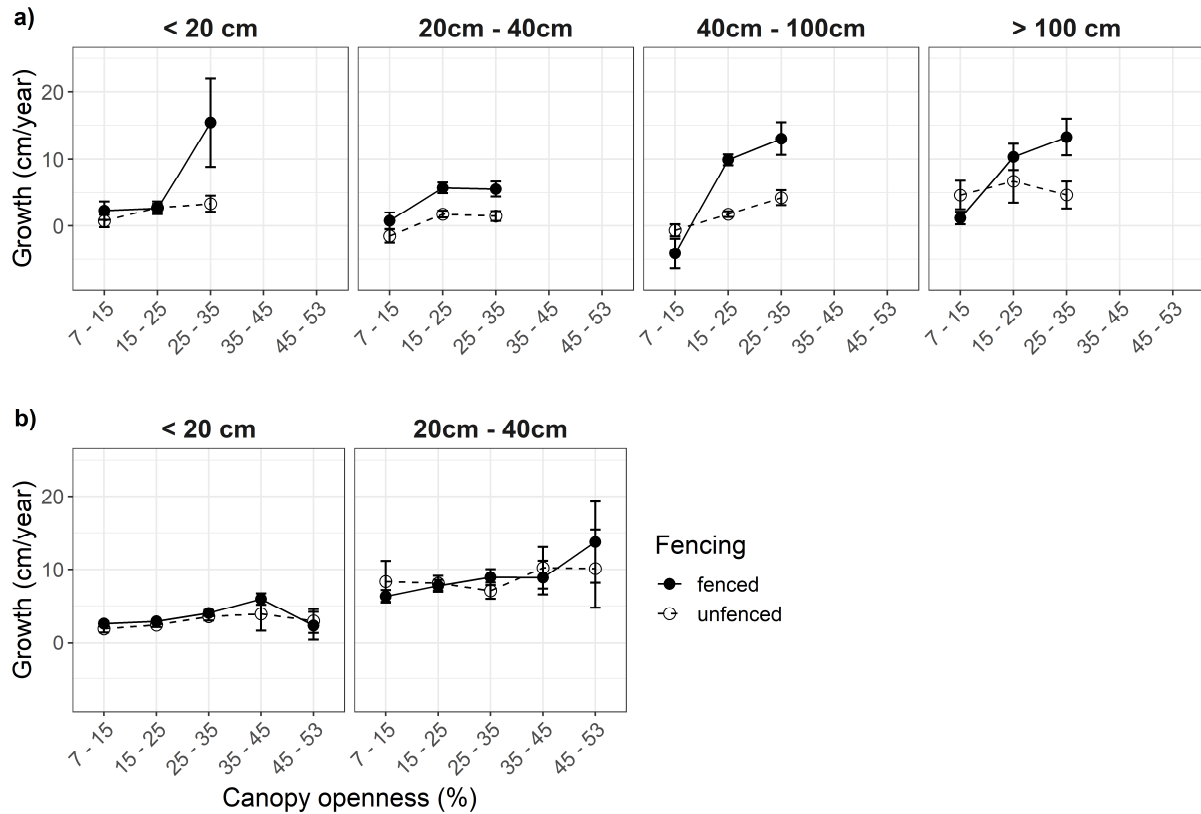
Prediction	Response variable	Selected model
<i>Sweden</i>		
P.1a	Growth rate (cm.year-1)	Ca + Hi + Fen + Ca*Hi + Ca*Fen + Hi*Fen + Ca*Hi*Fen
P.1b	Survival after two years (binary)	Ca + Hi + Fen
P.2	Occurrence of browsing (binary)	Ca + Hi + PreB + UCI
P.3	Growth rate (cm.year-1)	Ca + Hi + Br + Ca*Hi
<i>France</i>		
P.1a	Growth rate (cm.year-1)	Ca + Hi + Fen + Ca*Hi + Hi*Fen
P.1b	Survival after two years (binary)	Ca + Hi + Fen + Ca*Fen
P.2	Occurrence of browsing (binary)	Ca + Hi + PreB + Hi*PreB + UCI
P.3	Growth rate (cm.year-1)	Ca + Hi + Br + Ca*Hi + Hi*Br + UCI + UHI

367

368 3.1. Effect of fencing and canopy openness on oak seedlings growth (P1.a)

369 In Sweden, both canopy openness ($p = 0.02$) and fencing ($p < 0.01$) increased individual
 370 seedlings growth rate, and the interaction between the two variables was significant

371 ($p < 0.01$): the positive effect of fencing was higher under a relatively open canopy (Fig. 2.a).
 372 When canopy openness was above 25%, growth rate was on average three times higher in
 373 fenced plots than in unfenced plots, while below 15% of canopy openness, seedlings in fenced
 374 and unfenced plots had the same average growth rate (Fig. 2.a).



