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1 **Title:**

2 Combining partial cutting and direct seeding to overcome regeneration failures in dune forests.

3

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13

14 **Abstract:**

15 Stand regeneration is a crucial step in the management of many forests and its failure can  
16 jeopardize future forest growth and production. Thus, adapting forestry practices to improve  
17 seedling establishment is of prime importance to maintain sustainable forest management. In the  
18 coastal dune forests of maritime pine in SW France, regeneration failure after clear-cutting has  
19 greatly increased in the last decades. The aim of this study was to quantify the different stages  
20 involved in the regeneration process (seed rain, germination, survival), and to assess the impact of  
21 harvesting methods (partial cutting vs. clear-cutting) and of the use of direct seeding (seeding vs. no  
22 seeding) on these stages. We established five trials located in areas with contrasting regeneration  
23 statuses (of which two sites were in an area characterized by chronic regeneration failure), and we  
24 investigated the effect of the harvesting method and the use of direct seeding in a factorial design.  
25 We monitored the seed rain, germination and first-year survival for three years. Due to the transient  
26 nature of the seed bank, we found that the seed rain of the previous year was the only possible  
27 seed source for tree regeneration, and it increased with the proximity and size of surrounding  
28 mature trees. Nonetheless, seed rain did not limit regeneration in these stands. In fact, germination  
29 was the bottleneck stage of the regeneration process in all sites because it was short-lived and

30 consequently exposed to failure in case of unfavourable conditions. Once established, seedling  
31 death was mainly due to summer drought. Clear-cutting without seeding resulted in severe  
32 regeneration failures in 4 out of 5 sites, with the most severe in the failure area. Direct seeding  
33 increased seedling emergence only in the first year, while partial cutting had a longer-lasting effect  
34 by providing a regular seed supply over several years. Partial cutting also decreased biotic and  
35 abiotic stresses through microhabitat modification under the tree canopy, resulting in a higher  
36 number of germinations and greater seedling survival. This positive effect was more pronounced in  
37 the two sites within the failure area, suggesting that conditions were more stressful in this part of the  
38 forests. Consequently, we recommend avoiding clear-cutting in favour of partial cutting in all parts of  
39 these forests, and ensuring the maintenance of sufficient forest cover to promote regeneration.  
40 Direct seeding could be used in addition to partial cutting to maximize the chances of success, but  
41 only in areas where natural regeneration is low.

42

43 **Key words:** Direct seeding, Drought, Forest management, Germination, Partial cutting, *Pinus*  
44 *pinaster*, Seed availability, Seedling survival, Tree regeneration.

45

46

## 47 **1. Introduction**

48 The renewal of forest stands is a key step in forest dynamics and for their sustainable  
49 management. Natural regeneration is one way to do this and involves the stages of seed  
50 production, seed dispersal, germination and seedling survival, each being influenced by many  
51 interacting biotic and abiotic factors (Price et al., 2001; Kozłowski, 2002; Calama et al., 2017). The  
52 establishment of a species results from the interactions between the quantity of available seeds and  
53 the number of suitable microsites for regeneration (Harper, 1977; Schupp, 1995). The density of  
54 seeds reaching the ground depends on the seed production, on the spatial arrangement and the  
55 characteristics of the seed trees, and on the seed dispersal capacity (Greene et al., 1999; Viglas et  
56 al., 2013; Montoro Girona et al., 2018). Then, seedling emergence and survival depends on  
57 favourable local conditions such as soil moisture, soil temperature, or light (Harper, 1977;  
58 Kozłowski, 2002). These ecological conditions vary widely, both spatially and over time (Beckage

59 and Clark, 2003; Gómez-Aparicio et al., 2005), and can be influenced by biotic interactions with  
60 overstorey trees, herbaceous species or herbivore populations (Harmer, 2001; Wagner et al., 2011;  
61 Lavoie et al., 2019). Consequently, regeneration failure can also depend on the local environmental  
62 conditions.

63 Natural regeneration is frequently unsuccessful in temperate and Mediterranean managed  
64 forests (Calama et al., 2017; Dey et al., 2019), and could be increasingly threatened in the current  
65 context of global change in areas where droughts are expected to increase in frequency and  
66 intensity (IPCC, 2014). Thus, understanding the regeneration processes is very important in the  
67 adaptation of forest management practices to ensure the natural regeneration of stands. Forest  
68 harvesting, which is the starting point of the regeneration cycle, can be performed in two different  
69 ways in even-aged forests: i) clear-cutting, when all the trees are removed in a single harvesting  
70 operation and the new seedlings emerge from the soil seed bank. In the most difficult cases, natural  
71 regeneration can be assisted with a direct seeding using local seeds to overcome establishment  
72 limitations (Grossnickle and Ivetić, 2017); ii) partial cutting, when some of the mature trees are left  
73 unlogged in the stand to promote regeneration, and are harvested few years later, once  
74 regeneration is sufficient (Nyland, 2016). The degree of canopy closure induced by partial cuts can  
75 potentially influence several ecological processes and is therefore a key factor that can affect  
76 regeneration. First, the remaining trees can supply the viable soil seed bank for a few years to offset  
77 low seed availability for regeneration (Nyland, 2016). Second, forest cover can create more suitable  
78 conditions for seedling establishment by buffering microclimatic stresses (e.g. vapour pressure  
79 deficit, soil moisture or solar radiation) (Aussenac, 2000; Heithecker and Halpern, 2006). Partial  
80 cuts also modify light availability at the ground level and can influence the development of  
81 herbaceous and understorey species that may limit seedling establishment by competing for  
82 resources (Löf, 2000; Wagner et al., 2011). Finally, this habitat modification may also have an  
83 indirect impact on the behaviour of herbivores and therefore on the potential damage caused to  
84 seedlings (Reimoser and Gossow, 1996; Côté et al., 2004). In addition, partial cutting, which is  
85 increasingly used to ensure the sustainable management of many forests, can have other effects  
86 than promoting natural regeneration. Partial cutting also promote both economic and ecological  
87 features of mature stands, by increasing the radial growth of residual trees following the decrease in

88 stand density (Montoro Girona et al., 2016), and by supporting higher richness and greater  
89 abundance of flora and fauna than clear-cuts (Fedrowitz et al., 2014). However, these positive  
90 effects could be reduced in case of mortality of residual trees, as partially cut stands tend to be  
91 more sensitive to disturbance (particularly windthrow) than unharvested stands (Montoro Girona et  
92 al., 2019).

93 Maritime pine (*Pinus pinaster* Aiton) is a widely distributed conifer in the Mediterranean  
94 basin and along the Atlantic coast of Western Europe, and is of high ecological, economic and  
95 social importance in its native area (Alía and Martín, 2003) and in countries where it has been  
96 introduced (mainly Australia, New-Zealand, and South Africa). The coastal forests of maritime pine  
97 in southwestern France cover about 100 000 ha (IFN, 2017). Natural regeneration following clear-  
98 cutting has been used traditionally for many decades for the renewal of these forests to fulfil their  
99 multifunctional role (i.e. wood production, soil erosion protection, preservation of biodiversity,  
100 recreation usage and aesthetic value) and to improve the conservation of genetic diversity and the  
101 capacity to adapt to global change. However, regeneration failures (i.e. less than 3000 seedlings ha<sup>-1</sup>  
102 <sup>1</sup> – or 0.3 m<sup>-2</sup> – three years after harvest (Sardin, 2009)) have steadily increased in recent years,  
103 and persisted in spite of an additional supply of local seeds in some stands at the harvesting period.  
104 These failures were mainly observed in the central part of the coastal fringe occupied by dune  
105 forests (up to half of the regenerating stands may fail some years (Ouallet, 2012)), but this is  
106 beginning to spread to other areas, causing great concern among forest managers. In this type of  
107 ecosystem with freely draining sandy soils and regular severe summer drought, partial cutting is a  
108 method often used in other regions to renew pine forests, such as Spain (Calama et al., 2017). This  
109 method regularly results in sufficient seedling density in maritime pine forests (e.g. Rodríguez-  
110 García et al., 2010), but failures are also observed (e.g. González-Alday et al., 2009). This is  
111 because natural regeneration is highly dependent on site characteristics and on local climatic  
112 conditions, and is also variable between pine populations (Rodríguez-García et al., 2011b;  
113 Vergarechea et al., 2019).

114 The aim of this study was to identify the processes involved in failures of natural  
115 regeneration in the coastal forests of maritime pine, in interaction with silvicultural practices. For this  
116 purpose, we established five stands located in areas with contrasting regeneration successes, and

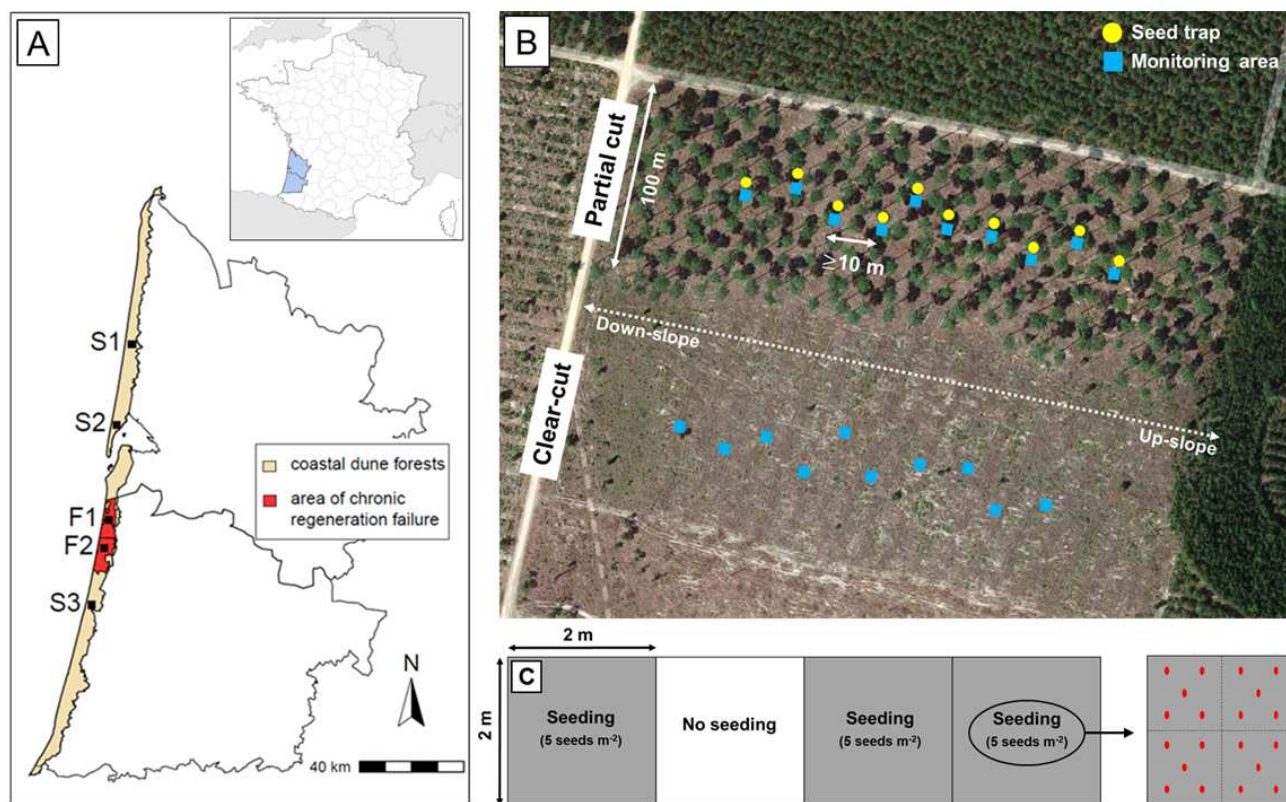
117 investigated the effect of the harvesting method (partial cutting compared to the usual clear-cutting)  
118 and of the use of direct seeding (compared to the absence of seeding). We hypothesized that: i)  
119 partial cutting could compensate for poor-regeneration years by supplying extra seeds each year,  
120 and by increasing germination and seedling survival rates due to improved microclimatic conditions,  
121 especially in the summer; ii) this positive effect would be more pronounced on sites within areas of  
122 high regeneration failures, so that the threshold of 3,000 seedlings ha<sup>-1</sup> necessary for a successful  
123 regeneration would be exceeded; and iii) direct seeding would improve the number of seedlings  
124 regardless of the harvesting method, but it might be less useful than partial cutting that provides a  
125 combination of seed supply and microhabitat amelioration. By improving our understanding of the  
126 ecology of maritime pine regeneration, our findings should enable us to propose adequate  
127 management strategies to ensure natural regeneration in these forests.

