



# Direct seeding for restoration of mixed oak forests: Influence of distance to forest edge, predator-derived repellent and acorn size on seed removal by granivorous rodents



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## ABSTRACT

Restoration of mixed oak forest in northern temperate regions is important for biodiversity and for adaptation of forest management to climate change. Direct seeding has been considered as a cost-effective method for the assisted regeneration of oaks. However, removal of acorns by granivorous rodents hinders its application. Patterns of acorn removal can vary with habitat type, presence of predators, and acorn size. In this field study, we tested the effects of distance to forest edge, predator excrement as a repellent, and acorn size on the performance of direct-seeded oak in southern Sweden. The experiment was carried out at two different sites. Our hypotheses were: (i) in clear-cuts, acorn removal is higher closer to the forest edge compared to open areas, (ii) treatment with predator excrement reduces acorn removal without affecting germination, and (iii) larger acorns will be removed more readily than smaller acorns. Finally, we also investigated if seedlings from larger acorns survive better and grow taller compared to smaller acorns in relation to habitat structure and predator excrement as repellent. Acorn removal differed at the two sites. At Skrylle (older clear-cut), no forest edge effects were found. At Klåveröd (new clear-cut site), our results suggest that removal of acorns was higher in the open clear-cut due to the presence of large slash piles. Less vegetation coverage correlated with lower rates of acorn removal, except near slash piles. Our results therefore suggest that forest managers should reduce understory vegetation and avoid slash piles during direct seeding of oak. Mink excrement failed to protect acorns against removal, but did not reduce acorn germination. Bigger acorns produced taller seedlings but did not enhance overall woodland establishment due to their higher removal rate. Our results further suggest a potential food satiation effect due to an extra supply of additional food. Satiation manipulation might potentially be a method of mitigating the impact of seed predation by granivorous rodents during the direct seeding of oak, but such an approach requires further research before it could be recommended.

## 1. Introduction

Previous land-use policies have transformed forest landscapes in many parts of Europe into conifer monocultures, mainly of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) (Zerbe, 2002). These forests have proven vulnerable to biotic and biotic disturbances which are worsened by climate change and threaten the provisioning of forest ecosystem services (Hanewinkel et al., 2013). A great challenge for European forestry is therefore to establish more resistant and resilient forests that have a more diverse species

composition and age structure (Bolte et al., 2009). Deciduous oaks (*Quercus* spp.) are relatively resistant to drought and wind damage (Epron and Dreyer, 1993; Götmark and Kiffer, 2014). An increasing proportion of oaks, as pure stands or in mixed forests, could help meet these challenges (Löf et al., 2010; Mette et al., 2013).

Direct seeding is a restoration technique with several potential benefits under future climatic conditions (Löf et al., 2019). Seedlings regenerated after direct seeding, develop a better tap-root architecture and are therefore more suitable to overcome stress conditions such as drought (Zadworny et al., 2014). In addition, stands established

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through direct seeding will often be mixed with other tree species and result in more complex stand structures due to increased natural regeneration of other woody species (Twedt and Wilson, 2002) that contribute to increased resilience and resistance (Pretzsch, 2020). It also has advantages over planting seedlings such as lower regeneration costs and more propagules can be transported by workers to sowing sites (Willoughby et al., 2004; Madsen and Löf, 2005; Löf et al., 2019). However, a major problem for direct-seeded acorns is predation by rodents (Nilsson et al., 1996; Dey et al., 2008; Löf et al., 2019). Acorns are strongly preferred by scatter-hoarding rodents due to their high energy and nutrient content (Jinks et al., 2012). Earlier studies have reported 80–100% removal of acorns from restoration sites within the first four months after sowing (Birkedal et al., 2009; Puerta-Piñero et al., 2010; Prévosto et al., 2011; Jinks et al., 2012; Van Ginkel et al., 2013; Martelletti et al., 2018). However, previous research has often used small experimental plots and has rarely been done in situations with simultaneous practical direct seeding over large areas.

Patterns of acorn removal by rodents can vary in time and space depending on multiple factors (Jensen and Nielsen, 1986; Pérez-Ramos et al., 2008). During spring and summer the year after a big acorn crop, small rodent populations grow which usually results in higher acorn predation (Ostfeld et al., 1996; Wolff, 1996; Schnurr et al., 2002). It has been therefore suggested that late spring is a proper timing of direct seeding which avoids the peak of rodent populations (Madsen and Löf, 2005; Löf and Birkedal, 2009; Birkedal et al., 2010). Many seed-eating mammals also change their foraging behaviors to reduce their own predation risk, which is driven by habitat structure (Lima and Bednekoff, 1999; Laundré et al., 2010). For example, several studies have reported higher acorn removal rates by rodents in areas with dense vegetation cover (Frost and Rydin, 2000; Pons and Pausas, 2007; Pérez-Ramos and Maranon, 2008; Perea et al., 2011). In this context, forest edges become an important factor in seed predation by small rodents (Ostfeld et al., 1997; Kollmann and Buschor, 2003; Meiners and LoGiudice, 2003). Clear-cuts larger than 1 ha without vegetation and other potential rodent habitats have been suggested to minimize acorn predation following seeding operations (Johnson, 1981). Understanding how these factors influence seed predation is important for restoration managers, but little published information is available.

Because nocturnal rodents depend on olfaction to detect potential predators, some studies have explored using predator odors as a repellent to hinder acorn consumption (Sunyer et al., 2013; Villalobos et al., 2019). For example, mink (*Neovison vison* Schreber) excrement was found to reduce acorn consumption by bank voles (*Myodes glareolus* Schreber) in a laboratory setting, suggesting its potential utility as a repellent (Villalobos et al., 2019). But its effectiveness under field conditions has not been verified.