375
 376 **Figure 2:** Annual seedling growth rate ($\text{cm}\cdot\text{year}^{-1}$) according to initial height and canopy
 377 openness (%) in fenced and unfenced plots, in Sweden (a) and France (b). Error bars show the
 378 standard error. Values for initial height and canopy openness classes were chosen for each
 379 country based on the distribution of each variable in each country (Supplementary Material,
 380 Appendix E).

381
 382 In France, fencing did not increase growth rate ($p = 0.48$). There was a significant interaction
 383 between canopy openness and initial height ($p < 0.01$; Supplementary Material, Appendix D,
 384 Table D.1): canopy openness had a positive effect on the growth rate only for intermediate
 385 and tall seedlings (i.e. higher than 20 cm) (Fig. 2.b).

386 In both countries, adding understory cover index and/or understory height index to the most
387 parsimonious models did not improve the models, based on the AIC. These variables were
388 therefore not included in the final model (Supplementary Material, Appendix B, Table B.1).

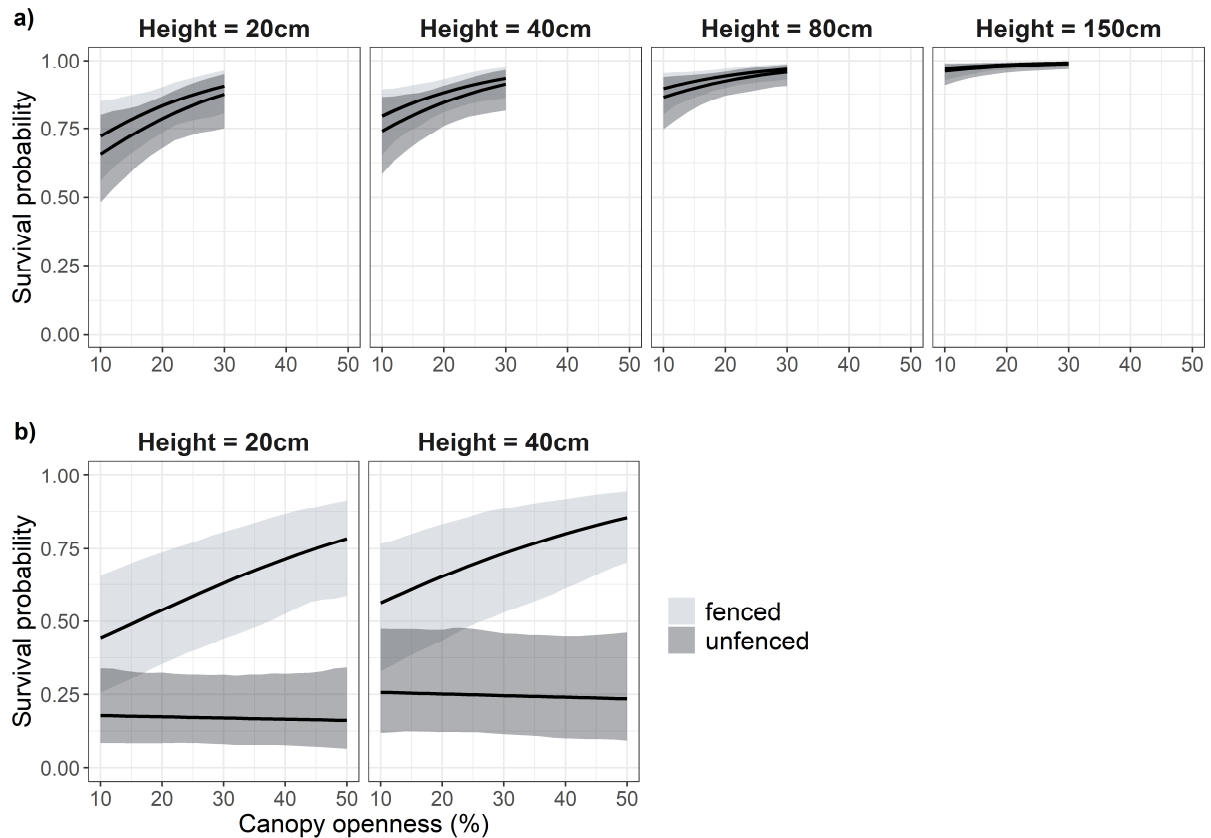
389

390 *3.2. Effect of fencing and canopy openness on oak seedlings survival (P1.b)*

391

392 In Sweden, survival after two years increased with canopy openness ($p = 0.03$)
393 (Supplementary Material, Appendix D, Table D.2). Survival was slightly higher in fenced
394 plots (Fig. 3.a.) but the trend was not significant ($p = 0.11$).