## 128 **2. Materials and methods**

### 129 **2.1. Study sites**

130 Our study combined experimentation (harvesting method and seeding as treatments, see  
131 2.2.) and exploration on a regional scale, integrating a major regeneration failure area. Thus, we  
132 established five trials along the coast in the maritime pine (*Pinus pinaster* Ait) sand dune forests of  
133 SW France in areas with contrasting regeneration statuses (Fig. 1A): two of the sites were within  
134 the area of chronic regeneration failure (hereafter referenced to as sites F1 and F2), while the three  
135 other sites were in areas with frequent regeneration success (S1, S2 and S3). The lower number of  
136 site in the failure area is explained by its geographically smaller area compared to the whole dune  
137 forests (Fig. 1A). Stand area ranged from 7.4 to 11.5 ha and tree age ranged from 58 to 77 years  
138 old (Table S1). The climate in the region is temperate oceanic. Average, minimum and maximum  
139 annual temperatures were 13.6 °C, 8.8 °C and 18.5 °C for S1 and about 14.1 °C, 9.3 °C and 19.2  
140 °C for the four other sites (Table S1). Average annual precipitation ranged from 840 mm to 1007  
141 mm (Table S1), with the wettest period in winter and the driest in July-August. All sites were chosen  
142 on westerly facing slopes at about 2.5 km from the ocean, with an average slope of 10°. Soils are  
143 young sandy soils (WRB classification: arenosols; USDA classification: entisols) mainly composed  
144 of coarse sands (96–97%), are slightly acidic (topsoil values of pH = 4.5–5.0), and are extremely

145 poor in nutrients (Augusto et al., 2010). These soils have a low water holding capacity which,  
 146 combined with low summer rainfall, results in an extremely low soil moisture content and a high  
 147 water stress for seedlings in summer (Guignabert et al., 2020).



148  
 149 **Fig. 1:** A) Location of the five study sites. B) Aerial photography of S3 showing the two harvesting treatments,  
 150 and the distribution of the monitoring areas. C) Schematic of one monitoring area and of the seed  
 151 arrangement pattern.

## 152 2.2. Experimental design

153 Two silvicultural practices were tested factorially at each site in early 2015: i) the harvesting  
 154 method (usual clear-cut vs newly tested partial cut using the uniform shelterwood system), and ii)  
 155 the use of direct seeding (vs no seeding). To that end, each of the two harvesting methods was  
 156 carried out on half of all stands (Fig. 1B). Tree harvesting was performed mechanically with a feller-  
 157 buncher between January and March 2015. For the partial cut treatment, trees were chosen on the  
 158 basis of their vigour and appearance, and tree density after harvest was ~70 stems/ha in all sites.  
 159 The basal area after partial cutting was between 7.5 and 13.2 m<sup>2</sup> ha<sup>-1</sup> (Table S1). Other  
 160 management practices were carried out before logging in all experimental treatments: understory  
 161 vegetation was removed mechanically to limit post-logging competition and was combined with light  
 162 mechanical tillage to increase soil aeration and nutrient availability. Then, at each site, we

163 positioned ten monitoring areas in the centre of each harvesting treatment (Fig. 1B), each area  
164 being split into four 4 m<sup>2</sup> quadrats (Fig. 1C). Three quadrats were sown with five seeds m<sup>-2</sup>, which  
165 corresponds to the quantity currently used by foresters in regeneration failure areas. Seeds were  
166 sown following an identical pattern (Fig. 1C; ca. 0.5 cm deep) and came from cones collected from  
167 stands of maritime pine located in the same forests. The fourth quadrat was unsown, and its  
168 position was determined randomly. Finally, we installed a 1.5 m<sup>2</sup> seed trap one meter away of each  
169 monitoring area in the partial cut treatment (Fig. 1C) to quantify the seed rain (10 seed traps per  
170 site). Traps were wooden frames filled with high-density polyethylene mesh and with 25 cm high  
171 edges in soft PVC, and were set up at about 25 cm above the ground (Fig. S1).

### 172 **2.3. Regeneration monitoring**

173 Seed rain was collected monthly in seed traps and counted from May to October in 2015,  
174 2016 and 2017, then air-dried and stored at 4 °C. Seed weight and seed length were measured on  
175 a random sample of 80 seeds per site of the 2015 seed rain, using a precision balance and a digital  
176 calliper respectively. Since seed rain is known to be dependent on tree basal area and tree density  
177 (Ruano et al., 2015b; Viglas et al., 2013), we measured the circumference of all trees within a 20 m  
178 radius of each seed trap and their distance from the trap . Then, from these two variables we  
179 calculated a seed source abundance index (SSAI) for each seed trap as follows:  $SSAI =$   
180  $\sum_{i=1}^n (TBA_i / d_i)$  with  $TBA_i (m^2) = (c_i/100)^2 / 4\pi$  and where  $c$  (cm) is the circumference at 1.30 m  
181 of tree  $i$ ,  $TBA$  is the basal area of tree  $i$  (m<sup>2</sup>) and  $d$  the distance (m) of tree  $i$  from the seed trap. The  
182 closer and bigger the tree, the more it contributes to the index value. The choice of a 20 m radius  
183 circle around each seed trap was based on previous studies about the dispersal distance  
184 corresponding to the majority of dispersed pine seeds (Juez et al., 2014; Ruano et al., 2015b).

185 Seedling emergence and first-year survival were monitored each year from 2015 to 2017.  
186 Censuses were carried out monthly from May to October in 2015 and 2016, and only three  
187 censuses were made in 2017: in late March, before the germination peak; in mid-June, after the  
188 germination peak and before the drought period; and in late September, after the drought period.  
189 Cause of seedling death was recorded: drought, when the seedling turned from green to red/brown;  
190 or due to herbivores, when the seedling died after browsing by ungulates or rodents (see



191 Guignabert et al. (2020) for more details on the distinction). Non-lethal ungulate browsing events  
192 were also noted at each survey. For each monitoring year, the survival of seedlings that emerged in  
193 the spring was only surveyed until the end of that specific year, and not throughout the whole study.  
194 Thus, a final count of all living seedlings was performed in March 2018 to obtain an assessment of  
195 the regeneration density comparable to the density value defined by foresters as the threshold  
196 value necessary for a successful regeneration (i.e. 0.3 seedlings m<sup>-2</sup>; Sardin, 2009).

## 197 **2.4. Complementary measurements**

### 198 *2.4.1. Soil seed bank*

199 Soil samples were collected from all sites to assess the soil seed bank, both in the clear-cut  
200 and in the partial cut. This sampling was performed at the beginning of the experiment in April 2015,  
201 after tree harvesting and before the beginning of the seed rain. A soil sample of 1/32 m<sup>2</sup> and 5 cm  
202 deep was collected in the proximity of the four corners of each monitoring area, giving a total of 400  
203 samples (5 sites x 2 harvesting methods x 10 monitoring areas x 4 samples) from a total surface  
204 area of 12.5 m<sup>2</sup>. Samples were then sieved using a 2 mm mesh and undamaged seeds were  
205 counted and stored at 4 °C.

### 206 *2.4.2. Seed germinative capacity*

207 We carried out a glasshouse germination test in March/April 2017 to evaluate the  
208 germinative capacity of the seeds in the five sites. This test was performed using the three pools of  
209 potential seed sources: i) seed rain, using seeds collected from seed traps in summer 2016; ii) soil  
210 seed bank, using seeds collected from soil sampled in April 2016 following the same procedure  
211 described above; and iii) seeds used for direct seeding by the French National Forestry Office  
212 (seeds ref: "PPA 303, dunes littorales de Gascogne", collected in winter 2015-16). All seeds were  
213 stored at 4 °C in the same place between their collection and the test. We sowed 11 batches of 50  
214 seeds in independent trays (50 x 30 cm) on March 15: five batches of soil seed bank and of seed  
215 rain (one per site), and one batch of seeds used for seeding. The soil used in all trays was collected  
216 from the F2 site and sieved to remove seeds potentially present in the collected soil. Trays were  
217 installed in a glasshouse at ambient temperature and watered every two days. New emergence was  
218 surveyed once a week for 8 weeks.

### 219 2.4.3. Dendrometric features of partial cuts

220 The dendrometric features of a mature stand (e.g. basal area, canopy cover) are partly  
221 related to the silviculture carried out during the forest rotation (e.g. thinning). We carried out this  
222 additional study in winter 2018-2019 in other forest stands to find out whether the stand structure of  
223 partial cuts might be a factor that should be integrated into the management considerations to  
224 improve regeneration. It should be noted that this study was not carried out at our five experimental  
225 sites, but at the scale of a large management canton. This area was located within the main failure  
226 area (i.e. near F1 and F2), the only area where partial cuts had been implemented in the region so  
227 far. We selected forest stands which had been harvested at least 3 years before (i.e. harvested in  
228 winter 2013-14, 2014-15 and 2015-16), which represented 29 stands and 280 ha (stand average =  
229 9.7 ha, min = 3.4 ha, max = 19.7 ha). For each stand, we measured: i) the seedling density, by  
230 counting the number of seedlings in 80 plots of 6 m<sup>2</sup> positioned according to a systematic grid  
231 pattern (all were summed and then reported as seedlings m<sup>-2</sup>); ii) the tree density by counting all  
232 trees in the stand; iii) the basal area, estimated from the tree diameter. The diameter of each tree  
233 (*d*, cm) was measured using a forest compensated calliper (i.e. graduated in 5 cm classes), the  
234 method which is regularly used in silviculture to carry out inventories and provides a good estimate  
235 of the basal area (Cordonnier et al., 2007). Stand basal area (*BA*) was then calculated for each  
236 stand as:  $BA (m^2/ha) = (\sum TBA)/stand\ area$ , with  $TBA (m^2) = \pi(d/100)^2/4$ ; iv) the forest cover,  
237 which was estimated using the normalised difference vegetation index (NDVI) based on analysis of  
238 multispectral images of the Pléiades satellite taken on 14 April 2018 and 03 September 2018, and  
239 performed with ArcGIS. This variable, obtained in m<sup>2</sup>, was then expressed as a percentage value by  
240 dividing the value by the stand area; and v) the individual tree crown surface area (m<sup>2</sup> tree<sup>-1</sup>), by  
241 dividing the forest cover (m<sup>2</sup>) by the number of trees.

