Received: 4 July 2022 | Accepted: 11 January 2023
DOI: 10.1111/afe.12563

ORIGINAL ARTICLE

Agricultural and Forest Entomology
Royal Entomological Society

Ten years after: Release cutting around old oaks still affects oak vitality and saproxylic beetles in a Norway spruce stand

Delphine Lariviere[1,2] | **Emma Holmström**[1] | **Lisa Petersson**[1] | **Line Djupström**[3,4] | **Jan Weslien**[3]

[1]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Alnarp, Sweden
[2]The Forestry Research Institute of Sweden (Skogforsk), Svalöv, Sweden
[3]The Forestry Research Institute of Sweden (Skogforsk), Uppsala, Sweden
[4]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

Correspondence
Delphine Lariviere, Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Sundsvägen 3, 23053 Alnarp, Sweden.
Email: delphine.lariviere@skogforsk.se, delphine.lariviere@slu.se

Funding information
FRAS - Future Silviculture in Southern Sweden research programme; Stiftelsen Extensus; Tranemålastiftelsen

Abstract

1. It is often suggested to release oaks (*Quercus robur*) from competition, to ensure their survival and boost their conservational value. However, few studies have explored how long-lasting this effect is and how it affects saproxylic beetles.
2. Ten years after cutting, we investigated effects of different release cutting levels (high, medium, and no release) around 140-year-old retained oaks in a commercial forest with Norway spruce (*Picea abies*).
3. We evaluated oak vitality using crown and dead wood measurements. Saproxylic beetles were caught in window traps, identified to species level, and grouped according to their association with oak and/or Norway spruce.
4. Released oaks had more light, higher temperatures, greater crown growth, and less dead wood in the crown compared to the no-release control.
5. After 10 years we still found a higher abundance of oak-associated beetles and higher overall species richness of saproxylic beetles in the released oaks. Beetle species composition significantly differed between released oaks and control.
6. We suggest avoiding planting trees beneath retained oaks when regenerating conifer forests and to proceed with conservation management during subsequent thinning by removing regeneration under the oak crowns. We emphasize the benefits of monitoring the retained oaks to maintain tree vitality, habitat quality, and insolation.

KEYWORDS
biodiversity, *Picea abies*, *Quercus robur*, release cutting, saproxylic beetles, tree retention

INTRODUCTION

Many species of beetles specialize in specific microhabitats that can mainly be found on ancient trees. Old, hollow oaks trees (*Quercus robur*) in forests can serve as a habitat for a particularly rich fauna, including many rare and red-listed beetles, and host a high proportion of threatened species (SLU Artdatabanken, 2020; Sundberg et al., 2019). These forest oaks can live for hundreds of years and provide crucial resources and dead wood of different decay stages and diameters (Lassauce et al., 2011; Parmain & Bouget, 2018; Sverdrup-Thygeson et al., 2010). Many species are tightly associated with forest oaks, and free-standing oaks seem to be particularly important because they harbour special communities of beetles (Sverdrup-Thygeson et al., 2010; Widerberg et al., 2012).

In the hemi-boreal zone of northern Europe, there has been a decline in wooded pastures, which started during the 20th century with urbanization and the intensification of agriculture (Dahlstrom et al., 2008; Eliasson & Nilsson, 2002; Eriksson et al., 2002; Scb, 2019). Especially during the last century, intensive forestry, in combination with a change in farmland management, has changed the structure and composition of the landscape. This has led to the homogenisation of the forest towards even-aged monocultures of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies* (L.) H. Karst.) (Dahlstrom et al., 2008; Lindbladh et al., 2014). Old broadleaved deciduous trees became scarce along with their array of specific microhabitats (deadwood, cavities, bark structure) that benefit many specialist species (SLU Artdatabanken, 2020; Siitonen & Ranius, 2015; Stokland et al., 2012). Numerous saproxylic or epixylic invertebrates, fungi and lichens have declined, and many are currently threatened (Clavel et al., 2011).

To mitigate the effects of the decline of broadleaved trees in Sweden, the strategy during the last decades has been to promote green tree retention in final harvest, meaning retaining individual or clustered broadleaf trees belonging to the previous tree generation (Fedrowitz et al., 2014; Gustafsson et al., 2012; Gustafsson et al., 2020). These retention trees are then surrounded by more recently planted trees (Drobyshev et al., 2019; Koch Widerberg, 2013). One purpose of the retention trees is that they may act as “lifeboats” and provide valuable refuge habitats for plants and animals, and promote the conservation of rare and red listed species (Jonsell et al., 1998; Mitchell et al., 2019; Parmain & Bouget, 2018). Green tree retention can also be practiced when old pastures are converted to Norway spruce plantations, and old trees are retained for the first rotation of the stand. This has been common practice in low-production former agricultural areas in Sweden, where many pastures and former croplands have been converted into production forest stands by planting Norway spruce (Kardell & Henckel, 1994; Koch Widerberg, 2013). Current legislation in Sweden does not forbid planting under the crown of retention trees, even though Norway spruce can rapidly shade and compete with the retained trees. Light can become a limiting factor and have repercussions on other ecological processes, and ultimately local biodiversity. Norway spruce plantations in southern Sweden usually have a 50–80-year rotation, whereas the age of retained oaks may be several hundred years. Therefore, adequate long-term management is crucial to preserve the oaks and the species associated with it.