395 In France, both fencing ($p < 0.01$), and canopy openness ($p < 0.01$) increased survival, and the
396 interaction between the two variables was significant ($p < 0.01$; Supplementary Material,
397 Appendix D, Table D.2). Canopy openness increased survival only in fenced plots (Fig. 3.b).
398 Seedlings located in unfenced plots had a very low survival after two years (e.g. 25% for a 40-
399 cm seedling), regardless of canopy openness. Overall, survival after two years was much
400 higher in Sweden than in France (Fig 3).



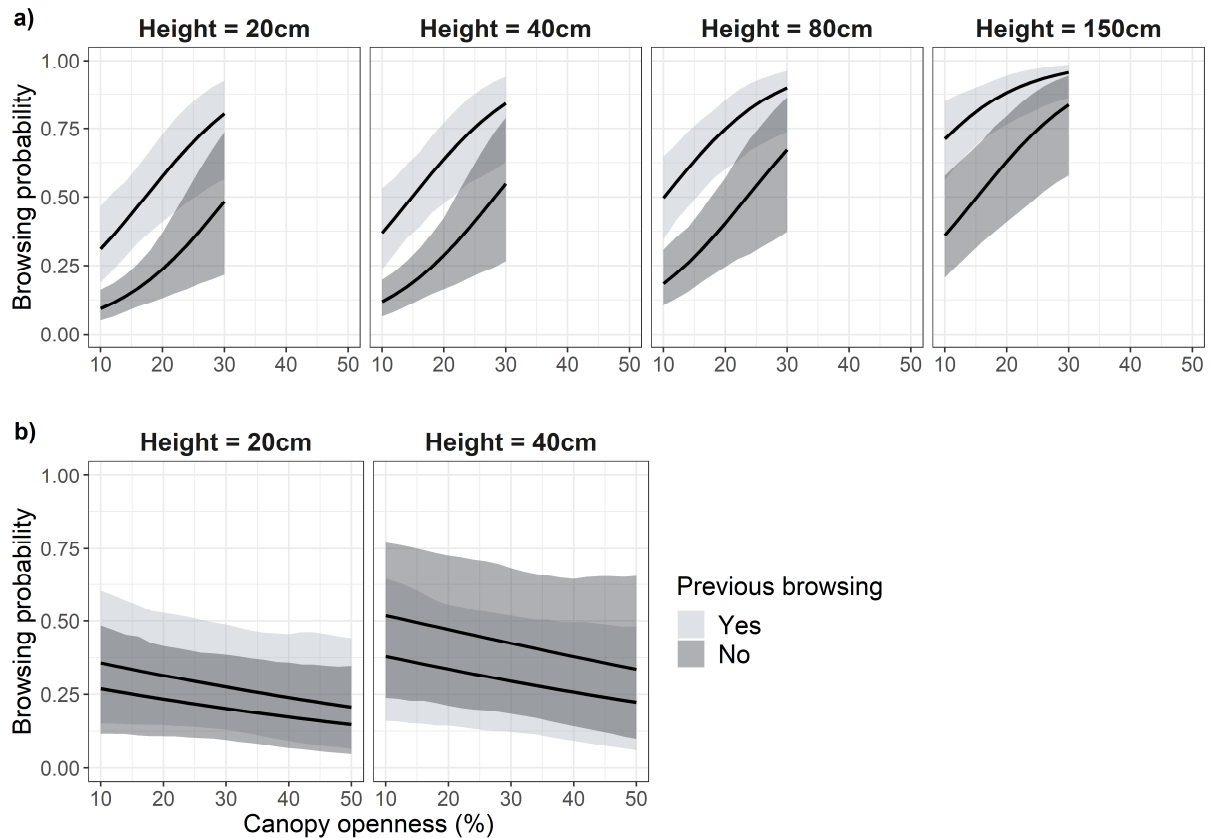
401

402 **Figure 3:** Predicted values and 95% confidence intervals from the generalized mixed models
 403 for seedling survival probability after 2 years as a function of canopy openness, fencing and
 404 initial height in (a) Sweden and (b) France, using models presented in Table 2. Initial height
 405 values and the range of canopy openness per country were chosen based on the distribution of
 406 each variable in each country (cf. Supplementary Material, Appendix E)

407

408 *3.3. Effect of canopy openness on browsing likelihood (P2)*

409 Canopy openness ($p < 0.01$) increased the likelihood of seedlings being browsed in Sweden
 410 but not in France (Supplementary Material, Appendix D, Table D.3) (Fig. 4). In France, the
 411 AIC test supported the inclusion of the shrub height index in the final model (Supplementary
 412 Material, Appendix B, Table B.3), but the factor was not statistically significant ($p = 0.06$). In
 413 Sweden, the AIC also supported the inclusion of the shrub height index in the final model
 414 (Supplementary Material, Appendix B, Table B.3) that significantly decreased browsing ($p <$
 415 0.01).