### 242 2.5. Data treatment and statistics

243 All statistical analyses were performed with R software version 3.5.2. (R Core Team, 2018).  
244 Data regarding seed and seedling density (i.e. seed rain, soil seed bank, germination and final  
245 seedling density) are expressed in number m<sup>-2</sup> and are continuous quantitative variables. Seedling  
246 survival and browsing occurrence are binomial variables, while the different types of mortality are

247 expressed as a percentage. Assumption of normality and homoscedasticity were checked for all  
248 models mentioned below, and the response variable was square root transformed when necessary.  
249 Post-hoc Tukey pairwise multiple comparisons were carried out when we found that a multilevel  
250 factor was significant.

### 251 *2.5.1. Seed rain and seed bank*

252 We tested the effects of site and year on seed rain, the effects of site and harvesting method  
253 on soil seed bank, and the effect of site on seed morphology using analysis of variance. To  
254 investigate the influence of tree size and distance on seed rain, we performed linear mixed  
255 modelling with our seed source abundance index as an explanatory variable of the mean annual  
256 seed rain and the site as random effect. Differences in germinative capacity of the seeds between  
257 the three pools of seed sources and between sites were compared using chi-square tests.

### 258 *2.5.2. Germination and seedling establishment*

259 Analyses regarding germination, survival, browsing occurrence and final seedling density  
260 were performed following a two-step procedure: i) full analyses with the site, harvesting method and  
261 seeding as explanatory factors, and all two- and three-way interactions; and ii) intra-site analyses of  
262 harvesting method and seeding separately. A random intercept for each monitoring area was  
263 included in all models to take into account the spatial dependence of the quadrats of the same  
264 monitoring area. Germination, tested for each year separately, and final seedling density were  
265 analysed using linear mixed models. Longitudinal analyses of seedling survival were performed on  
266 the first cohort of emerged seedlings (i.e. cohort of May, which represents 75.4% of the seedlings in  
267 2015) using Cox proportional hazard mixed models. We examined seedling survival only in 2015  
268 because the number of seedlings in clear-cuts was too low to compare harvesting treatments and to  
269 perform statistical tests for three out of five sites in 2016, and for all sites in 2017. Browsing  
270 occurrence was tested with generalized linear mixed models for binary data with a logit link function.  
271 The effects of the harvesting method on the distribution of causes of mortality (i.e. drought, rodents  
272 or ungulates) were tested using chi-square tests between sites and within sites.

273 In addition, one-sample *t*-tests were used to determine whether the final seeding densities  
274 were significantly different from the regeneration success threshold for the four possible  
275 management scenarios (i.e. clear-cut, clear-cut + seeding, partial cut, partial cut + seeding).

### 276 *2.5.3. Overall probability of recruitment*

277 In order to identify the limiting stages of regeneration capacity, we calculated the transition  
278 probabilities of passing the successive stages of the regeneration process successfully, for each  
279 harvest treatment of each site. We estimated the following stages:

- 280 i) Seed germinative capacity, estimated via our glasshouse test. .
- 281 ii) Germination, as the germination number divided by the viable seed rain (estimated by  
282 combining total seed rain and seed germinative capacity) plus the viable seeds from direct  
283 seeding. Since the germinations of a year resulted from the seed rain of the previous summer,  
284 we used the seed rain data from 2014-2016 and germination data from 2015-2017. Seed rain  
285 before harvest (i.e. 2014) was not measured in our study and was thus calculated from the  
286 2015-2017 data by estimating the contribution of one tree to the seed rain (number of  
287 seeds  $\text{m}^{-2} \text{year}^{-1}$ ), and relating it to stand density before harvest.
- 288 iii) 1<sup>st</sup> year survival, as the number of living seedlings one year after emergence divided by the  
289 germination number.
- 290 iv) 2<sup>nd</sup>/3<sup>rd</sup> year survival, as the number of seedlings counted three years after harvest divided by  
291 the number of living seedlings at the end of each year. This represented the seedlings from  
292 2015 that died in 2016 and 2017, and those from 2016 that died in 2017.

293 We finally calculated the overall probability of recruitment as the product of the successive  
294 probabilities.

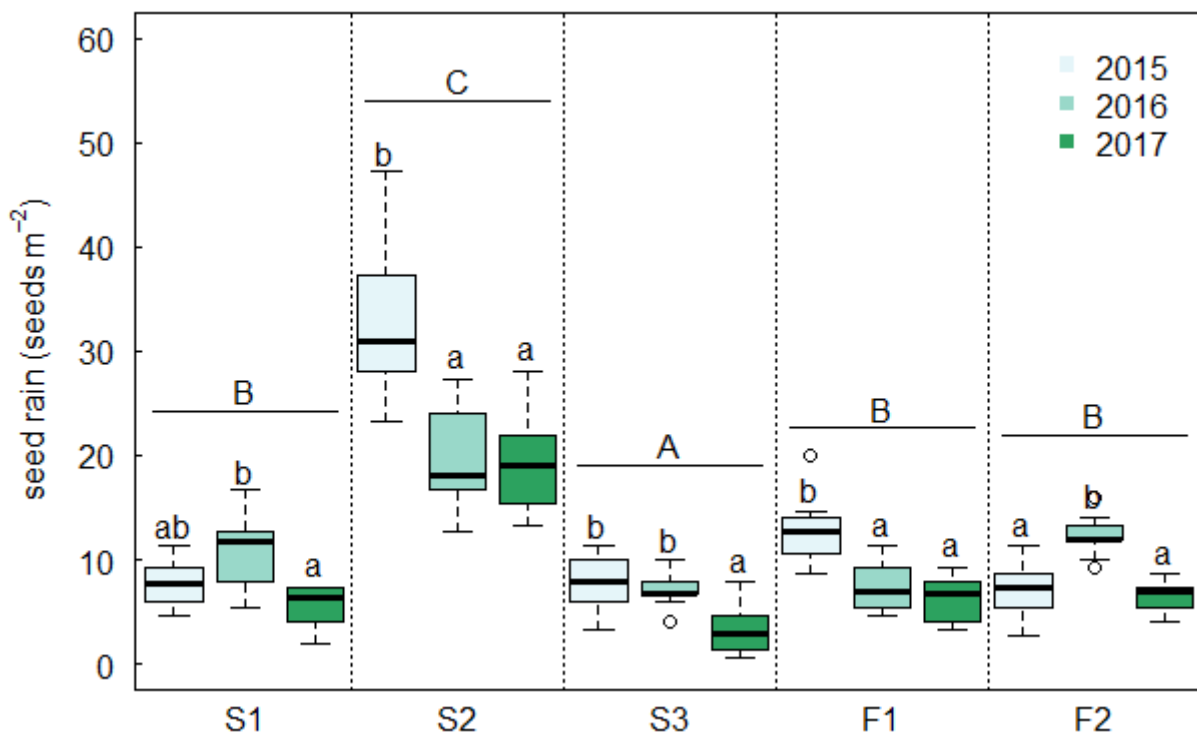
### 295 *2.5.4. Stand dendrometric features*

296 Relationships between dendrometric features of partial cuts (tree density, basal area, forest  
297 cover, and tree crown surface – see Table S2 for descriptive statistics of these variables) and  
298 seedling density were prospected with linear regression. As the year of harvesting had no effect on  
299 seedling density ( $p = 0.33$ ), these regressions were carried out using data from the 29 stands  
300 together.

301 **3. Results**

302 **3.1. Seed availability**

303 The number of seeds reaching the ground varied depending on the year and the site (both  $p$   
304  $< 0.001$ ; Fig. 2), with a different pattern of annual variation between sites (interaction  $p < 0.001$ ). All  
305 sites combined, seed rain averaged  $11.1 \pm 0.7$  seeds  $m^{-2}$  year $^{-1}$ , with a minimum of  $6.1 \pm 0.8$  seeds  
306  $m^{-2}$  year $^{-1}$  in S3 and a maximum of  $24 \pm 2.3$  seeds  $m^{-2}$  year $^{-1}$  in S2. Seed rain was influenced by tree  
307 size and density of mature trees in the vicinity of the seed traps, as seed rain was positively related  
308 to the seed source abundance index ( $F_{(1,44)} = 9.59, p = 0.004$ ).



309 **Fig. 2:** Amount of seed rain for each site per year ( $n = 10$  for each boxplot). Different uppercase letters  
310 indicate significant differences between sites, whereas different lowercase letters indicate significant  
311 differences between years within each site (post-hoc Tukey test).  
312

313 Seed weight and seed length were significantly different between sites (Fig. S2). With an  
314 average weight ranging from  $38.2 \pm 1.6$  mg (F2) to  $47.3 \pm 1.8$  mg (S2), and an average length  
315 ranging from  $7.28 \pm 0.1$  mm (F2) to  $7.71 \pm 0.1$  mm (S2), the seeds from all sites were within the  
316 range of known values for maritime pine seeds in Atlantic and Mediterranean forests (Fig. S2).

317 The amount of seeds in the soil seed bank also varied according to the site ( $p < 0.001$ ; Fig.  
318 S3), but not between clear-cut and partial cut areas ( $p = 0.215$ ). The average number of seeds was

319 119 ± 6.5 seeds m<sup>-2</sup>, with the largest amount in S1 with 196.6 ± 1.6 seeds m<sup>-2</sup> and the lowest in F1  
 320 with 79.6 ± 1.1 seeds m<sup>-2</sup>.

321 The germinative capacity of seeds showed very significant differences between the various  
 322 seed pools ( $\chi^2_{(2)} = 202.7, p < 0.001$ ; Fig. S4). The seeds used for the direct seeding had the highest  
 323 germinative capacity (86%), followed by the seeds from the seed rain (26 to 32% depending on the  
 324 site) and then the seed bank, of which no seeds from any stand germinated (Fig. S4). No difference  
 325 in germinative capacity was observed between the seed rain of the five sites ( $\chi^2_{(4)} = 0.57, p = 0.97$ ).