Tree species with larger seeds tend to germinate and establish more successfully (Ceccon et al., 2016; Grossnickle and Ivetić, 2017), suggesting that direct seedling could be more successful when using bigger acorns. However, because bigger acorns have a higher nutrient content than smaller acorns, they may be preferred by seed predators (Muñoz and Bonal, 2008; Pérez-Ramos et al., 2008; Zhang et al., 2008). Thus, less palatability of small acorns and their relative lower cost may therefore suggest a way to overcome predation pressure during direct seeding. On the other hand, larger acorns could also present disadvantages for rodents by requiring more time and energy to excavate and transport (Lichti et al., 2017). Rodents preferentially remove acorns lighter than 60% of their body mass (Muñoz and Bonal, 2008). Furthermore, acorn size preference seems to vary depending on the habitat structure. For example, Perea et al. (2011) showed that wood mice selected bigger acorns when foraging under shrub cover. In contrast, Pérez-Ramos et al. (2008) found that larger acorns are selectively removed by wood mice in open habitats. The balance of these factors in determining acorn predation in restoration contexts is little studied.

The goal of this study was to investigate a range of factors influencing seed removal by rodents, and hence the ultimate success of

direct seeding of oak. In a field experiment, we tested how removal rates of buried acorns and seedling size were related to distance to forest edge, mink excrement treatment, and acorn size. The experiment was replicated at two different clear-cut sites to account for site-specific factors, e.g. potential differences in granivorous rodent populations, and excluded acorn removal by large herbivores and birds via fencing and acorn burial respectively. Our hypotheses were: (i) removal of acorns is higher near forest edges in comparison to open areas of a clear-cut, (ii) mink excrement reduces acorn removal without affecting germination, and (iii) larger acorns will be removed in higher quantities than smaller acorns and removal rates will be related to habitat structure. Finally, we also investigated if unpredated larger acorns can improve seedling establishment rates compared to small acorns in relation to the other factors tested (habitat and mink excrement).

## 2. Material and methods

### 2.1. Site description

This study was conducted at two clear-cut sites between May and September 2019 in Scania, the southernmost part of Sweden. The clear-cut at Skrylle covered 3.6 ha (13°22'45"E, 55°40'43"N, 116 m a.s.l.) and was dominated by Norway spruce before felling in December 2017. The clear-cut at Klåveröd was 5.4 ha (13°10'32"E, 56°1'39"N, 196 m a.s.l.) where the previous stand was also dominated by Norway spruce and felled in June 2018. According to Hägglund and Lundmark (1977) the soil texture classification at both sites was sandy till. Ground vegetation was typically dominated by grass. At both sites, mechanical site preparation (patch scarification) was performed in spring 2019 before the start of the experiments. The scarified patches were ca 80 cm wide and 3 m long, and occurred in tracks at ca. 2 m spacing all over the clear-cuts. In all non-experimental areas of the clear-cuts, practical direct seeding (by the Scania Landscape Foundation) of pedunculate oak (*Quercus robur* L.) was performed manually at the same time as we laid out our experiments on April 30th and May 1st for Klåveröd and Skrylle, respectively. In the practical direct seeding that occurred in the surroundings of our experimental plots, acorns were placed ca. 1 m apart and at a soil depth of ca. 5 cm within the scarified patches, and ca 4500–5000 acorns were sown per hectare.

The surrounding forest at Skrylle was dominated by middle-aged monocultures of Norway spruce. However, at the eastern border of the clear-cut there was a 7 year old pedunculate oak plantation, and a ca. 60 cm high old stone wall occupied the southern part of the clear-cut. By the time of sowing (end of April 2019) naturally-regenerated Norway spruce and aspen (*Populus tremula* L.), and some wavy hair-grass (*Deschampsia flexuosa* L.) was observed covering circa 10% of the ground. At the end of August 2019, the patchily-distributed herbaceous vegetation at the clear-cut was mainly dominated by raspberry (*Rubus idaeus* L.) and wavy hair-grass, along with rushes (*Juncus* spp), and some naturally-regenerated Norway spruce and aspen. This vegetation covered ca. 50% of the ground (see Section 2.4).

In Klåveröd, the clear-cut was surrounded by middle-aged mixed forests dominated by pedunculate oak, European beech (*Fagus sylvatica* L.) and birch (*Betula pendula* Roth.). By the time of sowing (end of April 2019) no vegetation was present at the clear-cut. At the end of August 2019, the patchy herbaceous vegetation was dominated by raspberry and wavy hair-grass as well as rosebay willowherb (*Chamaenerion angustifolium* (L.) Scop.), and naturally-regenerated rowan (*Sorbus aucuparia* L.), aspen, and elderberry (*Sambucus nigra* L.). This vegetation covered about 18% of the ground at Klåveröd.

Both clear-cut sites were free from logs and fallen trees, but some harvesting residues were present, and in the middle of the clear-cut at Klåveröd large piles of slash had not yet been removed. To exclude large herbivores, both sites were enclosed with a 2 m high steel-wire fence in May 2019.