The release of retention trees—by removing the crop trees around the retained tree—is suggested as a solution for preserving some of the open forest environment that is often associated with high conservation values. Releasing, or “gap cutting” also promotes tree vitality and survival through multiple rotations, especially for tree species that are shade-intolerant such as oaks (Andersson et al., 2011; Götmark, 2009; Shifley, 2004; Widerberg et al., 2012). If early-stage plantations are dense and shaded, a release cutting in the first commercial thinning may be recommended. Such an opening reduces surrounding competition (Lariviere et al., 2020; Lindén, 2003) and increases insolation on the retained tree (Widerberg et al., 2012). It also changes the environment surrounding the tree, resulting in altered light intensity to the forest floor, and changes in soil humidity and soil biological properties (Muscolo et al., 2014). In turn, this may also favour other organisms associated with more open forest conditions, such as understorey vegetation (Gálhidy et al., 2006; Kelemen et al., 2012; Lariviere et al., 2020; Majasalmi & Rautiainen, 2020) or light-dependent beetles (Horak et al., 2014). The surrounding environment, including dead wood availability and temperature, are also important factors for beetle communities (Bouget et al., 2013; Müller et al., 2015). In some circumstances, an increase in temperature may compensate for poor habitat conditions in production forests, especially because shade-intolerant trees like oaks usually also support species adapted to open, light, and warm conditions (Horak et al., 2014; Jonsell et al., 1998).

One common denominator for beetle diversity and oak vitality is the amount of light entering the gap, which directly increases after release and causes an immediate response by saproxylic beetles (Widerberg et al., 2012). However light may gradually decrease with time as the released trees grow and fill the gap (Lariviere et al., 2020). There are no studies that explore the longer-term effect of gap creation on beetle diversity in planted conifer forest. In this study, the objective was to examine 10-year-effects of releasing old oaks on the richness, abundance, and composition of saproxylic beetle communities in a Norway spruce plantation.

The study is based on a thinning experiment established by Koch Widerberg (2013) in a stand a where Norway spruce trees were planted around oaks in 1975. In the experiment, during thinning in 2008, Norway spruce were removed under and around the oak crown at three levels of intensity (high-released oaks (HR); medium-released oaks (MR), and non-released oaks (NR)). Widerberg et al. (2012) found that the short-term effect (first 3 years) of releasing oaks was a higher species richness and abundance of oak-associated beetles compared to the non-released oaks. In this study, we re-examined the same stand 10 years after treatment, using the same experimental design and classification to test two hypotheses:

- The gap cutting still has a measurable effect on oak vitality and abiotic (light and temperature) variables 10 years post-treatment.
- The gap-cutting still has a measurable effect on oak-associated saproxylic beetles in terms of species richness, abundance, and composition.

METHODS

Study site

The study was conducted in 2018 and 2019 as part of an experiment located in the Swedish University of Agricultural Sciences (SLU) experimental forest at Asa (57.138°N, 14.756°E) in Kronoberg County, Sweden (Figure 1). The site elevation is around 220 m with a mean annual temperature of 6.6°C and mean annual precipitation of 458 mm (reference years 1990–2019 from Asa Reference climate data (Langvall, 2021)). The site is located on a 10% slope facing west. The soil conditions are predominantly mesic (90% of stand area), and

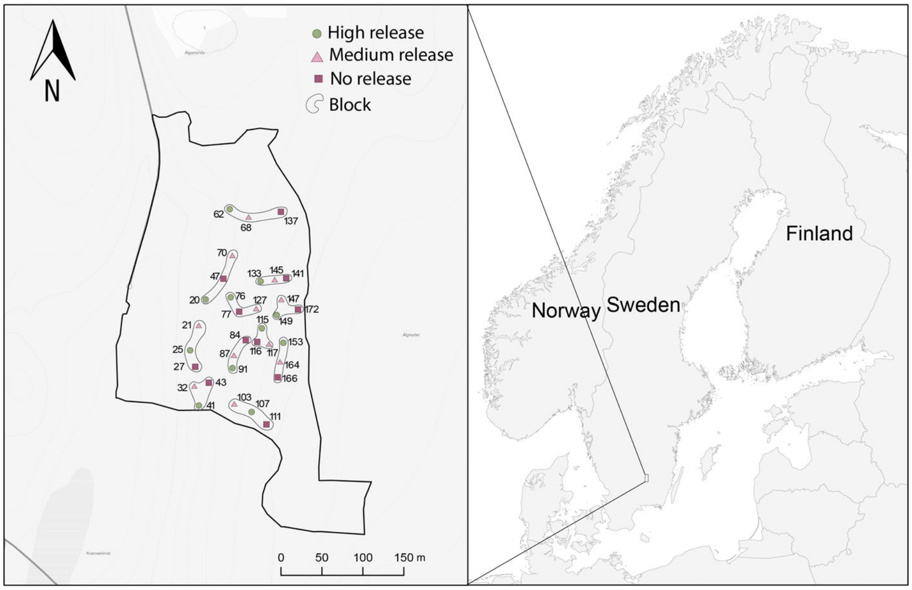

FIGURE 1 Map of the location of the stand used for the release experimentation near Asa. The map on the left shows the 33 focal oaks and the treatment they received: high release (green), medium release (light pink) or the control/no release (dark pink). The total stand area is 5.5 hectares.