416

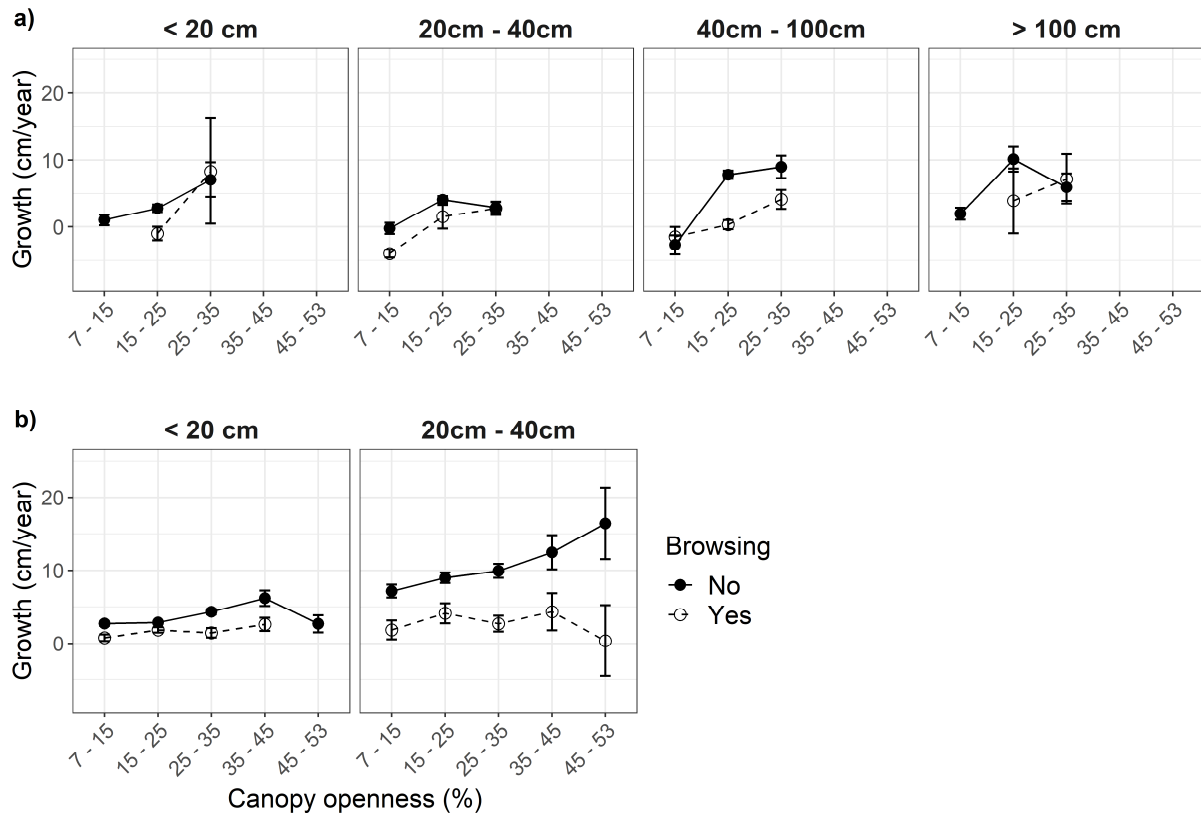
417 **Figure 4:** Predicted values and 95% confidence interval from the generalized mixed models
 418 for browsing probability as a function of canopy openness, previous browsing, and initial
 419 height in (a) Sweden and in (b) France using models presented in Table 2. Initial height values
 420 and the range of canopy openness per country were chosen based on the distribution of each
 421 variable in each country (cf. Supplementary Material, Appendix E)

422

423 *3.4. Effect of canopy openness on the reduction in growth rate induced by browsing (P3)*

424 Browsing had a negative effect on growth rate both in Sweden ($p < 0.01$) and in France ($p <$
 425 0.01) (Supplementary Material, Appendix D, Table D.4) but the model selection did not
 426 support the inclusion of an interaction between canopy openness and browsing in the final
 427 models (Supplementary Material, Appendix B, Table B.4) (Fig. 5). This means that the
 428 negative effect of browsing on growth rate was independent of canopy openness. Overall, the
 429 negative effect of browsing on growth rate was much higher in France than in Sweden – e.g.
 430 for seedlings between 20 and 40cm, browsing reduced the average growth rate by 5.94

431 cm.year⁻¹ in France, and only by 1.23 cm.year⁻¹ in Sweden. In France only, the AIC supported
 432 the inclusion of understory competition indices in the model, and both the understory height
 433 index ($p < 0.01$) and the understory cover index ($p = 0.04$) were positively correlated to the
 434 growth rate (Supplementary Material, Appendix D, Table D.4).