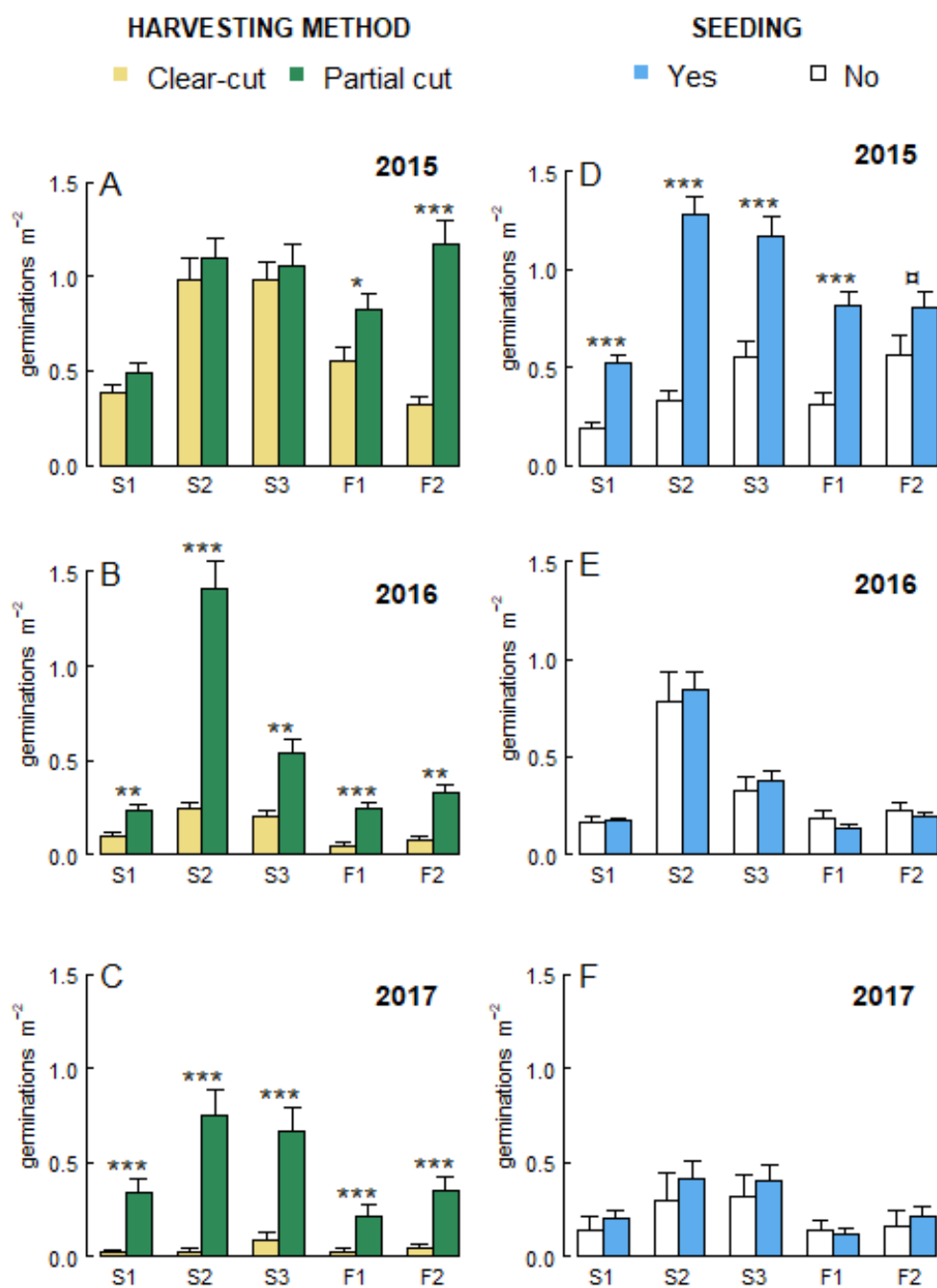
### 326 3.2. Germination

327 There was a significant site effect with, overall, a higher number of germinations in S2 and  
 328 S3, and a fewer in S1 (Table 1; Fig. 3). The interactions “site x harvesting method” and “site x  
 329 seeding” were also significant (Table 1), suggesting a major influence of site-specific conditions on  
 330 germination. The harvesting method had a highly significant effect on germination each  
 331 year (Table 1), with a higher number of germinations in partial cuts than in clear-cuts (Fig. 3). The  
 332 average number of germinations in partial cuts was 0.93 seedlings m<sup>-2</sup> in 2015, and this decreased  
 333 in the following two years (0.55 ± 0.06 seedlings m<sup>-2</sup> in 2016; 0.47 ± 0.09 seedlings m<sup>-2</sup> in 2017). In  
 334 clear-cuts, the number of germinations decreased sharply between the first and the second year  
 335 (0.65 ± 0.07 seedlings m<sup>-2</sup> in 2015; 0.14 ± 0.02 seedlings m<sup>-2</sup> in 2016), to reach nearly zero in the  
 336 third year (0.04 ± 0.02 seedlings m<sup>-2</sup> in 2017). Interestingly, when we examined the results site by  
 337 site, the positive effect of partial cuts was only observed in sites within the failure area in the first  
 338 year (Fig. 2A) while it was observed in all sites in the second and third year (Fig. 2B-C). The use of  
 339 direct seeding had a positive impact on germination only during the first year (Table 1; Fig. 2),  
 340 where the average number of germinations was 0.92 ± 0.08 seedlings m<sup>-2</sup> in the seeded quadrats  
 341 and 0.39 ± 0.07 seedlings m<sup>-2</sup> in the unseeded ones. This positive effect of seeding in the first year  
 342 was observed in all sites (Fig. 2D).

343 **Table 1:** Results of the linear mixed models for the effects of site, harvesting method, seeding and their  
 344 interactions on number of germinations for the three years. Significant effects ( $p < 0.05$ ) are indicated in bold.

<i>df</i>	2015		2016		2017	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>

Site	4,90	13.09	<0.001	23.41	<0.001	8.89	<0.001
Harvesting Method	1,90	23.93	<0.001	106.58	<0.001	195.77	<0.001
Seeding	1,290	95.72	<0.001	0.02	0.884	2.75	0.099
Site x Harvesting	4,90	6.35	<0.001	7.95	<0.001	4.90	0.001
Site x Seeding	4,290	4.52	0.002	0.67	0.615	0.98	0.422
Harvesting x Seeding	1,290	0.11	0.741	0.31	0.577	0.38	0.540
Site x Harvesting x Seeding	4,290	0.05	0.994	1.08	0.367	0.80	0.523



345

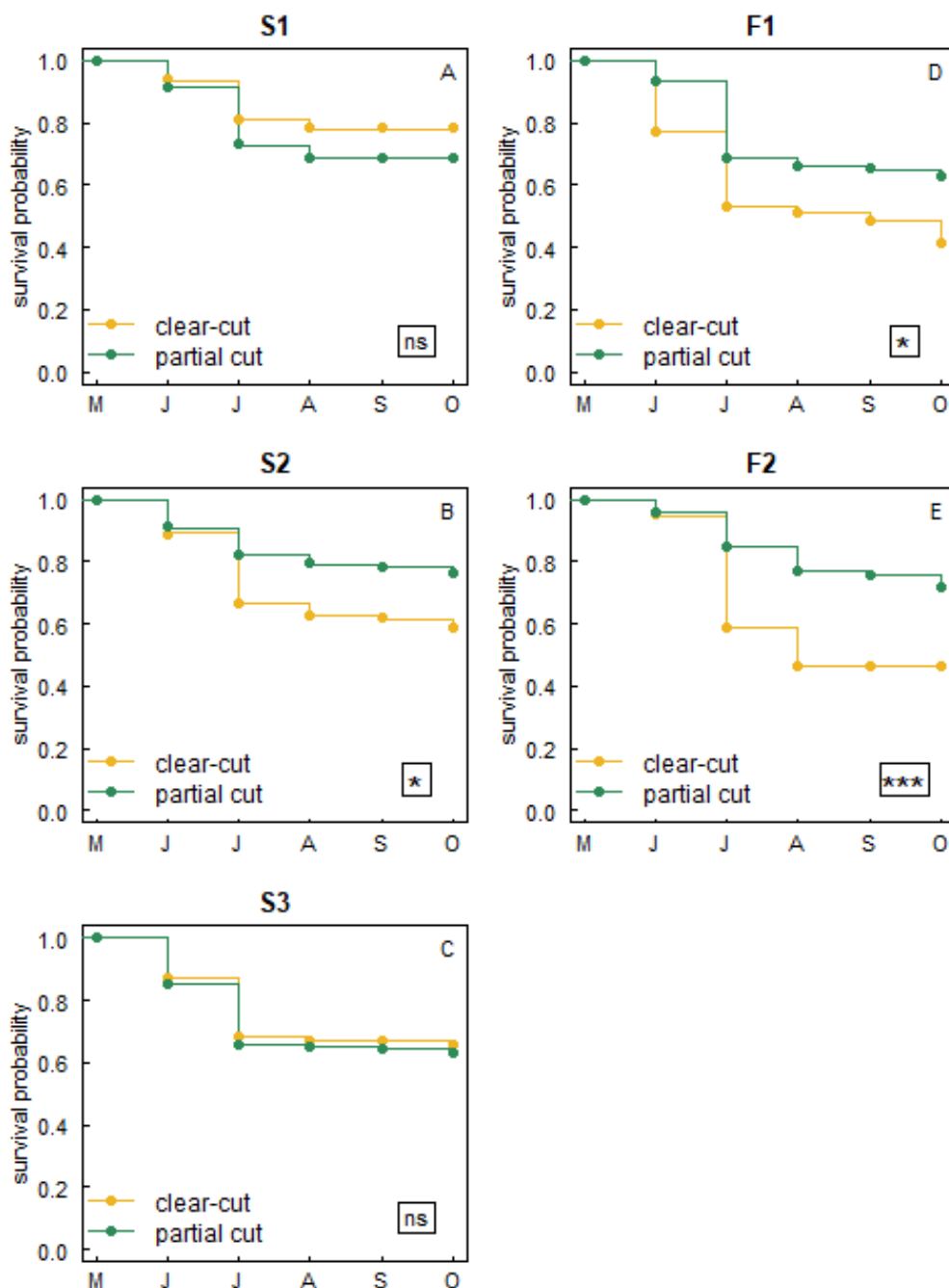
346 **Fig. 3:** Number of germinations m<sup>-2</sup> observed for each site according to the harvesting method (A-B-C) and  
 347 the presence of seeding (D-E-F). Panels A & D correspond to germinations from 2015, panels B & E to 2016,

348 and panels C & F to 2017. Asterisks indicate a significant difference between the two modalities within a site  
349 (linear mixed models: \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ ; °  $p < 0.1$ ).

### 350 **3.3. Survival**

351 Seedling survival was influenced by the harvesting method ( $\chi^2_{(1)} = 8.44$ ,  $p = 0.004$ ), but not  
352 by the site ( $\chi^2_{(4)} = 8.48$ ,  $p = 0.075$ ) or their interaction ( $\chi^2_{(4)} = 9.16$ ,  $p = 0.057$ ). Partial cutting had a  
353 positive impact on survival by decreasing mortality by 10.8% compared to clearcutting. On a site-by-  
354 site basis, partial cutting had a positive effect on three out of five sites, including the two in the  
355 failure area (mortality reduction of 17.5%, 21.5% and 25.6% for S2, F1 and F2 respectively; Fig. 4B-  
356 D-E). In addition, F1 and F2 were the only two sites where clear-cut survival rate was lower than  
357 50% (Fig. 4D-E).





358

359 **Fig. 4:** Seedling survival probability as a function of harvesting method in 2015, for each site separately.  
 360 Statistical significance between harvesting method is shown in the bottom right corner of each panel (Cox  
 361 mixed models: \*\*\*  $p < 0.001$ ; \*  $p < 0.05$ ; ns = non-significant).

362

363

364

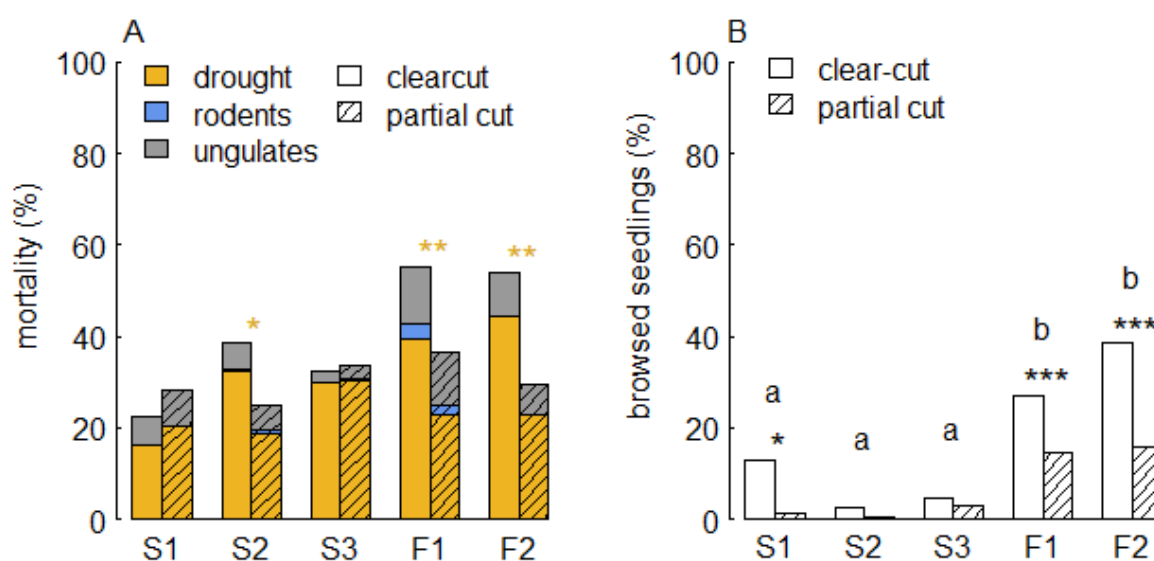
365

366

Drought was the main cause of mortality (Fig. 5A). All sites combined, we observed a higher mortality due to drought in clear-cuts than in partial cuts ( $\chi^2_{(4)} = 11.18$ ,  $p < 0.001$ ). Within sites, partial cutting significantly reduced the percentage of drought-killed seedlings in S2 ( $\chi^2_{(1)} = 7.39$ ,  $p = 0.007$ ), F1 ( $\chi^2_{(1)} = 6.28$ ,  $p = 0.012$ ) and F2 ( $\chi^2_{(1)} = 8.28$ ,  $p = 0.004$ ; Fig. 5A). Seedling death by herbivores was mainly caused by ungulates, while damage caused by rodents was almost nil,

367 except in F1 (Fig. 5A), and harvesting method had no influence on mortality caused by either type  
 368 of herbivore.