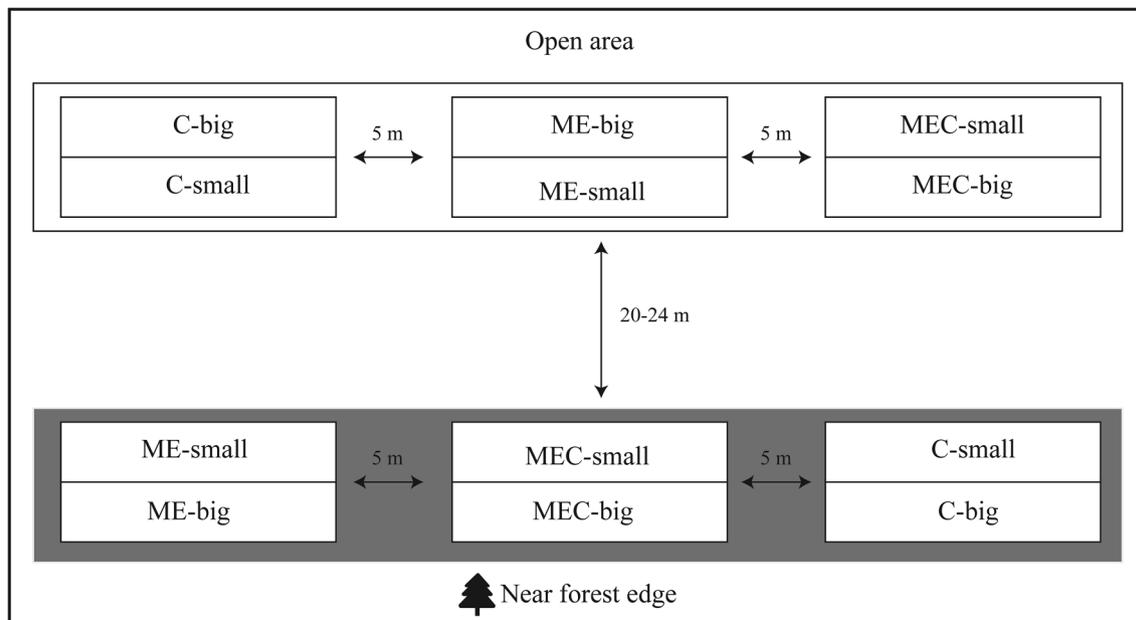


Fig. 1. Example of experimental design for one block with split-split plots. Main plot treatments were the open area of the clear cut and the area near the forest edge (gray rectangle). Subplots consisted of the sub treatments ME (mink excrement), MEC (Mink excrement coating) and C (control). Each split-split plot contained one row of 10 *small* acorns and another row with 10 *big* acorns.

## 2.2. Experimental design

The experimental design was randomized blocks with split-split plots (Fig. 1) and four blocks at each of the two sites. The distance between blocks was 50 m. The two main treatments (*habitat*) were placed in the clear-cuts with direct seeding near the forest edge (*near*) and in the open clear-cut (*open*). The distance from the *near* treatment to the forest edge was 5 m, and the distance from *open* treatment to forest edge was 30 m. At Klåveröd, slash piles were present at circa. 30 m from the open clear-cut treatments. Blocks were about 27 m × 16 m. The sub-treatments (*repellent*) were two types of repellent and a control: mink excrement (obtained from a mink farm in southern Sweden) directly applied on top of the acorn (ME), seed coating with mink excrement (MEC), and untreated acorns as a control (C). Each sub-plot was about 1 × 2 m, and the distance between sub-plots was ca. 5 m. In each sub-treatment, two rows (split-split plots) were created for direct seeding of acorns of two different sizes (Size: *big* and *small*; see Section 2.3). The distance between these split-split plots was ca. 1 m.

In each of these split-split plots, direct seeding was performed manually between the 29th and 30th of April 2019 by digging small holes and placing ten acorns 20 cm apart and 5 cm below the mineral soil surface. Disposable nitrile gloves (VMR, Leuven, Belgium) were used all times to avoid cross-treatment smell contamination or residual human scent. A total of 960 acorns were sowed in twelve treatment combinations, factorized as 2 habitats × 3 repellent treatments × 2 size classes (40 seeds per treatment at each site). All treatments were placed in the scarified patches, but separated at circa. 5–10 m from the practical restoration seeding in the non-experimental areas.

## 2.3. Seed material and preparation

Acorns of pedunculated oak were collected by the Scania Landscape Foundation (Stiftelsen Skånska Landskap) during autumn 2018 from different broadleaved forests in the region (Southern Sweden). After collection, all acorns were stored over winter submerged in a creek in jute sacks until seeding (Johnson et al., 2019). Before seeding, a float test (Gribko and Jones, 1995) was performed and all floating acorns were discarded. Then, remaining acorns were weighed and separated into two size classes according to Shi et al. (2019): small acorns

(< 4.8 g fresh weight; mean: 3.8 g; SD: 0.8) and big acorns (≥ 4.8 g fresh weight; mean: 6.4 g; SD: 1.4). The viability of the two acorn classes was determined by a cut-test (Bonner, 2008) on 100 randomly selected acorns per class (viability: small acorns 73%- and big acorns 62%).

To detect acorn presence or absence after sowing by metal detection, a small hole was drilled (0.8 mm ø) at the basal end opposite the embryo side of each acorn, and a flat metal washer (15 mm ø) was attached by using 5 cm of wire thread (0.6 mm ø). This added 0.1 g of additional weight to each acorn. This technique has been tested previously with no effects on seed removal by small mammals (Kempter et al., 2018). For the ME (mink excrement) treatment, 5 g (fresh weight) of pure mink excrement was placed on top of each acorn. For the MEC (mink excrement coating) treatment, acorns were soaked for 12 h prior to sowing in a solution of 400 g (fresh weight) mink excrement mixed with 3 l distilled water.

## 2.4. Measurements

All buried acorns were monitored after 15, 30, 60, 90, and 120 days following sowing using a pin-pointer metal detector (Miltenberger Snooper PXC2.2, Dinslaken, Germany) to determine acorn removal. We also recorded emergence of seedlings during each monitoring visit. In all emerged seedlings, the metal washer was still attached to the cotyledon, thus we excluded any confounding effects from natural regeneration. At the end of the experiment (September 16th), 120 days after sowing, seedling height was measured, and the percentage of ground vegetation was estimated visually in 10% classes (0–10%, 11–20% etc.) for each main plot at both sites.

## 2.5. Statistical analysis

All statistical analyses were performed using R version 3.5.0 (R Core Team, 2018). The factor effects of removal of acorns were analyzed using a mixed effects Cox survival models with the R package “coxme” (Therneau, 2019). The response (survival) variable represents acorn removal status (1 = removed, 0 = non-removed) over time. Since not all acorns were removed by the end of the experiment, remaining acorns were right-censored. We included the following factors and their interactions as fixed effects: *habitat* (two levels) × *repellent* (three