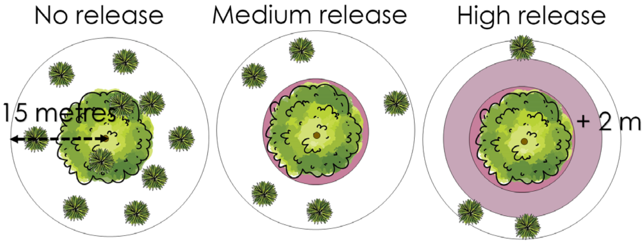

FIGURE 2 Representation of the different treatments in the release cutting experiment. The focal oak is the centre of the sample plot. The left image shows the control, or no release treatment (NR), where no Norway spruce were removed. The middle image shows the medium release (MR) where all Norway spruce were removed under the crown of the oak (dark pink area). The right image shows high release (HR) where all Norway spruce were removed under the crown of the oak (dark pink area) and 2 m beyond the crown area (lighter pink area).

the soil texture is sandy silt (80%) (Lindén, 2003). The experimental area is a 5.5 hectare which was originally a wooded pasture. Norway spruce (*Picea abies*) was planted in 1975 between the 84 pedunculate oaks (*Quercus robur*) and various retained deciduous trees, such as European aspen (*Populus tremula*) and Norway maple (*Acer platanoides*) distributed throughout the area.

Experimental design

The experiment was initially established in 2008 and was described by Koch Widerberg (2013) in further detail. Thirty-three oaks out of 84 were selected across the stand as "focal oaks" to undergo three different degrees of release cutting. On average, the oaks were 140 years old in 2018 (Drobyshev et al., 2019). The distance between the oaks was an average of 24.5 m from trunk to trunk, and the focal oak crown length was in average 4.7 m across all treatments and directions. The experiment was set up as a randomized block design with three treatments, each containing one focal oak, replicated in 11 blocks (Figure 1). Due to the death of one oak and one wrongly match oak from 2008 (Lariviere et al., 2020), we had to discard two oaks so our analyses included only 31 oaks.

In 2008, Norway spruce were removed at different intensities around each focal oak within a 15-m radius from each focal oak. High release (HR) consisted of removing all Norway spruce under and 2 m beyond the crown of the oak; medium release (MR) consisted of removing the Norway spruce directly under the oak's crown; and no release (NR) received no treatment other than normal thinning (Figure 2). Normal thinning was a removal of approximately 25% of the Norway spruce basal area, including strip roads. Most of the other retention trees (if not directly in the strip road area) were retained without any specific gap cutting surrounding them. The mean Norway spruce density (stems per plot) and treatment was 31 ± 9 SD in HR, 32 ± 11 in MR, and 44 ± 9 in NR, corresponding to 440, 450, and 623 stems per hectare, and representing a mean gap size of 8.8, 6.9, and 0 m radius. More details about the Norway spruce production aspects are found in Lariviere et al. (2020).

Insect sampling

Beetles were sampled in 2018 and 2019 using window traps placed approximately 5 m above the ground on the southern side of each focal oak stem, exactly as was done in 2008. Each window trap

FIGURE 3 Window trap used to catch beetles during the experiment. The trap was pulled up to 5 m above the ground using a rope system. The wood pole holding one 30 × 40 cm Plexiglas was inserted into the white container via two holes (one on each side) which also serve as drainage holes in case of heavy rain. At the top-right corner of the trap, a light and temperature logger can be seen (arrow).

consisted of a 40 × 17 × 14 cm white plastic container mounted with a single 30 × 40 cm Plexiglas transparent panel perpendicular to the stem (Figure 3). The containers were filled with 1.5 L of uncoloured monopropylene glycol (30%) and water (70%) solution to which a few drops of detergent were added to remove water surface tension. Traps were emptied every 3 weeks from May to September (six times per year). All saproxylic beetles (Coleoptera) were identified to the species level by entomologists Bengt Jan-Olof Andersson (Nybro, Sweden) and Hans Erik Wanntorp (Brottby, Sweden). The total number of individuals of each species was counted for each year. Only species characterized as saproxylic beetles (facultative and obligate saproxylic) included in Dahlberg and Stockland (2004) classification were used in the analysis.

Koch Wideberg (2013) assessed the beetles' association to oak and Norway spruce on the basis of their ability to use the wood of these tree species for at least some part of their life-cycle (Widerberg et al., 2018) following the classification by Dahlberg and Stokland (2004). We used the same non-nested beetle groups, as done in Koch Widerberg (2013), Widerberg et al. (2018). The four groups were:

- **Group I** saproxylic species associated with oak and Norway spruce.
- **Group II** saproxylic species associated with oak but NOT with Norway spruce.
- **Group III** saproxylic species not associated with oak.
- **Group I+ II** saproxylic species associated with oak.

Both oak- and spruce-associated beetles may also use other tree species present in southern Sweden.