369 Conversely to herbivory-killed seedlings, there was a strong effect of site ( $\chi^2_{(4)} = 72.67$ ,  $p <$   
 370  $0.001$ ) and harvesting method ( $\chi^2_{(1)} = 17.99$ ,  $p < 0.001$ ) on the percentage of non-lethal browsed  
 371 seedlings. Browsing was more frequent in clear-cuts and in the two sites within the failure area (Fig.  
 372 5B). It was also on these two sites that the positive effect of partial cutting was the most  
 373 pronounced, reducing the browsing occurrence by 12.6% in F1 and 22.5% in F2 (Fig. 5B).

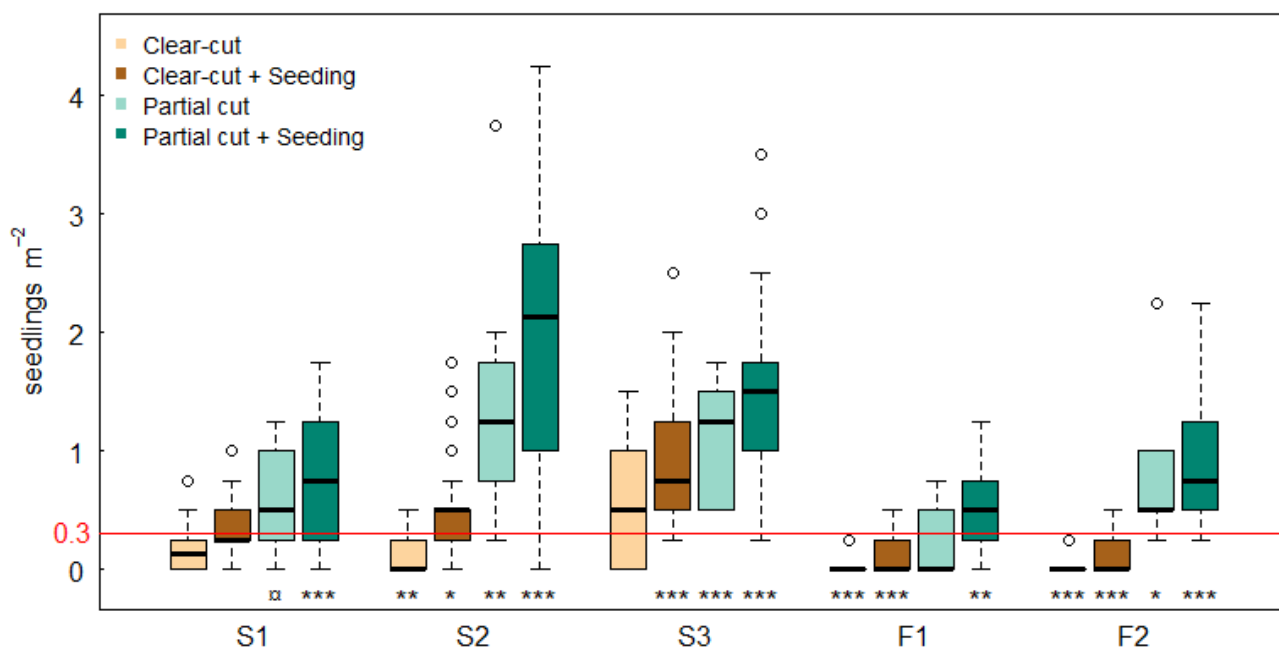


374 **Fig. 5:** A) Percentage mortality of each cause of death in 2015 according the site and harvesting method.  
 375 Yellow asterisks indicate a significant difference in the distribution of drought-killed seedlings between the two  
 376 harvesting method within a site (chi-square test: \*\*  $p < 0.01$ ; \*  $p < 0.5$ ). B) Seedlings non-lethally browsed by  
 377 ungulates in 2015 according to the site and the harvesting method. Different lowercase letters indicate  
 378 significant differences between sites (post-hoc Tukey test). Asterisks indicate a significant difference in  
 379 browsing occurrence between the two harvesting methods within a site (generalized linear mixed models: \*\*\*  
 380  $p < 0.001$ ; \*  $p < 0.5$ ).  
 381

### 382 3.4. Overall regeneration success

383 Three years after starting regeneration, seedling density was significantly higher in S2 and  
 384 S3 compared to the three other sites ( $F_{(4,90)} = 35.25$ ,  $p < 0.001$ ). The harvesting method had a very  
 385 significant effect on all the sites (Table S3) with a greater density of seedlings in partial cuts (Fig. 6),  
 386 whereas the use of seeding had a significant positive effect only in three sites (S2, S3 and F1;  
 387 Table S3). Interaction between harvesting method and seeding was not significant in all sites (Table  
 388 S3), suggesting that these two practices had independent effects on seedling densities. Clear-

389 cutting without seeding did not result in a sufficient seedling density to secure regeneration in any  
 390 site except for S3 (Fig. 6). Using direct seeding in addition to clear-cutting attained or exceeded the  
 391 threshold of 0.3 seedlings m<sup>-2</sup> for S1, S2 and S3, but was still largely insufficient for both sites in the  
 392 failure area (Fig. 6). Partial cutting without seeding had a very positive effect, as it allowed four out  
 393 of five sites to have a satisfactory regeneration, with F1 being around the predefined threshold (Fig.  
 394 6). Adding seeds to partial cuts increased seedling density in all sites, allowing all of them to  
 395 regenerate easily (Fig. 6).

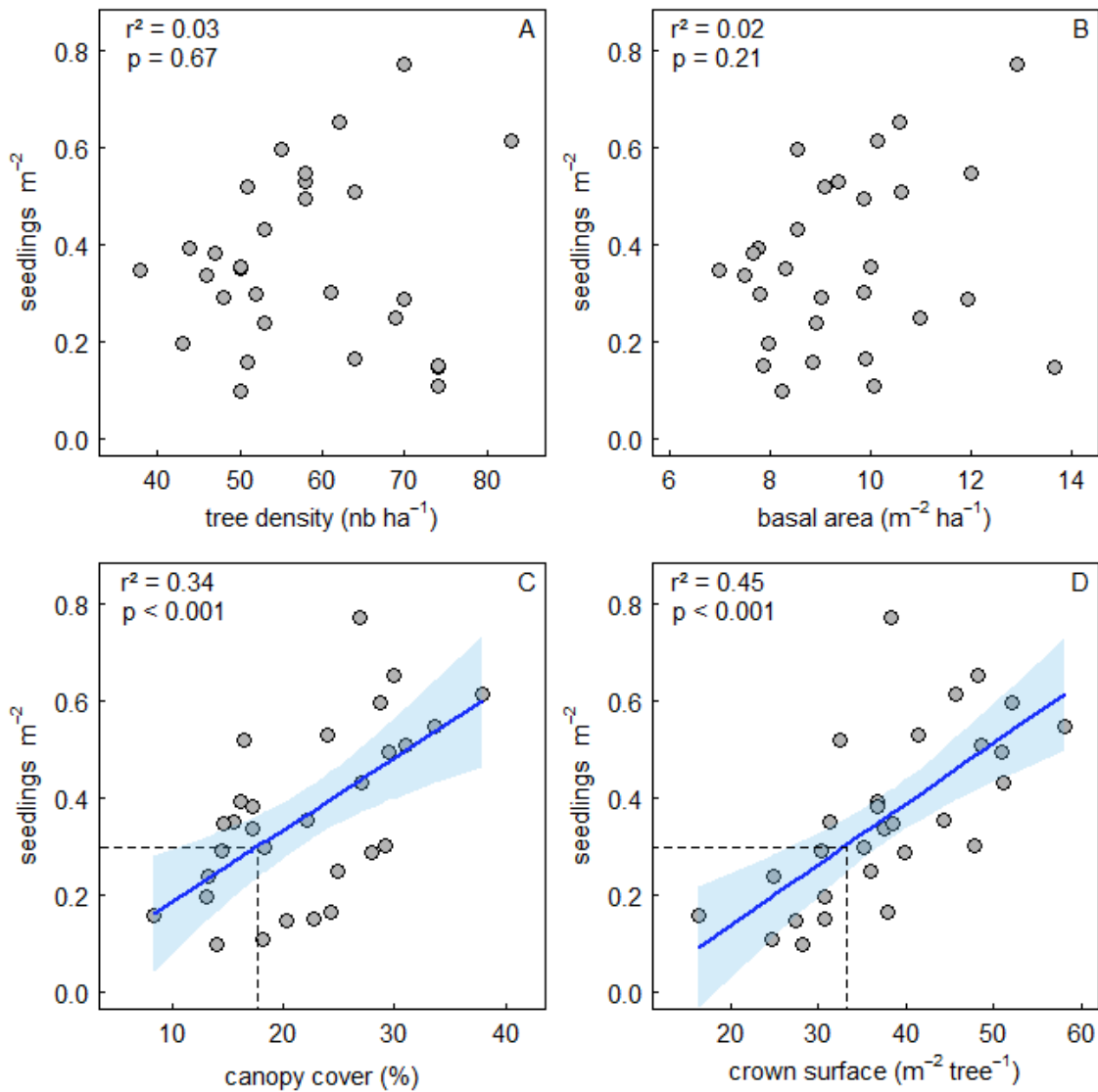


396 **Fig. 6:** Seedling density in March 2018 in each site (i.e. three years after harvest) as a function of the four  
 397 modalities of the harvesting method x seeding treatment combination. The red line represents the threshold of  
 398 0.3 seedlings m<sup>-2</sup> indicating sufficient regeneration. Asterisks indicate a significant difference from the  
 399 threshold values (one sample *t*-test: \*\*\* *p* < 0.001; \*\* *p* < 0.01; \* *p* < 0.05; ° *p* < 0.1).  
 400

401 In addition, results from the regional survey of the 29 stands harvested with partial cuts  
 402 showed that seedling density was not related to stand density (Fig. 7A) or basal area (Fig. 7B).  
 403 Conversely, stands with a higher forest cover (Fig. 7C) or with trees with well-developed crowns  
 404 (Fig. 7D) were associated with a more abundant regeneration.