levels) × size (two levels). We accounted for the hierarchical experimental design by including nested block/habitat/repellent/size as random effects in the model. In a first model including site as a fixed factor we found a strong effect of site ( $X^2 = 78.34$ ,  $df = 1$ ,  $p < 0.01$ ), and therefore sites were analyzed separately. In order to assess the validity of our model we performed a cox survival model with all the fixed effects but without the random factors (Velho et al., 2012) with the R package “survival” (Therneau and Lumley, 2014). We further evaluated the proportional hazard assumption using Schoenfeld residuals, and the influence of outliers (deviance residuals). For the factor effects on seedling emergence, false negatives were expected due to acorns been removed, presence of potential nonviable acorns and/or germination delay. We therefore performed a test for zero inflation using the function “testZeroInflation” from the DHARMA package (Hartig, 2019) and analyzed the data with a zero-inflated GLMM with binomial error distribution (package: “glmmTMB”, Brooks et al. (2017)) for Skrylle and a beta-binomial (for overdispersed data) error distribution for Klåveröd. The binary response variable was success or failure to germinate. Fixed and random factors were arranged as described for the acorn removal mixed survival model. To examine the model for overdispersion and residual distribution we used the functions “testDispersion” and “testUniformity” from the DHARMA package. An analysis of deviance (Wald  $X^2$  Type II) was tested *ad post* to evaluate the factor effects and their interactions. To assess the impacts of the habitat, repellent and size on seedling height, we used a generalized linear model (GLM) with a gamma error distribution and log link. In order to take into account the unequal number of seedlings per treatment combination, interactions of the factors were tested by a post analysis of deviance for unbalanced design (likelihood ratio  $X^2$  Type III). Post-hoc tests for multiple comparisons between factors were implemented using estimated marginal means with the “emmeans” package (Lenth, 2018). Correlation analysis between the percentage of acorns removed and the percent vegetation cover was performed with Kendall’s tau-b rank correlation test suited for discrete data with ties (McLeod, 2005). For analytical statistics the alpha level was set at  $\alpha = 0.05$  for all tests.

### 3. Results

#### 3.1. Acorn removal

In Skrylle, there were no effects of habitat or repellent alone as indicated by the hazard ratio (value close to 1.00) on the probability of acorns removed, but the significance of the factor size with a hazard ratio of 1.68 indicates a relationship between acorn size and an increased risk of acorn removal. A slight significant interaction between acorn size and the repellent treatment was observed suggesting an increased risk of acorn removal by the size in relation to the repellent treatment (Table 1). For small acorns only, the probability of acorn removal increased by ca. 60% when treated with repellent as compared to the control (25% of removal probability), but this effect was only significant near the forest edge (Fig. 2, Table A.1, Table A.2). In all other treatment combinations, the acorn removal probability was ca. 50–60%. For all treatments, most of the removal occurred between May (15 days after sowing) and July (60 days after seeding), with little removal thereafter (data not shown). In addition, in several cases, there was a trend toward faster removal of acorns in the ME and MEC-treatments, as compared to the C treatment.

In Klåveröd, only the effects of habitat were significant, indicating a strong relationship between habitat and the probability of acorn removal, with less acorn removal near the forest edge (ca. 10%–20% of removal probability) compared to the open areas (ca. 20–75%). There was almost a significant effect of the interaction between habitat and repellent (Table 1) where acorns in the MEC-treatment had a higher probability of acorn removal when compared to the control treatment but only significant for small acorns at the open area (Fig. 2, Table A1). Fewer small acorns were removed compared to large ones (Table A2). Although only a trend was observed indicated by the hazard ratio on the interaction between repellent and size. For all treatments, we found most acorns removed between May (15 days after sowing) and July (60 days after seeding) (data not shown).

For both habitats (*near* and *open*) at Skrylle (the older of the two clear-cuts), total acorn removal positively correlated with increased