Oak vitality and abiotic variables

A series of data were previously collected for Lariviere et al. (2020). For the present study, we used information about focal oak, such as diameter at breast height (DBH) measured with a calliper, height (metres), and crown area-growth in 10 years (m^2). The focal oak crown area-growth was calculated from the crown length, which was measured from the trunk of the focal oak to the end of the crown in four cardinal directions (north/south/east/west), then transcribed into a crown area in square metres. The crown area growth of the oak was calculated as the difference between the second (2018) and the first measurements (2008). We were also interested in dead wood characteristics, such as the percentage of dead wood in the crown and the diameter of the thickest dead branch on each focal oak. Dead wood was measured once in September 2018 before the leaves had fallen, which allowed easy detection of dead branches. The percentage of dead wood was estimated by counting the number and length of dead and alive branches on each oak. We used 2-dimensional tree architecture drawings (Appendix 2). Each drawing was scaled in relation to the tree's total height, which was measured with a vertex height-measuring instrument and an 8-m reference stick placed on the stem of the tree. Widerberg et al. (2012) found a positive correlation between species richness and the diameter of the thickest dead branch per oak, and therefore we also estimated the diameter of the thickest dead branch by holding a reference stick of 10, 20, 25, or 30 cm beside the branch on a long pole.

Light and temperature were recorded with HOBO Pendant MX Temperature/Light Data loggers, which were installed on the top right corner of the window traps (Figure 3). We used 22 loggers which were placed on focal oaks in the "no release" and "high release" treatments, representing the two extreme treatments. These recorded both light (lux) and temperature (°C) every hour from May to September in 2018 and 2019.

Data analyses

The analyses were conducted in R studio 3.4.3 (R Core Team, 2022). We investigated treatment differences for species richness, abundance, and species composition of saproxylic beetles. We also investigated difference between treatments for oak vitality variables, light, and temperature.

Beetle abundance and species richness

Abundance was calculated as the total number of saproxylic beetles captured at each focal oak for each year. Abundance data can often be overdispersed due to clusters of individuals (variance greater than the mean). For this reason, we used a negative binomial generalized linear mixed model (GLMM) using the function glmer.nb from the R package MASS by Ripley et al. (2013) to determine whether saproxylic beetle abundance differed between treatments.

Species richness was calculated as the total number of beetle species found at each focal oak in each year. We used generalized linear mixed models (GLMMs) with a Poisson distribution and log-transformed data to determine whether the total number of species per oak differed between treatments.

To assess the effect of different treatments, we used either beetle abundance or beetle species richness per oak for each year as the response variable. Treatment and sampling year were used as fixed factors, and block was set as a random factor. Species richness and abundance are often positively correlated in ecological data (Chao & Chiu, 2016). In our analyses, we controlled for this by including abundance as a covariate in the analysis of species richness.

Results for the general linear mixed models (GLMMs) were obtained from Wald Chi-Square Tests and interpreted based on a 0.05 critical alpha threshold. If an independent variable was significant, post-hoc pairwise comparisons between treatments were computed using estimated marginal means (function emmeans in packages lsmeans (v1.8.2; Lenth 2022) and multcomp (v1.4-20; Hothorn et al., 2022)). For all models, the assumptions were verified by inspecting the plots of the residuals, and if necessary, transformation of the response variable was performed before statistical testing. The analyses were conducted separately for each specific group of saproxylic beetles.

Species composition

We assessed the differences in species composition based on dissimilarity using a permutational multivariate analysis of variance (perMANOVA), using the adonis2 function in the vegan package (Oksanen et al., 2019). This model included treatment and block as random variables. To examine differences in beetle species composition between the different treatments, we used non-metric multidimensional scaling (NMDS), which is an unconstrained method. We used the metaMDS function from the R package vegan (Oksanen et al., 2019) with the Bray–Curtis dissimilarity index and interpreted the stress level according to Dexter et al. (2018) where a value of <0.3 is used as the threshold for a good fit and a reasonable interpretation. The analysis was conducted on the full beetle species dataset, with species aggregated per oak.

To see the effect of treatment on species composition we used a canonical correspondence analysis (CCA). We started by running a detrended correspondence analysis (DCA) with the decorana function from the vegan package (Oksanen et al., 2019). The DCA including treatment showed that the length of the first axis is equal to two SD units, and we therefore proceeded to a unimodal test with a CCA (Borcard et al., 2011; Lepš & Šmilauer, 2003). The species data set was used as the dependent variable, and treatment (the three factorials, HR, MR, and NR) was set as the explanatory variable. To obtain the total explained variation for each axis, we compared eigenvalues with the total inertia. The full CCA model and each axis were tested using ANOVA. Ordination plots were produced from the ggplot2 package by extracting the CCA axis values (v3.4.0; Wickham, 2016) and with the basic R plotting function from the vegan package (Oksanen et al., 2019). Plotting all species in the graph made the plot too hard to read. This was solved by using the function orditorp, which automatically adds labels, prioritizing species with higher frequencies.

Oak vitality and abiotic variables

Vitality variables for each oak were averaged at the treatment level and the means were compared in a linear mixed model (LMM) with treatment (fixed) and block (random) as explanatory variables. The proportion of dead wood followed a sigmoidal distribution and was then square root and arcsin transformed for the analyses. The abiotic variables (air temperature and light) were measured and calculated for the two extreme treatments, High Release and No Release. The mean values per oak were calculated, then averaged per treatment for each year. Treatment-related differences in the response variables light and temperature per oak each year were tested using a linear mixed model (LMM) with year as a fixed factor and block as a random factor.