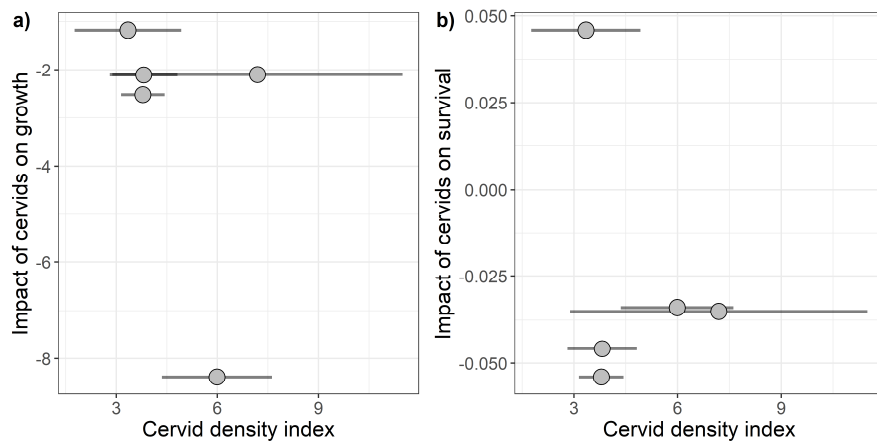


435
 436 **Figure 5:** Annual seedling growth rate (cm.year⁻¹) according to browsing, initial height and
 437 canopy openness (%), in Sweden (a) and France (b). Error bars show the standard error.
 438 Values for initial height and canopy openness classes were chosen for each country based on
 439 the distribution of each variable in each country (Supplementary Material, Appendix E).

440
 441 *3.5. Relationship between cervid density and the impact of cervids on oak growth and*
 442 *survival in Sweden.*

443 Neither the impact of cervids on growth ($p = 0.48$) nor their impact on survival ($p = 0.59$)
 444 were correlated to our cervid density index (Fig. 6). Results were similar when we compared

445 the impact of cervid on growth and survival with the more narrowly defined density indices
446 (moose and deer density indices) (Supplementary Material, Appendix F).



447

448 **Figure 6:** Variations in the impact of cervids on growth and survival with cervid density
449 index (animal.km⁻²) in Sweden. Negative values of the impact of cervids on growth and
450 survival indicate a negative effect of deer on seedling growth and survival respectively.
451 Horizontal error bars show the standard error of the cervid density index.

452

453 **4. Discussion**

454

455 *4.1. How do canopy openness and fencing affect oak seedlings growth and survival?*

456 Our observation that oak seedling growth (Fig. 2) and survival (Fig. 3) increase with canopy
457 openness corroborates our first prediction (P1). This result supports the already well-
458 documented finding, applied in everyday use by foresters, that high canopy openness
459 promotes the regeneration of oak (Ligot et al., 2013; Petersson et al., 2020) and more
460 generally of shade-intolerant tree species, by increasing understory light availability (Iverson
461 et al., 2017; Lu et al., 2018). We also showed that fencing improved oak seedling growth in
462 Sweden and survival in France, which is consistent with many studies where the exclusion of
463 wild ungulates improved the natural regeneration of oak (Leonardsson et al., 2015; Petersson
464 et al., 2020), and of other palatable tree species (Kumar et al., 2006; Rhodes et al., 2018).
465 Overall, these findings confirm that opening the canopy, through thinning or natural
466 disturbance, and excluding wild ungulates through fencing may effectively assist oak
467 seedlings during the first stages of the natural regeneration. Although forest managers
468 commonly control wild ungulates and manipulate canopy openness, the interaction between
469 the effects of these two disturbances on forest dynamics has received little research attention
470 so far.