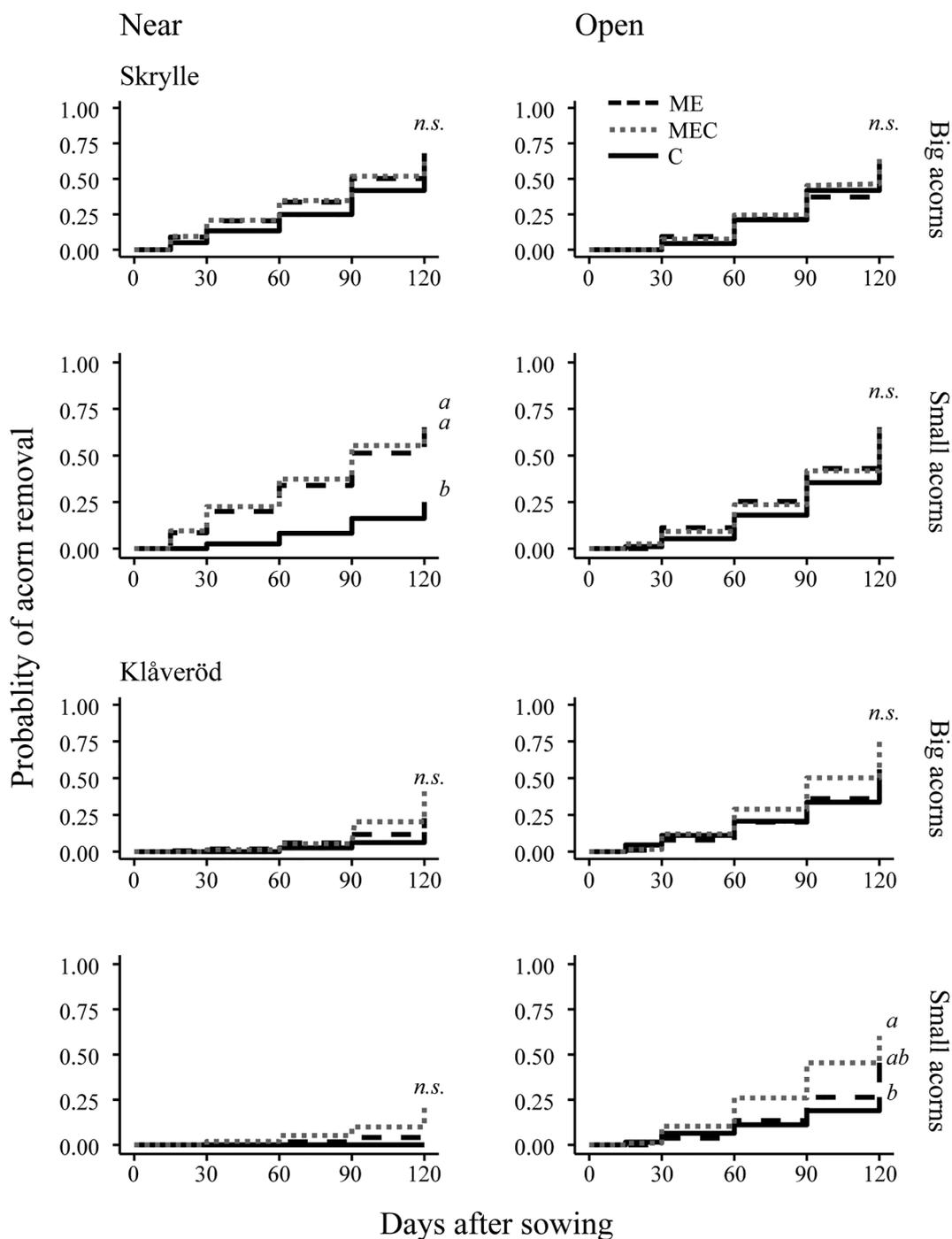
**Table 1**

Analysis of the probability of acorn removal over time at two sites in southern Sweden following direct seeding. Main factor and their interaction coefficients and hazard ratios were derived from mix effects Cox proportional hazard model. For description of treatments see Section 2.3.

Site, fixed factors and interactions	Coefficient	Hazard ratio <sup>a</sup>	SE	Z	p (>  z )
<b>Skrylle</b>					
Habitat	0.14	1.15	0.57	0.25	0.80
Repellent (ME) <sup>b</sup>	−0.04	0.96	0.69	−0.06	0.95
Repellent (MEC) <sup>b</sup>	0.28	1.33	0.69	0.41	0.68
Size	0.52	1.68	0.19	2.78	< 0.01
Habitat × repellent (ME) <sup>b</sup>	1.02	2.77	0.66	1.55	0.12
Habitat × repellent (MEC) <sup>b</sup>	0.90	2.46	0.66	1.37	0.17
Habitat × size	−0.42	0.66	0.26	−1.61	0.11
Repellent (ME) <sup>b</sup> × size	−0.61	0.54	0.30	−2.04	0.04
Repellent (MEC) <sup>b</sup> × size	−0.59	0.56	0.29	−1.82	0.04
Habitat × repellent (ME) <sup>b</sup> × size	0.29	1.34	0.40	0.74	0.46
Habitat × repellent (MEC) <sup>b</sup> × size	0.57	1.76	0.40	1.41	0.16
<b>Klåveröd</b>					
Habitat	−0.38	0.67	0.17	−2.35	< 0.01
Repellent (ME) <sup>b</sup>	−0.06	0.93	0.15	−0.42	0.67
Repellent (MEC) <sup>b</sup>	−0.06	0.94	0.15	−0.46	0.16
Size	0.07	1.08	0.12	0.64	0.52
Habitat × repellent (ME) <sup>b</sup>	−0.29	0.75	0.22	−1.31	0.06
Habitat × repellent (MEC) <sup>b</sup>	0.33	0.83	0.22	1.15	0.08
Habitat × size	0.18	1.19	0.18	0.99	0.32
Repellent (ME) <sup>b</sup> × size	−0.55	0.94	0.17	−0.34	0.08
Repellent (MEC) <sup>b</sup> × size	0.05	0.95	0.16	0.11	0.74
Habitat × repellent (ME) <sup>b</sup> × size	−0.04	0.95	0.26	−0.18	0.86
Habitat × repellent (MEC) <sup>b</sup> × size	−0.05	0.96	0.25	−0.21	0.84

<sup>a</sup> Ratio expressed as exponential coefficient (exp(coef), gives effect sizes of covariates.

<sup>b</sup> Control treatment used as a reference level.



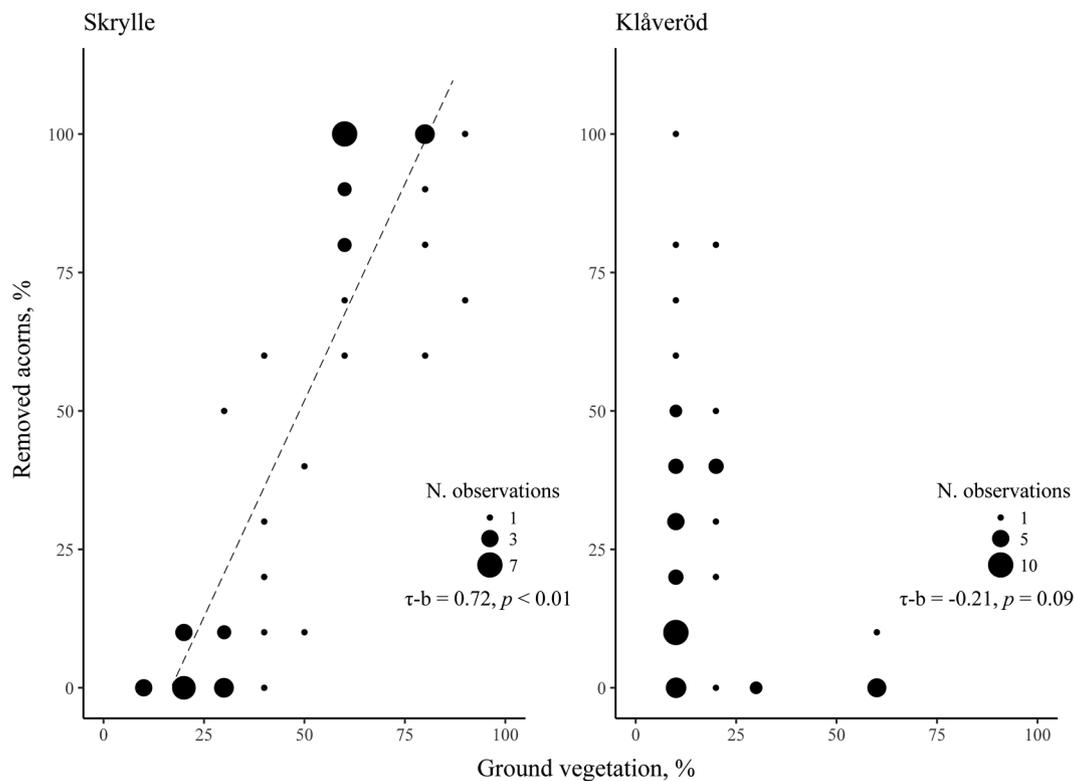
**Fig. 2.** Probability of removal of big and small acorns in two habitats (*near* forest edge and *open* clear-cut) at Skrylle (top) and Klåveröd (bottom) under three repellent treatments (ME = Mink excrement, MEC = Mink excrement coating and C = Control). Different letters show significant differences ( $p < 0.05$ ) between the repellent treatments. For acorn size comparison, see [Table A2](#).

coverage of ground vegetation as measured at the end of the experiment (Fig. 3). There was no such correlation at the younger clear-cut in Klåveröd with less ground vegetation cover.