RESULTS

Insect sampling

A total of 6602 saproxylic beetles representing 157 different species were sampled across both years, where 2285 individuals were found in high release (HR), 2215 in medium release (MR), and 2102 in no release (NR) trees. A total of 4249 beetles were found in 2018 and 2353 in 2019, belonging to 120 and 115 different species, respectively (Figure 4). In 2018, the most abundant species was *Quedius mesomelinus*, a facultative saproxylic beetle from group II (associated with both on oak and Norway spruce), with a total of 1803 individuals. In 2019, the most abundant species was *Cychramus luteus*, a facultative saproxylic species from group III (not associated with oak), with 647 individuals. Forty-three species (27% of all species) were represented by only one individual (Appendix 1).

Abundance, species richness, species composition

The abundance was similar in all treatments when all species were included (Table 1). When host tree association was considered, two groups showed treatment-related differences in abundance, Group I (both oak and spruce) ($p < 0.001$; Table 1) and group I + II (associated with oak) ($p < 0.05$; Table 1), whereas group II (associated with oak but not Norway spruce) and group III (species not associated with oak) showed no significant difference between treatments (Table 1).

The mean number of different species found at each oak differed significantly between treatments ($p < 0.001$; Table 2). The released oaks had more species than the control. When considering each group separately, only group I + II (associated with oak), had significantly more species at HR and MR compared to NR ($p < 0.05$; Table 2, Appendix 3).

Species composition significantly differed between HR and NR treatments (PERMANOVA, $F_{2/28} = 1.844$, $p = 0.009$, $r^2 = 0.116$). The analysed species composition at the individual oak level in the NMDS resulted in a stress level of 0.24. The NMDS ordination of the saproxylic beetles for the three treatments revealed a cluster for NR sample plots, indicating similarities in species composition among these oaks (Appendix 4). In contrast, HR and MR stands were more widely distributed, indicating less distinctive community compositions separating these treatments. There was a larger variation in the communities in HR and MR compared to NR, as they take up more of the ordination space (Appendix 4).

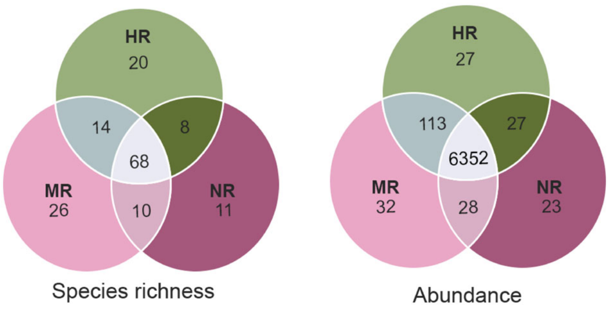

FIGURE 4 The left Venn diagram shows the number of different species appearing in each treatment. It shows the number of species of saproxylic beetles unique to a treatment or shared by two or three treatments, HR (High release), MR (Medium release), and NR (No release). The right Venn diagram shows the number of individuals in each pool of species. For example, in MR, there are 26 exclusive species only appearing in that treatment, and altogether they represent 32 individuals. In HR, there are 20 exclusive species only occurring in HR, altogether representing 27 individuals. Dataset includes both years (2018 and 2019). In total, 6602 individuals of 157 different saproxylic beetle species were sampled.

The detrended correspondence analysis (DCA) showed that the length of the first axis is equal to two SD units (Appendix 5); we therefore proceeded to a unimodal test with a canonical correspondence analysis (CCA). The constrained axes (treatments) of the CCA explained 8.3% of the variation in the model, and 91.15% of the variation was explained by unconstrained axes (ANOVA, $\chi^2 = 0.123$, $p = 0.009$) (Appendix 5). The ordination diagram (Figure 5) shows the species association with the different treatments. It indicated that a larger proportion (CCA1, 5.98%, $F = 1.837$, $\chi^2 = 0.083$, $p = 0.007$) of variation in species communities was explained by differences between communities in these treatments compared to the MR treatment, which was mainly explained by the y-axis (CCA2, $F = 0.880$, $\chi^2 = 0.040$, 2.98%, $p = 0.717$).

Some beetle species were clearly associated with the NR treatment (right/bottom), such as *Denticollis linearis* (3 ind.), *Trypodendron lineatum* (11), and *Trypodendron domesticum* (38). The other species aggregated at the bottom left of the ordination, including *Dasytes niger* (29), *Calambus bipustulatus* (3), a near threatened (NT) species, *Cetonia aurata* (6), and *Clytus arietis* (5) were associated with the HR treatment. Some species were clearly associated with the MR treatment such as *Hapalarea melanocephala* (3), *Polygraphus poligraphus* (5), and *Soronia punctatissima* (7). However, some beetle species located in the centre of the plot were not clearly distinguished between the treatments. These beetle species were recorded at a high or relatively high frequency throughout the survey. The pool of common species was similar in all three treatments and dominated by *Quedius mesomelinus*, *Cychramus luteus*, *Anaspis rufilabris*, *Cryptophagus scanicus*, and *Dasystes plumbeus*. A total of 57 species were found in only one of the treatments (Figure 4, Appendix 1).