471 Two recent studies showed that the exclusion of wild ungulates enhanced the positive effect
472 of gap creation on understory species richness and cover (Sabo et al., 2019) and on the
473 abundance of several tree species (Thomas-van Gundy et al., 2014). In our study, we show
474 that, in two contrasted forest regions, the effects of canopy openness and fencing also acted in
475 synergy to improve oak natural regeneration: the positive effect of fencing on oak seedling
476 growth or survival increased with canopy openness both in France and in Sweden. Different
477 mechanisms could explain the observed pattern. A first assumption would be that ungulates

478 browse more frequently and/or intensively on oak seedlings when canopy openness increases,
479 which would be consistent with our second hypothesis. A second possibility is that oak
480 responds differently to browsing depending on light availability, with a stronger reduction in
481 growth under high light availability. Such pattern could relate to the higher growth rates of
482 seedlings growing under open canopies, leading to a greater height difference between
483 browsed and unbrowsed seedlings in the absence of compensatory growth. Although it has
484 been observed in holm oak (*Quercus ilex*) (Baraza et al., 2010) in controlled conditions, this
485 would, however, go against our third prediction (P3), and most results found in the literature
486 for other tree species (Baraza et al., 2010; Kupferschmid et al., 2014).

487 It is noteworthy that fencing did not significantly influence seedling growth in France. This
488 may be the result of a lower browsing pressure exerted on the understory vegetation and/or
489 more specifically on oak seedlings. Cervids have species-specific browsing height that
490 generally corresponds to their shoulder height (Duncan et al., 1998; Nichols et al., 2015) and
491 our results, along with other similar studies, confirmed that height positively influences the
492 probability of browsing (Hartley et al., 1997; Renaud et al., 2003). Because the regeneration
493 was more advanced in Sweden, seedlings and other understory vegetation were on average
494 much higher than in France (Supplementary material, Appendix E, Fig. E.1), and this could
495 have resulted in an overall higher browsing pressure in the Swedish plots. The observed
496 pattern could also be the result of a difference in the palatability of oak relative to the other
497 woody species present in the two countries. Indeed, cervid browsing preference for a given
498 plant species – and the associated damages – is not only dependent on the plant species’
499 palatability and availability, but also on the palatability of the alternative forage available
500 (Bee et al., 2009; Milligan and Koricheva, 2013; Ohse et al., 2017). The ‘attractant-decoy
501 hypothesis’ predicts that, within a patch, an individual plant that grows among more palatable
502 plants will be somewhat protected from herbivores, as their attention is on the preferred

503 neighbors (Hjältén et al., 1993). In Sweden, studies on cervid selectivity show that oak is one
504 of the most palatable species (Bergqvist et al., 2018; Kullberg and Bergström, 2010). At the
505 French sites, several of the co-occurring woody (hornbeam) and shrub (bramble) species (see
506 Supplementary material, Appendix G, Fig. G.2 for the height and cover of the main
507 understory species) have been shown to be more often selected by red deer and roe deer than
508 oak (Boulanger et al., 2009; Tixier et al., 1997). The high availability of these more palatable
509 species in the French sites may have contributed to the fact that fencing did not affect oak
510 seedling growth. In addition, the alternative forages present may also influence the timing of
511 herbivory – e.g. cervids browse evergreen species in winter when deciduous species are
512 scarce. Since oak responds differently to summer or winter browsing (Woolery and Jacobs,
513 2014), the existence of differences in the seasonality of browsing between the two countries
514 could also explain the observed pattern.

515 *4.2. Do cervids preferentially browse seedlings growing under open canopies?*

516 In Sweden, consistent with our second prediction (P2), seedlings growing under an open
517 canopy were more likely to be browsed than those growing under a closed canopy (Fig. 4).
518 This pattern is consistent with other studies documenting a higher frequentation of wild
519 ungulates in canopy gaps (Kuijper et al., 2009; Mangas and Rodríguez-Estival, 2010), and is
520 likely driven by a combination of several mechanisms. First, increasing canopy openness may
521 lead to a higher abundance, biomass and diversity of herbs, shrubs and tree species in the
522 forest understory (Alexander and Mack, 2017; Burton et al., 2014; Sabo et al., 2019; Willms
523 et al., 2017), all of which influence the browsing probability of a given individual seedling
524 (Milligan and Koricheva, 2013; WallisDeVries, 1996). Second, canopy gaps also modify the
525 species composition of the understory in favor of light demanding species (Lu et al., 2018).
526 Studies linking browse quality for cervids and plant shade-tolerance have shown that light
527 demanding species generally have lower leaf toughness, fewer chemical defenses (e.g.

528 phenolic compounds) and higher nutritional content (Giertych et al., 2015; Kitajima et al.,
529 2012), and may therefore be more palatable to cervids. By increasing the quantity, quality and
530 diversity of the surrounding vegetation, canopy gaps may therefore create better foraging
531 conditions for herbivores, hence increasing the likelihood for oak to be browsed (Hjältén et
532 al., 1993). At the intra-specific scale, an increase in light availability can also influence plant
533 chemical composition, though it remains unclear how these changes actually affect plant
534 palatability. Nutrient content or digestibility are considered good proxies for plant nutritional
535 value for cervids, and are often drivers of food selection (Felton et al., 2018; Van Soest,
536 1996). It has been shown that at the intra-specific scale, light availability may increase the
537 digestibility of several woody species (Agrell et al., 2000), though it may also decrease the
538 leaf nutrient content (Giertych et al., 2015). More knowledge on the consequences of
539 increased light availability on plant nutritional properties is therefore necessary before
540 drawing any conclusions on this issue.