405 In terms of recruitment probability, we observed strong differences between sites with a  
 406 minimal overall probability of 0.7% in F1 and a maximum probability of 3.4% in S3. The probability  
 407 of finding a seedling three years after seed dispersal was higher in partial cuts than in clear-cuts in  
 408 all sites because of higher germination and greater survival (Table 2). Between all stages, the

409 transition from viable seed rain to germination showed the lowest probability in all sites (Table 2).  
 410 Sites in failure areas showed the lowest recruitment probability in clear-cuts because of the lowest  
 411 level of survival, while lowest probabilities of germination were observed in S1 (Table 2). Overall,  
 412 the probability of final recruitment was between 0.4% and 3.1% in clear-cuts and between 0.9% and  
 413 3.6% in partial cuts.



414  
 415 **Fig. 7:** Influence of dendrometric characteristics of partial cuts on seedling density. A) tree density; B) basal  
 416 area; C) forest cover; and D) tree crown surface area. *P*-values and *r*<sup>2</sup> of the regressions are shown in the top  
 417 left corner. Blue lines represent significant regressions, with the 95% confidence intervals in light blue. The  
 418 dashed line represents the threshold of 0.3 seedlings m<sup>-2</sup> indicating sufficient regeneration.

419 **Table 2:** Stage-specific transition probabilities leading to the recruitment of *Pinus pinaster* seedlings,  
 420 according to the site and harvesting method.

Stage	S1		S2		S3		F1		F2	
	Clear-cut	Partial cut	Clear-cut	Partial cut	Clear-cut	Partial cut	Clear-cut	Partial cut	Clear-cut	Partial cut
Seed germinative capacity	0.300	0.300	0.320	0.320	0.300	0.300	0.260	0.260	0.320	0.320
Germination	0.036	0.053	0.042	0.073	0.154	0.182	0.055	0.079	0.037	0.114
1 <sup>st</sup> year survival	0.707	0.678	0.537	0.690	0.681	0.688	0.465	0.631	0.438	0.632
2 <sup>nd</sup> /3 <sup>rd</sup> year survival	0.891	0.965	0.771	0.885	0.981	0.961	0.693	0.709	0.822	0.834
Overall probability of recruitment for a given seed	0.007	0.010	0.006	0.014	0.031	0.036	0.005	0.009	0.004	0.019

421

## 422 **4. Discussion**

423 Partial cutting and direct seeding, the two practices evaluated as alternatives to clearcutting,  
 424 had a positive effect on regeneration in these dune forests. However, their effects on each stage  
 425 showed site-specific differences, suggesting the importance of local factors on the success of the  
 426 regeneration process (Rodríguez-García et al., 2010, 2011b). These two practices have two main  
 427 axes of influence on the regeneration process: the increase of seed availability, improving seed rain  
 428 and germination; and the modification of microhabitat beneath the tree canopy, affecting both  
 429 germination and survival.

### 430 **4.1. Influence of forestry practices on seed availability**

431 Seed rain showed large spatial and temporal variations but did not appear to be a limiting  
 432 factor in our context, as the two failure sites did not differ from the others and as S3, with the lowest  
 433 seed rain, was one of the sites with the highest number of germinations and with the greatest  
 434 regeneration three years after harvest. Two recent studies on maritime pine stands suggesting that  
 435 neither seed production nor seed dispersal are limiting factors for regeneration showed similar  
 436 results, with 7–24 seeds m<sup>-2</sup> (Ruano et al., 2015b) and 7–15 seeds m<sup>-2</sup> (Juez et al., 2014).  
 437 However, it will be important to pay attention to these issues in the future as extreme climatic  
 438 conditions are expected to increase and could lead to a decrease in seed production (Mutke et al.,

439 2005; Ruano et al., 2015b). In our context, the main problem seems to be seed storage and  
440 conservation in the belowground seed bank until germination, which is a highly variable stage  
441 between provenances and populations of this species (Wahid and Bounoua, 2013; Calvo et al.,  
442 2016). In particular, the Atlantic provenance, which includes our coastal forests (de la Mata et al.,  
443 2012), showed the lowest germination rates in response to drought (Nuñez Paniagua et al., 2013).  
444 Here, we observed a probability of germination of only 4–18%, a fairly low percentage compared to  
445 other studies on maritime pine in situ (13–62%; Ruano et al., 2015a) or under controlled conditions  
446 (14–27%; Cruz et al., 2019). As seed weight was similar in our study and previous ones, this low  
447 germination rate is more likely to be explained by: high post-dispersal predation by many different  
448 organisms (Ruano et al., 2015a), the presence of a litter layer and harvest debris acting as a  
449 physical barrier preventing seeds from reaching the soil (Facelli and Pickett, 1991), or a very poor  
450 conservation of seed germinative capacity in the soil (Kozłowski, 2002). Indeed, the number of  
451 germinations in 2015 was slightly over one seedling m<sup>-2</sup> at the most, while the soil seed bank was  
452 high, with an average of 119 seeds m<sup>-2</sup>. Although pine species form only a short-lived soil seed  
453 bank with an expected minor role for regeneration (Izhaki et al., 2000), such quantities of seeds in  
454 the soil is not surprising with regard to other pine forests, where 150 and 187 seeds m<sup>-2</sup> were  
455 reported for *P. pinaster* and *P. halepensis* stands respectively (Daskalidou and Thanos, 1996; Luis-  
456 Calabuig et al., 2002). However, most seeds in the belowground seed bank are not viable, as  
457 shown by two studies on Aleppo pine: Izhaki et al. (2000) found that the density of germinable pine  
458 seeds was 0.83 seeds m<sup>-2</sup>, while Daskalidou and Thanos (1996) showed that only 8 to 18% of the  
459 seeds stored in the soil were sound. Our glasshouse test of germination capacity correspond to  
460 those results, showing that only seeds from the seed rain of the previous summer could contribute  
461 to germination in the following spring, while those stored in the seed bank were not viable for  
462 germination. Moreover, the significant decrease in number of germinations in clear-cuts between  
463 the first and second year, and then near-zero in the third year confirmed that seeds do not remain  
464 viable for more than a year in the soil in most cases. Finally, although seeds from direct seeding  
465 had a germination capacity of 86%, their effect on germination was only observed in the first year.  
466 This confirms the short life span of the soil seed bank, and that the regeneration of maritime pine  
467 depends almost exclusively upon the seed rain falling during the year before harvest.

468 Partial cutting and direct seeding were therefore two effective practices to increase seed  
469 stocks and improve germination. Direct seeding had an instantaneous impact by significantly  
470 increasing the number of germinations on all sites, up to 4-fold greater than in the unseeded plots,  
471 but only in the first year. This strong impact can be explained by their higher germination capacity  
472 as a result of a prior selection during which only the heaviest –and hence those most likely to be  
473 viable– seeds were selected. It can also be explained by the shorter time spent in the soil by these  
474 seeds, as seed rain occurred in summer while direct seeding was done in winter, and was therefore  
475 less vulnerable to predation or detrimental environmental conditions. However, the effect of seeding  
476 in our study was probably overestimated because seeds were sown manually one-by-one and were  
477 thus incorporated into the soil under better conditions, in contrast to the broadcast seeding  
478 practiced by foresters. Conversely to seeding, partial cutting had a longer-lasting effect with a  
479 regular yearly seed supply, leading to higher germination in all sites in the second and third years.

#### 480 **4.2. Influence of partial cutting on microhabitat**

481 Our results showed a positive effect of partial cuts, both for germination and survival stages.  
482 However, the outcome of partial cutting is affected by local site conditions (Rodríguez-García et al.,  
483 2010), and this was also observed in our study, with large variations between the five sites. Effect of  
484 partial cutting was significantly positive in two sites for germination (F1 and F2) and three sites for  
485 survival (S2, F1 and F2). The similar differences in germination found in S1, S2 and S3, which also  
486 had very different survival rates, and the fact that S2 was similar to F1 and F2 for survival but not  
487 germination, suggests that the mechanisms of canopy-induced effects are different depending on  
488 the stage of regeneration considered. In general, the positive effects of partial cutting increased  
489 gradually with the increase of forest cover, as demonstrated in our regional survey (Fig. 7).

490 However, the influence of partial cutting on the microhabitat can only be discussed for the  
491 first year of the study for two reasons: i) germination in 2015 was linked to the seed rain in 2014  
492 (before exploitation and so were similar in the two harvest modalities), and differences observed  
493 that year were therefore mainly due to the influence of harvesting method and not related to seed  
494 availability. In contrast, the role of microhabitat on germination became indistinguishable in the  
495 second and third years because differences in germination were essentially the consequence of an

496 additional seed supply by seed-trees; and ii) we could not perform statistical analyses regarding  
497 seedling survival as the number of seedlings was too low in clear-cuts in the second and third  
498 years.

#### 499 *4.2.1. Influence on germination*

500 Soil moisture and soil temperature, which are closely related to the light reaching the forest  
501 floor, are the main drivers of germination and could be affected by forest canopy structure  
502 (Aussenac, 2000; Castro et al., 2005). In our study, the effect of canopy cover had a strong impact  
503 in the two sites within the failure area, as well as a slightly positive effect in the other three sites, as  
504 confirmed by the greater probability of germination in partial cuts than in clear-cuts for all sites. This  
505 suggests that partial cutting induced slightly more suitable conditions for germination in all sites, and  
506 that another factor was involved at this stage within the failure area which was reduced by the  
507 presence of a canopy. Canopy mitigation of light intensity in partial cuts was similar in the five  
508 stands (Guignabert et al., 2018). This could explain the slight positive effect on all sites because it  
509 was the only factor similarly impacted by the partial cutting in all sites. This positive effect was more  
510 likely to be due to a decrease in soil temperature than an increase in soil moisture, since the effects  
511 of harvesting method were identical in the driest site and the wettest site (see S2 and S3 in Table  
512 S1). However, soil moisture was probably a primordial factor for germination in our forests because  
513 the site with the highest amount of precipitation (S3) was by far the one with the highest probability  
514 of germination. Thus, we may not have preserved enough forest cover in the experimental partial  
515 cuts to have a real impact on soil moisture, because the regional sandy soils do not hold enough  
516 water, or to maintain a low light intensity as pine forests usually have low LAI values (Gonzalez et  
517 al., 2013). Further studies are therefore needed to investigate the role of light and water availability  
518 on the germination process to better understand the canopy-induced effects on seedling  
519 emergence. The large difference in the number of germinations between the two harvesting  
520 methods in the failure area is intriguing and could be the result of a biotic component rather than  
521 improved microclimate, such as rodent seed predation. Indeed, rodent seed predation is one of the  
522 main bottlenecks in some Spanish pine stands (Ruano et al., 2015a), and a former study has  
523 already shown higher rodent damage in this area of our coastal forests (GEREA, 1990). As rodent



524 foraging activity increases with the volume of coarse woody debris on the stand (Puig-Gironès et  
525 al., 2020), this may explain the lower number of germinations in clear-cuts where woody debris was  
526 more abundant.