TABLE 1 Results from the negative binomial generalized linear mixed model (GLMM) of saproxylic beetle abundance, as well as the mean and standard error (SE) per oak in each treatment for each beetle group

ABUNDANCE	Year			Treatment			High release			Medium release			No release		
Beetles	Chisq	DF	*p*	Chisq	DF	*p*	Mean	SE	Group	Mean	SE	Group	Mean	SE	Group
All	82.66	1	**0.000**	4.09	2	0.129	97.2	7.3	-	92.3	7.1	-	83.8	6.5	-
Group I	5.18	1	**0.023**	13.50	2	**0.001**	15.8	1.8	**a**	10.9	1.3	**b**	9.6	1.2	**b**
Group II	166.27	1	**0.000**	2.89	2	0.236	52.1	4.3	-	48.6	4.2	-	43.7	3.8	-
Group III	13.65	1	**0.000**	0.28	2	0.870	25.7	2.6	-	27.0	2.7	-	27.0	2.7	-
Group I + II	139.64	1	**0.000**	6.00	2	**0.050**	68.7	5.5	**a**	60.4	5.1	**b**	54.3	4.6	**c**

Note: High release (HR) consisted of removing all Norway spruce under and 2 m beyond the crown of the oak; medium release (MR) consisted of removing the Norway spruce directly under the oak's crown; and no received no treatment other than normal thinning and used as control. "All" included all individuals found during the experiment. Significant p-values are shown in bold. If significant, the results of the Kenward–Roger post-hoc test are illustrated with letters. Means sharing a letter are not significantly different from each other at $p \leq 0.05$. Group I saproxylic species associated with oak and Norway spruce. Group II saproxylic species associated with oak but NOT with Norway spruce. Group III saproxylic species not associated with oak. Group I+ II saproxylic species associated with oak.

TABLE 2 Results from the Generalized Linear Model (GLM) with saproxylic beetles species richness and the mean and standard error (SE) per oak in each treatment High release (HR) consisted of removing all Norway spruce under and 2 m beyond the crown of the oak; medium release (MR) consisted of removing the Norway spruce directly under the oak's crown; and no treatment other than normal thinning and used as control

SP. RICHNESS	Year			Abundance			Treatment			High release			Medium release			No release		
Beetles	Chisq	DF	*p*	Chisq	DF	*p*	Chisq	DF	*p*	Mean	SE	Group	Mean	SE	Group	Mean	SE	Group
All	0.04	1	0.837	13.09	1	**0.000**	10.49	2	**0.005**	23.50	1.17	a	23.30	1.21	a	19.20	1.09	b
Group I	6.18	1	**0.013**	31.14	1	**0.000**	2.99	2	0.224	6.62	0.56	-	7.50	0.62	-	6.07	0.57	-
Group II	3.23	1	**0.072**	7.21	1	**0.007**	2.97	2	0.226	9.39	0.74	-	9.31	0.77	-	7.94	0.70	-
Group III	2.14	1	0.143	3.91	1	**0.048**	3.64	2	0.162	6.56	0.55	-	6.55	0.57	-	5.27	0.51	-
Group I + II	0.85	1	0.356	12.70	1	**0.000**	6.97	2	**0.031**	16.90	0.99	a	16.70	1.02	a	13.90	0.92	b

Note: "All" included all species found during the experiment (157 species). Significant *p*-values are shown in bold. If significant, the results of the Kenward–Roger post-hoc test are illustrated with letters; means sharing a letter are not significantly different from each other. Group I saproxylic species associated with oak and Norway spruce. Group II saproxylic species associated with oak but NOT with Norway spruce. Group III saproxylic species not associated with oak. Group I+ II saproxylic species associated with oak.

Oak vitality and abiotic factors

The oak crowns grew 16–17 times more when released (HR and MR) compared to the non-released treatment (NR) (Table 3). The highest proportion of dead branches was in the NR treatment (39% ± 3.26 SE) and the lowest was in the HR treatment (23.8% ± 3.09 SE). Both the mean proportion of dead branches and canopy growth were affected by treatment ($p < 0.01$; Table 3). The thickest dead branch size did not significantly differ between treatments ($p = 0.149$; Table 3).

Temperature differed between treatments (Table 3) and sampling years (ANOVA, $F_{1/29,141} = 3557.07$, $p < 0.001$). The temperature was higher in HR oaks than NR oaks, and the year 2018 was warmer than 2019 (Table 3). Light differed significantly between treatments, with double lux values for HR versus NR (Table 3). Light did not differ significantly between 2018 and 2019 (Table 3).

DISCUSSION

In this study, we tested two main hypotheses concerning the long-lasting effects of gap creation on (1) oak vitality and abiotic factors and (2) abundance, species richness, and species composition of saproxylic beetles. Both main hypotheses were supported by the data. Ten years after the release, tree vitality was slightly higher in released oaks than in unreleased oaks, and it was warmer and lighter around the released oaks. More beetle individuals and more species of oak-associated saproxylic beetles were trapped on released versus unreleased oaks and species composition differed between treatments. These results are novel and have important implications for management of beetle diversity with different light preferences over time in planted conifer stands.