541 The fact that canopy openness did not influence browsing likelihood in France could relate to
542 the importance of the understory – especially shrubs – in the French sites. Indeed, understory
543 height is relatively similar between the two countries (Table 1) while seedlings are higher in
544 Sweden, thus suggesting that the understory competition is developing rapidly in France. It is
545 thus likely that in most French sites, oak seedlings are still growing beneath the shrub layer.
546 Our results confirm that the understory protects the seedlings from browsing (Jensen et al.,
547 2012), as understory height or cover decreased the browsing probability in both countries.
548 However, several species that dominate the shrub layer in France – e.g. bramble, raspberry –
549 are highly competitive regarding light interception (Balandier et al., 2013). Because light
550 availability also promotes growth for these shrub species (Supplementary material, Appendix
551 G, Fig. G.2) (Gaudio et al., 2008), a higher canopy openness may not necessarily increase
552 light availability for seedlings growing beneath the shrub layer, and therefore may not

553 influence their palatability. The fact that in France, canopy openness only improved the
554 growth of higher seedlings tend to support this hypothesis.

555 *4.3. Does the impact of browsing on growth vary with canopy openness?*

556 The ability of trees to recover from browsing may depend on the available light
557 (Kupferschmid et al., 2014) but this relationship is highly variable among different tree
558 species (Baraza et al., 2010). In our study, we observed a consistent trend in both countries:
559 browsing significantly reduced seedling annual growth rate, but contrary to our third
560 prediction (P3), the effect was independent of canopy openness (Fig. 5). This is even more
561 notable, as the short duration of the study in most sites (2-3 years), along with the relatively
562 shady conditions, could have limited the possibility to detect differences in growth rates. This
563 finding confirms that the synergy between the effects of fencing and canopy openness on oak
564 seedling growth observed in Sweden is related to a higher browsing frequency in canopy gaps
565 (result of P2) rather than to a light-mediated response to browsing.

566 At the individual seedling level, reduction in growth rate induced by browsing seems to be
567 higher in France than in Sweden. This pattern could be related to differences in site conditions
568 that we did not measure - e.g. soil composition, moisture, or climate; factors that have
569 interacted with the effect of browsing on understory vegetation dynamic (Danell et al., 1991;
570 Randall and Walters, 2011). These inter-site differences could therefore explain differences in
571 tree species' tolerance to browsing between French and Swedish sites. This pattern could also
572 be related to different cervid compositions between the two countries. Indeed, the effect of
573 browsing on seedlings growth is conditioned by both the timing and intensity of herbivory
574 (Danell et al., 1994; Woolery and Jacobs, 2014), and these two factors are known to vary
575 depending on the cervid species (Nichols et al., 2015). The identification of the relative effect
576 of each cervid species, as has been done in recent studies (Barasona et al., 2013; van Beeck
577 Calkoen et al., 2019), would be necessary to confirm this hypothesis. Lastly, we may assume

578 that because oak is under higher browsing pressure in Sweden, it has developed local genetic
579 adaptations to better tolerate browsing as has been shown for the Japanese nettle (*Urtica*
580 *thunbergiana*) (Kato et al., 2008), or the orange jewelweed (*Impatiens capensis*) (Martin et
581 al., 2015). Strong inter-specific differences are known to exist in the ability of trees to recover
582 from herbivory (Baraza et al., 2010; Kupferschmid and Heiri, 2019) but the existence of such
583 differences at the intra-specific scale has been far less documented. A study by Mann et al.
584 (2012) showed that two distinct populations of *Eucalyptus morrisbyi* were not equally tolerant
585 to browsing, through differences in chemical and physical leaf traits. Vourc'h et al., (2002)
586 also found that the ability of western red cedar (*Thuja plicata*) to tolerate deer browsing varies
587 between populations, and more specifically with the browsing history of each population.
588 However, several recent studies conducted in temperate forests for Scots pine (O'Reilly-
589 Wapstra et al., 2014) and for beech (Frank et al., 2019) do not support population-specific
590 responses to browsing. Our results suggest that this question should be investigated for oak, as
591 it could have major management implications.

592

593 4.4. Does the impact of cervids on growth and survival correlate with cervid density?