#### 527 *4.2.2. Influence on seedling survival*

528 Summer drought was the main cause of mortality in all sites, and was reduced by partial  
529 cuts in three sites (S2, F1 and F2). This is in agreement with previous studies on maritime pine that  
530 demonstrated enhancement of seedling recruitment beneath conspecific mature trees where  
531 canopy cover buffered abiotic stresses (Ruano et al., 2009; Rodríguez-García et al., 2011a, 2011b).  
532 The positive impact of canopy cover on survival would mainly be characterized by a decrease in  
533 vapour pressure deficit, as demonstrated on oak seedlings in the same coastal forests (Muhamed  
534 et al., 2013), where higher vapour pressure deficit increased seedling transpiration demand and  
535 seedling sensitivity to drought (Will et al., 2013). Even if we did not have accurate microclimate  
536 measurements in each harvesting method x site locations, we observed that S1 had lower  
537 temperatures and S3 had higher precipitation. Consequently, they should both have a lower aridity  
538 level than the other three sites especially in summer (Ouallet, 2012). This may explain why the  
539 effect of partial cutting was positive only in S2, F1 and F2. It is also important to mention that the  
540 summer of 2015 was an average summer, while the summer of 2016 was the driest of the last  
541 decade, particularly the July-August period (precipitation: 94-110 mm in 2015 vs. 15-26 mm in  
542 2016). We were unable to compare survival during that year because we lacked seedlings in clear-  
543 cuts. However, survival in partial cuts in 2016 was between 42% and 76% (Fig. S5), whereas in  
544 comparison with another study carried out in the same year in a clear-cut within the failure area,  
545 only 10% of seedlings survived (Fig. S5; Guignabert et al., 2020). This suggests that the benefit of  
546 partial cutting is even more positive during an extremely dry summer. This drier summer in 2016  
547 also showed that mortality after the first year could be high as well (up to 30% in F1) although it  
548 remained lower than the first summer mortality. In this previous study, we also found that  
549 understory vegetation could facilitate seedling establishment at intermediate water stress and that  
550 damage by deer and rodents, which were quite important, could be modulated by shrub presence  
551 (Guignabert et al., 2020). Therefore, further studies investigated the effect of partial cutting on

552 seedling establishment should consider these biotic interactions, as overstorey canopy may modify  
553 the outcome of plant-plant interactions (Rodríguez-García et al., 2011a).

554 At a larger scale than the seed-seedling microsite, harvesting method also affects habitat  
555 and therefore the behaviour of ungulate and rodent species (Reimoser and Gossow, 1996; Fisher  
556 and Wilkinson, 2005). Browsing by herbivores can kill seedlings or reduce height growth leading to  
557 recruitment failure of tree species or to poorly shaped trees, thus reducing their commercial value  
558 (Côté et al., 2004). In our study, ungulate browsing on pine seedlings was higher at both sites in the  
559 failure area, and higher in clear-cuts than in partial cuts. Post-harvest development of herbaceous  
560 vegetation is greater in clear-cuts than partial cuts because of differences in light intensity,  
561 increasing food supplies for ungulates. This results in higher risk of browsing damage in clear-cuts  
562 than partial cuts (Reimoser and Gossow, 1996), a risk that is more severe in areas with high  
563 ungulate abundance (Tremblay et al., 2007). This was potentially the case for the sites within the  
564 failure area, because they were located within a military area where hunting is controlled and lower  
565 in comparison to other parts of the coastal forests (Guignabert, 2018). In addition, it has been  
566 shown that rodents could have a negative impact on seedling survival in a recently clear-cut stand  
567 in the failure area (Guignabert et al., 2020), but this seems not systematic as it was rarely observed  
568 in the five sites of the present study.

### 569 **4.3. Conclusion and management implications**

570 Overall, seedling density in all sites three years after harvest was higher in partial cuts than  
571 clear-cuts, and was higher in seeded than unseeded plots (but only significant in three sites). These  
572 practices influenced the whole regeneration process by various mechanisms discussed in the  
573 foregoing paragraphs, validating our three initial hypotheses. Indeed, partial cutting had a positive  
574 effect in the long term by providing seeds each year, and by reducing biotic and abiotic stresses,  
575 which improved germination and survival (hyp. 1). This positive effect was actually more  
576 pronounced in the failure area, as the only two sites where partial cutting had an impact on both  
577 germination and survival were within this area (hyp. 2). Lastly, direct seeding had a positive impact  
578 on germination, but seedling density was always higher in partial cuts than in clear-cuts + seeding,  
579 which makes its use less beneficial (hyp. 3). Thus, sufficient regeneration can be achieved in all

580 stands by using these two practices appropriately. Their effects are independent, thus enabling us  
581 to propose a revision of silvicultural practices currently applied in these forests, while additional  
582 research with longer-term monitoring and more replications, particularly in the area of chronic  
583 regeneration, should be pursued to optimize these management recommendations.

584 Clear-cutting without seeding led to severe regeneration failure in 4 out of 5 sites, the last  
585 one being around the threshold limit. Applying direct seeding enabled only two sites to significantly  
586 exceed the required seedling density. Consequently, the practice of clear-cutting currently used in  
587 these forests should be avoided, even with the addition of direct seeding. Indeed, seeding had an  
588 immediate effect and if the harvesting followed a poor year of seed production or if the spring and/or  
589 summer following harvest was very dry, regeneration would not be sufficient resulting in a  
590 silvicultural stalemate in the stand, making forest renewal impossible. In contrast, partial cutting had  
591 a strong positive impact on all sites and should be the method preferred here, as already performed  
592 in the Iberian peninsula in the same type of pine forests with sandy soils and severe summer  
593 drought (Calama et al., 2017). The forest cover and to a lesser extent the basal area should be  
594 considered when carrying out partial cutting, which should not be based on a specific tree density.  
595 The forest cover retained for partial cutting should be at least 18%, preferably with trees with well-  
596 developed crowns ( $>33 \text{ m}^2$ ). In areas of regeneration failures where the canopy effects are  
597 important for both germination and survival, leaving a denser forest cover (around 30%) would be  
598 better. Even if the basal area had no effects on the final seedling density, it was positively related to  
599 a higher seed rain. Thus, keeping trees with high diameter and great vigour is also recommended  
600 as they are a good indicator of higher cone production (Bravo et al., 2017), and should be  
601 distributed as homogeneously as possible throughout the stand. In addition, partial cutting could be  
602 combined with a direct seeding to maximize the chances of success, but only in failure areas.

603

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## 615 **References**

- 616 Alía, R., Martín, S., 2003. EUFORGEN: Technical guidelines for genetic conservation and use for  
617 Maritime pine (*Pinus pinaster*). Int. Plant Genet. Resour. Inst.  
618 <https://doi.org/10.1016/j.jhazmat.2010.10.029>
- 619 Augusto, L., Bakker, M.R., Morel, C., Meredieu, C., Trichet, P., Badeau, V., Arrouays, D., Plassard,  
620 C., Achat, D.L., Gallet-Budynek, A., Merzeau, D., Canteloup, D., Najjar, M., Ranger, J., 2010. Is  
621 'grey literature' a reliable source of data to characterize soils at the scale of a region? A case  
622 study in a maritime pine forest in southwestern France. Eur. J. Soil Sci. 61, 807–822.  
623 <https://doi.org/10.1111/j.1365-2389.2010.01286.x>
- 624 Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects  
625 and consequences for silviculture. Ann. For. Sci. 57, 287–301.  
626 <https://doi.org/10.1051/forest:2000119>
- 627 Beckage, B., Clark, J.S., 2003. Seedling survival and growth of three forest tree species: the role of  
628 spatial heterogeneity. Ecology 84, 1849–1861.
- 629 Bravo, F., Maguire, D.A., González-Martínez, S.C., 2017. Factors affecting cone production in *Pinus*  
630 *pinaster* Ait.: lack of growth-reproduction trade-offs but significant effects of climate and tree  
631 and stand characteristics. For. Syst. 26, e07S. <https://doi.org/10.5424/fs/2017262-11200>
- 632 Calama, R., Manso, R., Lucas-Borja, M.E., Espelta, J.M., Piqué, M., Bravo, F., Del Peso, C.,  
633 Pardos, M., 2017. Natural regeneration in Iberian pines: A review of dynamic processes and  
634 proposals for management. For. Syst. 26. <https://doi.org/10.5424/fs/2017262-11255>
- 635 Calvo, L., Hernández, V., Valbuena, L., Taboada, A., 2016. Provenance and seed mass determine  
636 seed tolerance to high temperatures associated to forest fires in *Pinus pinaster*. Ann. For. Sci.  
637 73, 381–391. <https://doi.org/10.1007/s13595-015-0527-0>
- 638 Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2005. Ecology of seed germination of *Pinus*  
639 *sylvestris* L. at its southern, Mediterranean distribution range. Investig. Agrar. Sist. y Recur.  
640 For. 14, 143. <https://doi.org/10.5424/srf/2005142-00879>
- 641 Cordonnier, T., Tran-ha, M., Piat, J., François, D., 2007. La surface terrière: méthodes de mesure et  
642 intérêts. Rendez-vous Tech. ONF n°18, 9–16.
- 643 Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological Impacts of  
644 Deer Overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147.  
645 <https://doi.org/10.1146/annurev.ecolsys.35.021103.105725>
- 646 Cruz, O., García-Duro, J., Casal, M., Reyes, O., 2019. Role of serotiny on *Pinus pinaster* Aiton  
647 germination and its relation to mother plant age and fire severity. iForest 12, 491–497.  
648 <https://doi.org/10.3832/ifor2968-012>
- 649 Daskalakou, E.N., Thanos, C.A., 1996. Aleppo pine (*Pinus halepensis*) postfire regeneration: The  
650 role of canopy and soil seed banks. Int. J. Wildl. Fire 6, 59–66.  
651 <https://doi.org/10.1071/WF9960059>

- 652 de la Mata, R., Voltas, J., Zas, R., 2012. Phenotypic plasticity and climatic adaptation in an Atlantic  
653 maritime pine breeding population. *Ann. For. Sci.* 69, 477–487. [https://doi.org/10.1007/s13595-](https://doi.org/10.1007/s13595-011-0173-0)  
654 011-0173-0
- 655 Dey, D.C., Knapp, B.O., Battaglia, M.A., Deal, R.L., Hart, J.L., O'Hara, K.L., Schweitzer, C.J.,  
656 Schuler, T.M., 2019. Barriers to natural regeneration in temperate forests across the USA.  
657 *New For.* 50, 11–40. <https://doi.org/10.1007/s11056-018-09694-6>
- 658 Facelli, J.M., Pickett, S.T.A., 1991. Plant litter: Its dynamics and effects on plant community  
659 structure. *Bot. Rev.* 57, 1–32. <https://doi.org/10.1007/BF02858763>
- 660 Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W.,  
661 Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L.,  
662 2014. REVIEW: Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl.*  
663 *Ecol.* 51, 1669–1679. <https://doi.org/10.1111/1365-2664.12289>
- 664 Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the  
665 North American boreal forest. *Mamm. Rev.* 35, 51–81. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2907.2005.00053.x)  
666 2907.2005.00053.x
- 667 GERE, 1990. Etude de la prédation exercée par les vertébrés sur les graines de pin maritime  
668 dans les forêts dunaires. ONF, Université de Bordeaux I.
- 669 Gómez-Aparicio, L., Valladares, F., Zamora, R., Luis Quero, J., 2005. Response of tree seedlings to  
670 the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different  
671 scales. *Ecography (Cop.)*. 28, 757–768. <https://doi.org/10.1111/j.2005.0906-7590.04337.x>
- 672 González-Alday, J., Martínez-Ruiz, C., Bravo, F., 2009. Evaluating different harvest intensities over  
673 understory plant diversity and pine seedlings, in a *Pinus pinaster* Ait. natural stand of Spain.  
674 *Plant Ecol.* 201, 211–220. <https://doi.org/10.1007/s11258-008-9490-2>
- 675 Gonzalez, M., Augusto, L., Gallet-Budynek, A., Xue, J., Yauschew-Raguene, N., Guyon, D.,  
676 Trichet, P., Delerue, F., Niollet, S., Andreasson, F., Achat, D.L., Bakker, M.R., 2013.  
677 Contribution of understory species to total ecosystem aboveground and belowground biomass  
678 in temperate *Pinus pinaster* Ait. forests. *For. Ecol. Manage.* 289, 38–47.  
679 <https://doi.org/10.1016/j.foreco.2012.10.026>
- 680 Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M.J., 1999. A  
681 review of the regeneration dynamics of North American boreal forest tree species. *Can. J. For.*  
682 *Res.* 29, 824–839. <https://doi.org/10.1139/x98-112>
- 683 Grossnickle, S., Ivetić, V., 2017. Direct Seeding in Reforestation – A Field Performance Review.  
684 *REFORESTA* 94–142. <https://doi.org/10.21750/REFOR.4.07.46>
- 685 Guignabert, A., 2018. Etude des processus de régénération naturelle du pin maritime en contexte  
686 de dune forestière gérée. Influence de la sylviculture, du climat et des interactions biotiques.  
687 PhD Thesis - Université de Bordeaux.
- 688 Guignabert, A., Augusto, L., Gonzalez, M., Chipeaux, C., Delerue, F., 2020. Complex biotic  
689 interactions mediated by shrubs: Revisiting the stress-gradient hypothesis and consequences  
690 for tree seedling survival. *J. Appl. Ecol.* 57, 1341–1350. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2664.13641)  
691 2664.13641
- 692 Guignabert, A., Delerue, F., Gonzalez, M., Augusto, L., Bakker, M., 2018. Effects of Management  
693 Practices and Topography on Ectomycorrhizal Fungi of Maritime Pine during Seedling  
694 Recruitment. *Forests* 9, 245. <https://doi.org/10.3390/f9050245>
- 695 Harmer, R., 2001. The effect of plant competition and simulated summer browsing by deer on tree  
696 regeneration. *J. Appl. Ecol.* 38, 1094–1103. <https://doi.org/10.1046/j.1365-2664.2001.00664.x>
- 697 Harper, J.L., 1977. Population biology of plants. Academic Press, London.
- 698 Heithecker, T.D., Halpern, C.B., 2006. Variation in microclimate associated with dispersed-retention