Different indices of vitality have been used to document that gap cutting improves oak vitality (Gálhidy et al., 2006; Götmark, 2009; Harrington & Warren, 2006; Lariviere et al., 2020; Shifley, 2004). We used crown growth and proportion of dead branches and showed that the oak crown was growing and colonizing the gap when released, while unreleased oaks had higher proportion of dead wood. Götmark (2009) used dead wood in the crowns as a negative predictor of growth and also found that the openness around the oak crown was a positive predictor for oak growth. In addition, he showed a positive effect of release on oak basal area, which we did not find. However, these external cues for oak vitality still cannot address the complete picture of the oaks' response to the release. Other studies are emphasizing the potential negative effects thinning may have on oak vitality (Bergquist & Isacsson, 2002; Drobyshev et al., 2019). Drobyshev et al. (2019) used dendrochronological methods to show that oak growth is negatively correlated with the amount of dead oak crown but is positively related to oak age. They argue that summer drought could potentially be a negative factor for older oaks. Oak responses to thinning are generally positive and gap cutting will reduce the risk of mechanical damage to the tree from potential regrowth as well as reduce competition for water, light, and nutrients, which are factors that can trigger oak death (Andersson et al., 2011).

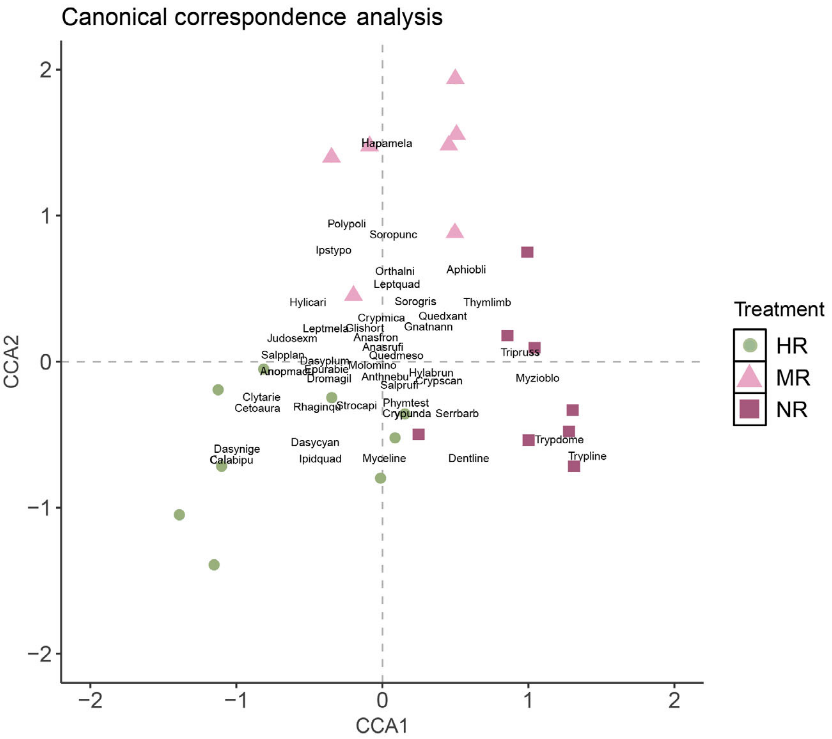

FIGURE 5 Biplot from the canonical correspondence analysis (CCA) of saproxylic beetle composition around 31 oaks in different release treatments. The plot shows the two first axes from the CCA and specific species association with three different gap treatments around the oaks (HR, high release; MR, medium release and NR, no release). The biplot only represent oaks that are within the x and y limit. Only species with the highest overall frequency are presented in the plot. Singletons were therefore excluded. The full species list is available in Appendix 1.

TABLE 3 Relationship between release treatments and different environmental variables

					High release		Medium release		No release		ANOVA		
Variable	***n***	**Transf.**	**Year**	**Unit**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	***F***	**Df, dendf**	***p***
Thickest DB (cm)	31	NT	2018	cm	17.50	1.80	19.00	1.91	22.70	1.91	2.038	2/28	0.149
Dead wood (%)	31	Arcsin(sqrt)	2018	%	23.80	3.09	27.90	3.26	39.00	3.26	5.6216	2/28	**0.007**
Crown area 2018	31	log	2018	m^2	66.10	10.27	63.70	10.44	40.20	6.59	3.278	2/19.54	0.059
Crown growth	31	NT	2018	m^2	24.46	5.12	22.86	5.40	1.43	5.40	6.065	2/19.64	**0.009**
DBH	31	log	2018	mm	624.00	38.30	607.00	39.30	546.00	34.40	1.278	2/18.21	0.303
Height	31	NT	2018	m	23.80	0.83	22.30	0.87	22.90	0.87	0.953	2/19.31	0.403
Temperature	44	NT	2018/2019	°C	16.10	0.08			15.80	0.08	26.201	1/29.52	**0.000**
Light	44	log	2018/2019	Lux	842.00	145.90			399.00	71.30	24.689	1/29.97	**0.000**

Note: The table shows the mean and its standard errors (SE) for three different release treatments of retained oak trees in a Norway spruce stand (high release, HR; medium release, MR; and no release, NR). Temperature and light were only measured in the two extremes treatment HR and NR. Transformed variables are mentioned in the Transf. column where NT = Not transformed, Arcsin(sqrt) = Arcsine square root transformed and log = log10 transformed. The table also shows the *F*-value (*F*), degrees of freedom (df), denominator df (dendf) and *p*-value (*p*). *p*-values from the ANOVA in bold are significant ($p < 0.05$). Thickest DB = diameter of the thickest dead branch (cm), Dead wood = proportion of dead wood in the oak, Crown area = size of the crown in square metre, Crown growth = difference in crown area between 2008 and 2018, DBH = diameter at breast height (mm), Height = height of the focal oak (m).