### 3.2. Seedling emergence

At Skrylle, there were no treatment effects alone on seedling emergence (Table 2) but a significant interaction of the factor *repellent* with *habitat* and *size* (Table 2). At the near forest edge, a higher emergence for the small acorns was observed for the C treatment compared to the MEC treatment (estimate = 2.18,  $t$ -ratio = 3.50,

SE = 0.63,  $p < 0.01$ ). Seedling emergence started in July (60 days after sowing) and increased until August (90 days after sowing; Fig. 4). Thereafter, the rate of seedling emergence leveled off. The removal of acorns was slightly higher in Skrylle compared to Klåveröd, and more seedlings emerged at the latter site. In addition, there were significant treatment effects for both habitat and the interaction between repellent and size at Klåveröd (Table 2). Thus, more seedlings emerged near the forest edge where acorn removal was less compared to the open area (Fig. 2, Fig. 4, and Table A.3). From the small acorns in the open area, fewer seedlings emerged in the MEC treatment compared to C treatments (estimate = 2.02,  $t$ -ratio = 3.15, SE = 0.64,  $p < 0.01$ ) (Fig. 4).



**Fig. 3.** Total removal of acorns in relation to the ground vegetation cover at the end of August at Klåveröd and Skrylle. Bigger size black dots represent more observations within the same value of acorns removed and ground vegetation. Shown are the regression lines and the values from Kendall’s rank correlation analysis.

**Table 2**

Direct and interacting predictors of seedling emergence at two sites in southern Sweden following direct seeding of pedunculated oak. Main factors interactions were derived *a posteriori* from a zero-inflated generalized linear mixed model with a binomial error distribution for Skrylle and a betabinomial error distribution for Klåveröd. An analysis of deviance for balanced design (Wald  $\chi^2$  Type II) was used for both sites. For description of treatments see text.

Site, fixed factors and interactions	$\chi^2$	Df	$p (>  \chi^2 )$
<b>Skrylle</b>			
Habitat	0.85	1	0.36
Repellent	2.14	2	0.34
Size	0.30	1	0.58
Habitat × repellent	9.90	2	< 0.01
Habitat × size	0.01	1	0.91
Repellent × size	6.96	2	0.03
Habitat × repellent × size	2.93	2	0.23
<b>Klåveröd</b>			
Habitat	13.80	1	< 0.01
Repellent	5.49	2	0.06
Size	1.34	1	0.25
Habitat × repellent	1.64	2	0.44
Habitat × size	3.30	1	0.07
Repellent × size	6.22	2	0.04
Habitat × repellent × size	2.17	2	0.34

As for Skrylle, the rate of seedling emergence increased until August and leveled off thereafter.

By the end of the experiment (120 days after sowing), seedlings were around 10 cm tall in all treatments (Fig. 5). There was a strong effect of acorn size on seedling height, with big acorns producing taller seedlings than small acorns (Fig. 5, Table A.4).