594 Our results did not show any correlation between cervids density indices and the impact of
595 these animals on oak seedlings' growth or survival (Fig. 6). A weak statistical relationship
596 between cervid population density and browsing impact on trees is not an unusual finding,
597 due to the multitude of other factors influencing the foraging choices of free-ranging animals
598 (e.g. Jarnemo, Minderman, Bunnefeld, Zidar, & Mansson, 2014; Putman, Langbein, Green, &
599 Watson, 2011; Reimoser & Putman, 2011) and to the difficulty to accurately estimate cervid
600 density (Pfeffer et al., 2018). Indeed, it is possible that the variation in deer densities among
601 our sites was insufficient to enable us to identify a differential impact on seedling growth and
602 survival. Also, while dung pellet counts have been found to accurately predict winter habitat

603 use by moose (Månsson et al., 2011), the method may under-estimate population densities of
604 roe deer (Pfeffer et al., 2018). In addition, our study was of relatively short duration,
605 compared to most of the studies that show significant correlations between deer densities and
606 forest regeneration (Horsley et al., 2003; Kuijper et al., 2010).

607

608 *4.5 Top-down and bottom-up processes in managed forests*

609 Many recent studies converge on the idea that the relative importance of the effects of bottom-
610 up and top-down processes on the development of living organisms is highly dependent on
611 the environmental conditions – e.g. resource availability (Gilliam, 2006; Hillebrand, 2005;
612 Moran and Scheidler, 2002) or climate (Lynam et al., 2017; Rosenblatt and Schmitz, 2016). In
613 this study, we show that under closed canopies, oak seedling growth and survival were
614 constrained by low light availability (bottom-up control), but were not influenced by the
615 presence of ungulates. Inversely, under open canopies, seedlings were more frequently
616 browsed (top-down control), leading to a strong effect of fencing on growth and survival. As
617 resource availability increased, the regulation of seedlings development thus shifted from a
618 bottom-up to a top-down control. In the context of a managed forest, the review by Gilliam
619 (2006) revealed a similar pattern: N fertilization to increase nutrient availability for the
620 understory vegetation also tended to increase the importance of insect herbivory. In a study of
621 deer and their predators, Crête (1999) also reached the conclusion that top-down effects are
622 more pronounced in high productivity systems than in systems with low resource availability.
623 Our results support the hypothesis that net outcome for forest regeneration is the result of a
624 balance between enhanced resource availability for primary productivity and limitation of
625 predation. From a more general perspective, our findings support the pattern already observed
626 in marine communities (Hillebrand, 2005) or in cultivated fields (Moran and Scheidler, 2002):

627 an increase in resource acquisition does not always benefit the organism consuming the
628 resource as it may also increase predation.

629

630 **5. Conclusions**

631 Based on consistent patterns in two contrasted European forest regions, our results contributed
632 to improve our understanding of the interaction between the effects of wild ungulates and
633 canopy openness on oak regeneration. We have thus provided new insights into how these
634 top-down and bottom-up processes can interact with each other to influence the development
635 of forest trees. Fencing only improved oak growth or survival when the canopy was
636 sufficiently open, this was explained by a higher browsing frequency in canopy gaps. Gap
637 creation is generally necessary to achieve successful oak regeneration, but our results show
638 that moderate canopy operations may increase the damage caused by ungulates. From a
639 management point of view, these findings suggest that in forests with high ungulate densities,
640 gap creation alone may be insufficient to successfully regenerate oak stands if it is not
641 combined with protection from browsing. As anthropogenically increasing resource
642 availability to promote organisms of high ecological or economic value is common in
643 ecosystem management, our study highlights the importance of considering the interactions
644 between bottom-up and top-down processes before implementing measures.

645

646 **Acknowledgments**

647 We thank all the students and technicians who helped us with data collection, especially
648 Agathe Le Goff, James Lambert and Hubert Holveck. We are also grateful to Adam Flöhr and
649 Jan-Eric Englund for their help with the statistical analyses. We thank Victoria Moore for
650 correcting the linguistic mistakes. This study was conducted in the context of a PhD co-
651 funded by the French Office for Biodiversity (OFB) and the French National Forest Office
652 (ONF) under partnership agreement CNV-REC-2018-07. This work was also supported by
653 the Ministry of Agriculture (MAA) [convention E12-2018], the French National Research
654 Agency (ANR) as part of the "Investissements d'Avenir" program [ANR-11-LABX-0002-01,
655 Laboratory of Excellence ARBRE], and the Foundation Oscar and Lili Lamms Memory. The
656 DrEAM mobility program at the Lorraine University funded the collaboration between France
657 and Sweden.

658

659

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