- 699 harvests in coniferous forests of western Washington. *For. Ecol. Manage.* 226, 60–71.  
700 <https://doi.org/10.1016/j.foreco.2006.01.024>
- 701 IFN, 2017. Inventaire Forestier National [WWW Document]. URL <https://inventaire-forestier.ign.fr/>  
702 (accessed 12.18.17).
- 703 IPCC, 2014. *Climate Change 2014: Synthesis Report*. Cambridge University Press, Cambridge.
- 704 Izhaki, I., Henig-Sever, N., Ne'Eman, G., 2000. Soil seed banks in Mediterranean Aleppo pine  
705 forests: the effect of heat, cover and ash on seedling emergence. *J. Ecol.* 88, 667–675.  
706 <https://doi.org/10.1046/j.1365-2745.2000.00486.x>
- 707 Juez, L., González-Martínez, S.C., Nanos, N., De-Lucas, A.I., Ordóñez, C., del Peso, C., Bravo, F.,  
708 2014. Can seed production and restricted dispersal limit recruitment in *Pinus pinaster* Aiton  
709 from the Spanish Northern Plateau? *For. Ecol. Manage.* 313, 329–339.  
710 <https://doi.org/10.1016/j.foreco.2013.10.033>
- 711 Kozłowski, T.T., 2002. Physiological ecology of natural regeneration of harvested and disturbed  
712 forest stands: implications for forest management. *For. Ecol. Manage.* 158, 195–221.  
713 [https://doi.org/10.1016/S0378-1127\(00\)00712-X](https://doi.org/10.1016/S0378-1127(00)00712-X)
- 714 Lavoie, J., Montoro Girona, M., Morin, H., 2019. Vulnerability of Conifer Regeneration to Spruce  
715 Budworm Outbreaks in the Eastern Canadian Boreal Forest. *Forests* 10, 850.  
716 <https://doi.org/10.3390/f10100850>
- 717 Löf, M., 2000. Establishment and growth in seedlings of *Fagus sylvatica* and *Quercus robur*:  
718 influence of interference from herbaceous vegetation. *Can. J. For. Res.* 30, 855–864.  
719 <https://doi.org/10.1139/x99-257>
- 720 Luis-Calabuig, E., Torres, O., Valbuena, L., Calvo, L., Marcos, E., 2002. Impact of large fires on a  
721 community of *Pinus pinaster*. *Fire Biol. Process.* 1–12.
- 722 Montoro Girona, M., Lussier, J.-M., Morin, H., Thiffault, N., 2018. Conifer Regeneration After  
723 Experimental Shelterwood and Seed-Tree Treatments in Boreal Forests: Finding Silvicultural  
724 Alternatives. *Front. Plant Sci.* 9, 1–14. <https://doi.org/10.3389/fpls.2018.01145>
- 725 Montoro Girona, M., Morin, H., Lussier, J.-M., Ruel, J.-C., 2019. Post-cutting Mortality Following  
726 Experimental Silvicultural Treatments in Unmanaged Boreal Forest Stands. *Front. For. Glob.*  
727 *Chang.* 2, 1–16. <https://doi.org/10.3389/ffgc.2019.00004>
- 728 Montoro Girona, M., Morin, H., Lussier, J.-M., Walsh, D., 2016. Radial Growth Response of Black  
729 Spruce Stands Ten Years after Experimental Shelterwoods and Seed-Tree Cuttings in Boreal  
730 Forest. *Forests* 7, 240. <https://doi.org/10.3390/f7100240>
- 731 Muhamed, H., Touzard, B., Le Bagousse-Pinguet, Y., Michalet, R., 2013. The role of biotic  
732 interactions for the early establishment of oak seedlings in coastal dune forest communities.  
733 *For. Ecol. Manage.* 297, 67–74. <https://doi.org/10.1016/j.foreco.2013.02.023>
- 734 Mutke, S., Gordo, J., Gil, L., 2005. Variability of Mediterranean Stone pine cone production: Yield  
735 loss as response to climate change. *Agric. For. Meteorol.* 132, 263–272.  
736 <https://doi.org/10.1016/j.agrformet.2005.08.002>
- 737 Nuñez Paniagua, M., Sierra de Grado, R., Alía, R., Bravo, F., 2013. Efecto del estrés hídrico y la  
738 oscilación de las temperaturas sobre la germinación de semillas de diversas procedencias de  
739 *Pinus pinaster* Ait., in: 6° Congreso Forestal Español. Vitoria, junio, pp. 1–12.
- 740 Nyland, R.D., 2016. *Silviculture: Concepts and Applications*. 3rd edn. Waveland Press, Long Grove,  
741 Illinois.
- 742 Ouallet, P., 2012. Quels peuvent-être les facteurs écologiques responsables des échecs de  
743 régénération naturelle du pin maritime sur les dunes littorales des forêts domaniales de  
744 Biscarrosse et de Sainte-Eulalie? MsC Thesis - BSA, ONF.
- 745 Price, D.T., Zimmermann, N.E., van der Meer, P.J., Lexer, M.J., Leadley, P., Jorritsma, I.T.M.,

- 746 Schahber, J., Clark, D.F., Lasch, P., McNulty, S., Wu, J., Smith, B., 2001. Regeneration in gap  
747 models: priority issues for studying forest responses to climate change. *Clim. Change* 51, 475–  
748 508. <https://doi.org/10.1023/A:1012579107129>
- 749 Puig-Gironès, R., Imbeau, L., Clavero, M., Rost, J., Pons, P., 2020. Does post-fire salvage logging  
750 affect foraging activity by rodents? *Eur. J. For. Res.* <https://doi.org/10.1007/s10342-020-01285-5>  
751 5
- 752 R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for  
753 Statistical Computing, Vienna, Austria. <https://www.r-project.org/>.
- 754 Reimoser, F., Gossow, H., 1996. Impact of ungulates on the silvicultural system. *For. Ecol. Manage.*  
755 88, 107–119.
- 756 Rodríguez-García, E., Bravo, F., Spies, T.A., 2011a. Effects of overstorey canopy, plant–plant  
757 interactions and soil properties on Mediterranean maritime pine seedling dynamics. *For. Ecol.  
758 Manage.* 262, 244–251. <https://doi.org/10.1016/j.foreco.2011.03.029>
- 759 Rodríguez-García, E., Gratzer, G., Bravo, F., 2011b. Climatic variability and other site factor  
760 influences on natural regeneration of *Pinus pinaster* Ait. in Mediterranean forests. *Ann. For.  
761 Sci.* 68, 811–823. <https://doi.org/10.1007/s13595-011-0078-y>
- 762 Rodríguez-García, E., Juez, L., Bravo, F., 2010. Environmental influences on post-harvest natural  
763 regeneration of *Pinus pinaster* Ait. in Mediterranean forest stands submitted to the seed-tree  
764 selection method. *Eur. J. For. Res.* 129, 1119–1128. <https://doi.org/10.1007/s10342-010-0399-7>  
765 7
- 766 Ruano, I., del Peso, C., Bravo, F., 2015a. Post-dispersal predation of *Pinus pinaster* Aiton seeds:  
767 key factors and effects on belowground seed bank. *Eur. J. For. Res.* 134, 309–318.  
768 <https://doi.org/10.1007/s10342-014-0853-z>
- 769 Ruano, I., Manso, R., Fortin, M., Bravo, F., 2015b. Extreme climate conditions limit seed availability  
770 to successfully attain natural regeneration of *Pinus pinaster* in sandy areas of central Spain.  
771 *Can. J. For. Res.* 45, 1795–1802. <https://doi.org/10.1139/cjfr-2015-0257>
- 772 Ruano, I., Pando, V., Bravo, F., 2009. How do light and water influence *Pinus pinaster* Ait.  
773 germination and early seedling development? *For. Ecol. Manage.* 258, 2647–2653.  
774 <https://doi.org/10.1016/j.foreco.2009.09.027>
- 775 Sardin, T., 2009. Guide des sylvicultures Forêts littorales atlantiques dunaires. Office National des  
776 Forêts, Paris.
- 777 Schupp, E.W., 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am.  
778 J. Bot.* 82, 399–409. <https://doi.org/10.1002/j.1537-2197.1995.tb12645.x>
- 779 Tremblay, J.P., Huot, J., Potvin, F., 2007. Density-related effects of deer browsing on the  
780 regeneration dynamics of boreal forests. *J. Appl. Ecol.* 44, 552–562.  
781 <https://doi.org/10.1111/j.1365-2664.2007.01290.x>
- 782 Vergarechea, M., del Río, M., Gordo, J., Martín, R., Cubero, D., Calama, R., 2019. Spatio-temporal  
783 variation of natural regeneration in *Pinus pinea* and *Pinus pinaster* Mediterranean forests in  
784 Spain. *Eur. J. For. Res.* <https://doi.org/10.1007/s10342-019-01172-8>
- 785 Viglas, J.N., Brown, C.D., Johnstone, J.F., 2013. Age and size effects on seed productivity of  
786 northern black spruce. *Can. J. For. Res.* 43, 534–543. <https://doi.org/10.1139/cjfr-2013-0022>
- 787 Wagner, S., Fischer, H., Huth, F., 2011. Canopy effects on vegetation caused by harvesting and  
788 regeneration treatments. *Eur. J. For. Res.* 130, 17–40. <https://doi.org/10.1007/s10342-010-0378-z>  
789 0378-z
- 790 Wahid, N., Bounoua, L., 2013. The relationship between seed weight, germination and biochemical  
791 reserves of maritime pine (*Pinus pinaster* Ait.) in Morocco. *New For.* 44, 385–397.  
792 <https://doi.org/10.1007/s11056-012-9348-2>

793 Will, R.E., Wilson, S.M., Zou, C.B., Hennessey, T.C., 2013. Increased vapor pressure deficit due to  
794 higher temperature leads to greater transpiration and faster mortality during drought for tree  
795 seedlings common to the forest-grassland ecotone. *New Phytol.* 200, 366–374.  
796 <https://doi.org/10.1111/nph.12321>

797