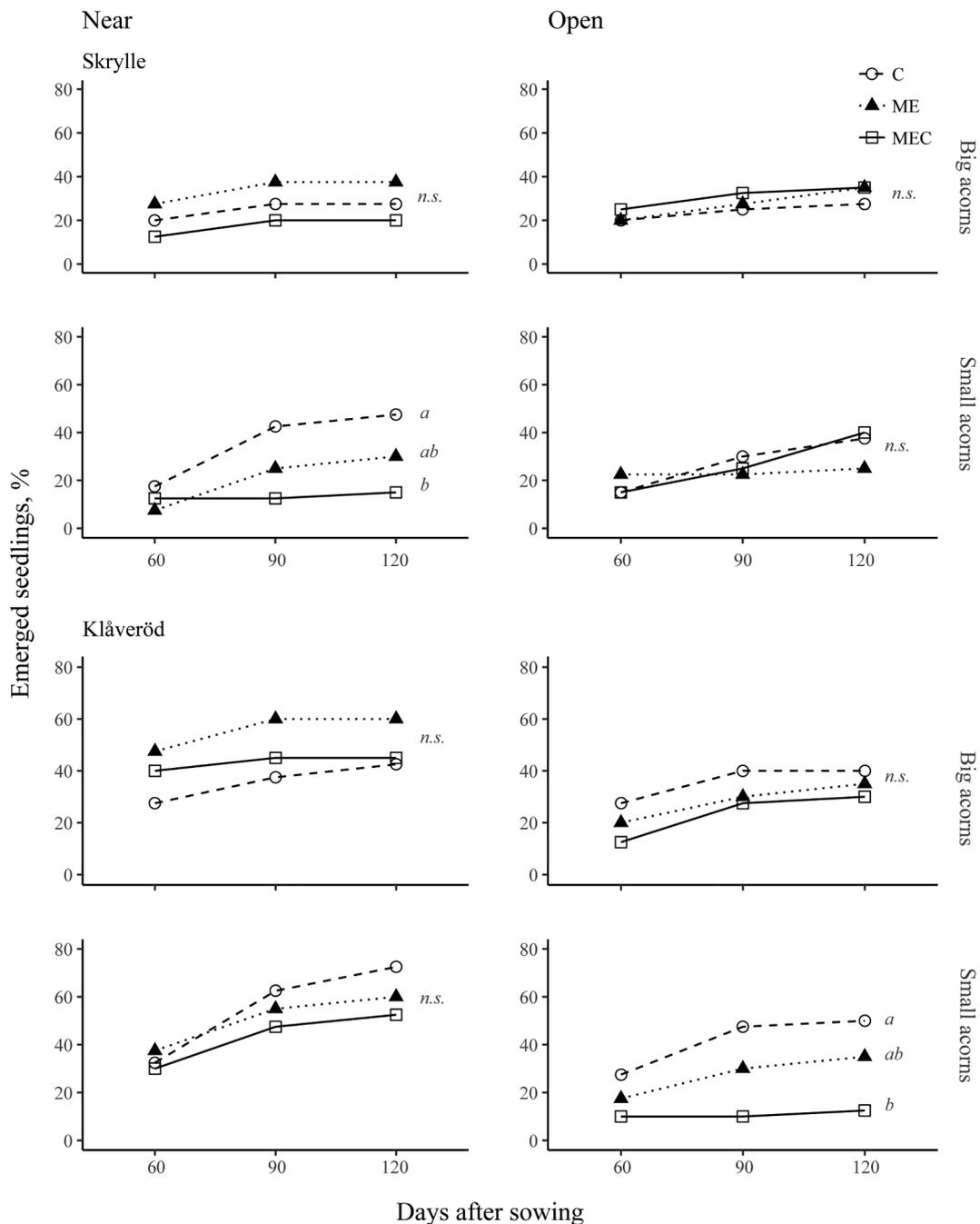
**4. Discussion**

At the end of the experiment, after 120 days, the probability of acorn removal was between 0% and 60% depending on treatment. This

is in contrast to several previous studies where a near total removal of acorns has been reported during direct seeding (Schnurr et al., 2002; den Ouden et al., 2005; Madsen and Löf, 2005; Birkedal et al., 2009; Van Ginkel et al., 2013; Martelletti et al., 2018). Our study was conducted the year after a heavy mast, suggesting that the population size of granivorous rodents was not at its minimum and high removal rate could thus be expected. The low percentage of removal in our study may be explained by the presence of more direct-seeded acorns outside our study plots. Thus, our results are most likely related to the predator-satiation hypothesis (Janzen, 1971), where it is expected that a higher availability of food resources leads to an increased probability of seeds to escape predation.

Although we did not attempt to capture rodents in order to estimate population size, we are confident that the majority of acorn removal was due to granivorous rodents. Removal by birds is likely to have been low because they rely mainly on visual cues to allocate food (Land, 1999), thus sowing at 5 cm depth may represent a certain degree of protection (Birkedal, 2009). Moreover, ungulates were excluded with fencing (Dey et al., 2008; Castro et al., 2015; Löf et al., 2019). Previous seed studies in the same region have also observed the three major acorn predators to be the bank vole, yellow-necked mouse (*Apodemus flavicollis* Melchoir) and wood mouse (*Apodemus sylvaticus* L.) (Hansson, 1971; Birkedal et al., 2009).

Contrary to our first hypothesis and to previous research (Kollman and Buchor, 2003), we did not find higher acorn removal near the forest edge. Instead, acorn removal was significantly higher in the open area at one of the sites (Klåveröd). This can probably be explained by the presence of large post-harvest slash piles relatively near (ca. 30 m) the open area plots. This is in accordance with the findings of Birkedal et al. (2010) who reported that rodent captures were more frequent closer to slash piles in a clear-cut. However, granivorous rodents can have home ranges of up to 300 m (Szacki, 1999) and therefore further studies including a bigger range of distances from habitats like slash piles would be needed to determine a “safe distance” from such areas.



**Fig. 4.** Percentage of emerged seedlings in two habitats from small and big acorns at Skrylle and Klåveröd under three repellent treatments (ME = Mink excrement, MEC = Mink excrement coating and C = Control). Different letters show significant differences ( $p < 0.05$ ) between the repellent treatments.

Open areas such as clear-cuts or former pastureland are considered as zones of high predation risk for prey mammals (Frost and Rydin, 2000; Brown and Kotler, 2004; Pons and Pausas, 2007). According to the “landscape of fear” concept, vegetated habitats have a low predation risk, so they will be used more intensively than higher-risk open habitats (Laundré et al., 2001, 2010). However, after cutting operations at both of our sites, habitats providing suitable shelter for rodents emerged, such as slash piles and ground vegetation that colonized the sites (Hansson, 1978; Takahashi et al., 2006; Dey et al., 2008). Thus, our results suggest a habitat preference by the rodents at both of our sites. Such habitat preferences are well known for scatter-hoarding rodents (Dickman, 1992; Jacob and Brown, 2000; van der Merwe and Brown, 2008; Martelletti et al., 2018).

At the end of the experiment, the percentage of ground vegetation

positively correlated with the percentage of acorn removal in Skrylle whereas this effect was not found for Klåveröd. This can probably be explained by a higher abundance of vegetation at the older clear-cut in Skrylle compared to the younger clear-cut in Klåveröd. This is also in line with the results of Birkedal et al. (2010) who found that longer time after scarification at clear-cuts correlates with an increase of vegetation cover and a subsequent larger rodent population.

Olfactory signals from mammalian predators could influence seed predation by rodents, but there are only a few field studies addressing this phenomenon (Sunyer et al., 2013; Gallego et al., 2017). In the present study, we did not observe the expected repellent effects. In some cases, the opposite was observed, i.e., removal on acorns was higher in the ME and MEC treatments. This is in contrast to our previous results from a laboratory experiment (Villalobos et al., 2019).

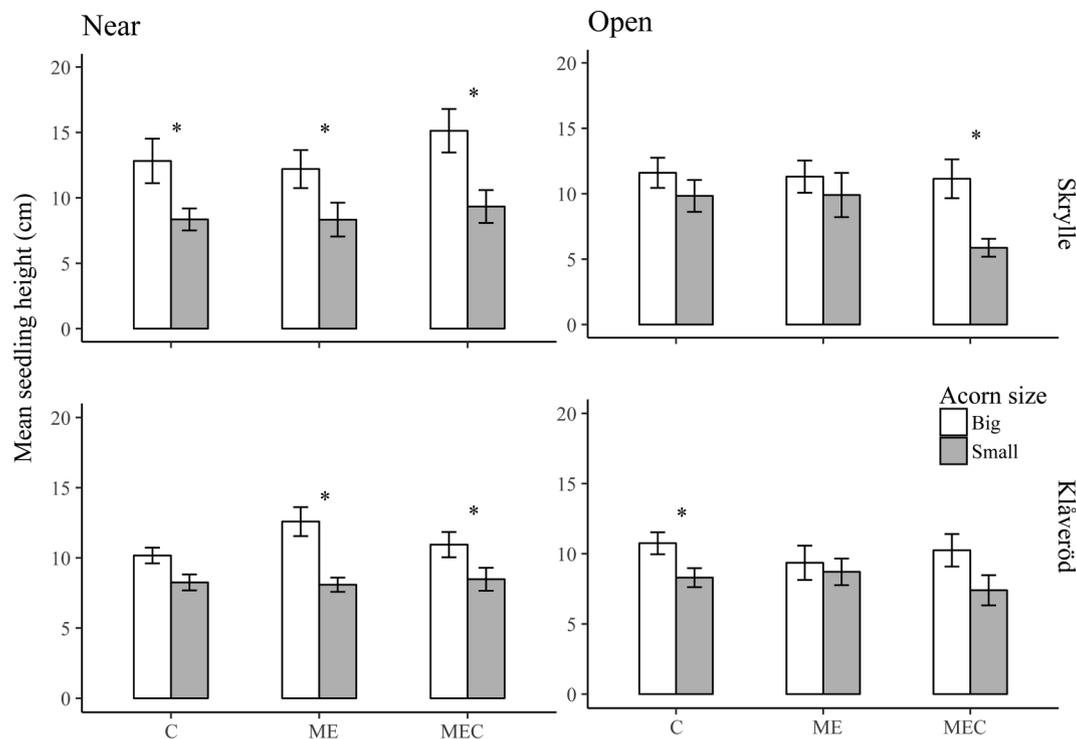


Fig. 5. Mean seedling height (cm) for each sub-treatment (ME: Mink excrement, MEC = Mink excrement coating and C: Control) in the two habitats (*open* clear cut and *near* forest edge) at Skrylle and Klåveröd. White bars and gray bars represent the acorn size (*big* and *small*). Asterisks indicate differences ( $p < 0.05$ ) between small and big acorns (error bars show  $\pm$  SE,  $n = 4$ ).

There may be several reasons for this contradiction. First, it is possible that mink excrement, despite having been buried in the soil, desiccated fast and the olfactory cues dissipated quickly (Bytheway et al., 2013). Second, a habituation to the predator's smell by rodents may have occurred. For example, if the olfactory signal was lost but previously identified by rodents, it could have had a counter-productive effect, so that rodents learned where the acorns were buried. There are strong possibilities of habituation effects after long exposure to a predator's odor cue (Apfelbach et al., 2005). Some previous field studies have found similar results when predator feces were located close to foraging seed stations (Sundell et al., 2004; Bakker et al., 2005; Navarro-Castilla and Barja, 2014).

At Klåveröd, large acorns had higher removal rates than small acorns. Similar results have been observed for acorns by Muñoz and Bonal (2008), Perez-Ramos and Maranon (2008) and Zhang et al. (2008). However, at Skrylle both small and large acorns were removed in equally high proportions. This result suggests no acorn discrimination or selection by rodents at this site. The reasons for non-selection by rodents are still not well understood (Xiao et al., 2004). It is possible that rodent population at Skrylle was higher, resulting in less acorn selection due to a higher pressure for rodents to rapidly perform a catch (Lichti et al., 2017). Furthermore, spending less time for selecting acorns by size may be explained by the lack of protective habitats, such as the large slash piles that were present at Klåveröd. This result is in line with the findings of Pons and Pausas (2007) where a lack of acorn selection by the wood mouse was observed in high predation risk areas.

In our study, acorn size had no effect on the number of emerged seedlings, but bigger acorns produced larger seedlings regardless of any repellent or different habitats. Similar results by Xiao et al. (2004), did not find higher seedling emergence with bigger acorn sizes of the jolcham oak (*Quercus serrata* Murray). However, for northern red oaks (*Quercus rubra* L.), there is evidence that bigger acorns increase germination rates and overall seedling performance during direct seeding (Kormanik et al., 1998; St-Denis et al., 2013).

With the exception of the MEC treatment for small acorns in the

open area in Klåveröd, repellent treatments had no negative impact on seedling emergence or the early performance of seedlings. This result is also in accordance with a previous study by Villalobos et al. (2019) where germination of mink excrement-coated acorns did not show a significant reduction in germination when compared to control acorns.

## 5. Conclusion

Our work suggests that in clear-cuts, acorn removal increases due to the presence of protective habitats for rodents such as ground vegetation or large slash piles regardless of whether the direct seeding is carried out close to forest edges or in open areas. Consequently, for improved direct seeding of oak we recommend avoiding long-term storage of slash piles within clear-cuts and measures for ground vegetation control such as small scale prescribed burning or mechanical site preparations. In this study however, we do not have statistical evidence to support this recommendation. We further demonstrated that mink excrement, in the way we applied it, cannot be recommended as a method to improve direct seeding of oak. Finally, we also found that whilst selecting big acorns may improve the early growth of seedlings, this will only be the case if the acorns themselves survive predation. However, a conflicting trade-off between small and big acorns emerged as big acorns are preferred by rodents. It is therefore not possible to suggest practical implications related to acorn size classes from our study. Our overall results suggest a food satiation effect when an additional food supply is available in a clear-cut. Therefore, the predator-satiation hypothesis should be further tested by providing supplemental sources of alternative food such as cheaper seeds (e.g. oats or sunflower seeds) on success rates of direct seeding.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Authors' contribution

Adrian Villalobos, Fredrik Schlyter, Gert Olsson and Magnus Löf planned and designed the study. Adrian Villalobos performed the experiment and analyzed the data. Adrian Villalobos, Fredrik Schlyter, Johanna Witzell and Magnus Löf led the writing of the manuscript. All authors contributed to the final manuscript and gave approval for submission.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118484>.

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