In our study, the amount of dead wood was lower in the released than unreleased oaks, whereas the species richness and abundance of certain beetle groups were higher. This indicates that dead wood quantity is not always a good predictor or the only predictor of saproxylic beetle diversity. Müller et al. (2015) concluded that dead wood indeed plays a crucial role in saproxylic beetle diversity, but that temperature was also an important driver. Increasing temperature may even compensate for poor habitat conditions in production forests (Bouget et al., 2013; Müller et al., 2015).

We showed that still 10 years after gap-cutting the amount of light reaching the oak trunks was greater for released compared to the non-released oaks. The amount of light reaching the oak is a key factor for saproxylic oak-associated beetles. It promotes the development of a microclimatic variability within the oak crown, bark, trunk, and other structures that are important for saproxylic beetles (Ranius & Jansson, 2000; Seibold et al., 2018). Active management, such as release cutting, can modify these environmental variables to the benefit of the oak itself and its attached conservation value (Gough et al., 2014). Several studies have shown that light is essential for many species associated with oak trees (Bouget et al., 2013; Härdtle et al., 2003; Horak et al., 2014; Jonsell et al., 1998). Shade-intolerant trees, like oaks (*Quercus* spp.), will support species adapted to open, light, and warm conditions and appear to harbour more beetle species dependent on high levels of insolation than more shade-tolerant tree species (Horak et al., 2014; Jonsell et al., 1998; Ranius & Jansson, 2000). Lindhe et al. (2005) showed that high oak stumps have much larger proportions of species favoured by exposed conditions than Norway spruce, which is in accordance with the positive effect of release we found for beetle groups associated with oak. Gran and Götmark (2019) found more saproxylic beetles species following thinning in an oak-dominated mixed forest. This increase was likely due to both increased sun exposure and the addition of new dead wood from the oak. In agreement with Gran and Götmark (2019), we speculate that together with higher insolation, the released oaks provide a more continuous supply of sunny substrates than unreleased oaks. Widerberg et al. (2012) found a positive relationship between the diameter of the thickest dead branch and species richness of oak-associated beetles, which we did not find. Their study did not have an experimental setup with treatments, but instead used a gradient from small to large gaps where the large gaps extended 3–8 m outside the crown edge. They, thus, had much larger gaps than in our study, possibly allowing for high amounts of sun-exposed coarse dead wood.

There were clear differences in temperature between the two sampling years, with 2018 being warmer than 2019. In fact, 2018 was one of the warmest summers ever recorded in southern Sweden (Langvall, 2021). The abundance, species richness, and species composition of beetles differed between years. The higher abundance in 2018 was probably due to higher flight activity and more days with temperatures above the flight threshold, which can increase the number of beetles trapped in a season. Faster insect development, leading to multiple generations of some species might have also played a role (Ratte, 1984; Zaslavski, 1988). The differences in species composition between years were an effect of longer species lists and more year-specific species in 2018 than in 2019. Temperature, as a result of differences in insolation, differed between treatments, and consequently, the window traps on the warmer and sunnier released oaks had a higher flight activity than shaded control oaks. Thus, the trap catches do not only depend on the number of beetles attracted to an oak but also the amount of time they spend flying there (Bouget et al., 2014). In our analyses, we controlled for this by including abundance as a covariate in the analysis of species richness, and found that control oaks (NR) still had lower species richness compared to released oaks for the group I (both oak and spruce) and group I + II (using oaks during at least part of their life cycle).

The species composition differed clearly between the HR and NR treatments. We found patterns in species composition that relate to the life history of some species. For instance, *Trypodendron* spp. probably have an affinity for NR oaks; they are so-called ambrosia beetles that depend on a sufficiently moist microclimate to cultivate ambrosia fungus for their larvae. The HR treatment was characterized by the presence of species that breed in the wood of broadleaf trees and visit flowers for pollen or nectar. For example, *Clytus arietis* is a wasp-mimicking longhorn beetle with adults that visit flowers. Adults of the scarabid *Cetonia aurata* feed on pollen and nectar and were only found in the released treatments. We also found red listed species in the released oaks, such as *Dryophthorus corticalis* (Vulnerable (VU)) and *Calambus bipustulatus* (Near Threatened (NT)), which are associated with broadleaf trees. We did not further explore any possible causal links between species composition among trapped beetles and the local stand structure, but it is clear that the creation of a gap in the forest alters many biotic and abiotic factors, which may affect species composition even at a small spatial scale.

Our findings add to those by Widerberg et al. (2012), who showed that even 3 years post-treatment the diversity and abundance of oak-associated beetles was positively affected by the release (Widerberg et al., 2012). We found that 10 years after there was still a positive effect of the release treatment on the diversity and abundance of oak-associated beetles, and a change in beetle species composition. We added a temporal dimension to the efficiency of oak release and showed a long-lasting targeted effect of release management over time. In contrast, Toivanen and Kotiaho (2010) found that the positive effect of partial cutting on saproxylic beetles in coniferous forests had disappeared after 2 years, probably because the dead wood resource was rapidly exhausted. If the oaks remain healthy, they may provide long-lasting habitats (crown, trunk) for saproxylic beetles. The present study, together with Koch Widerberg (2013) and our earlier study (Lariviere et al., 2020), contributes to the understanding of how saproxylic beetle species richness, abundance, and assemblages are linked to environmental conditions over time.

Since our study was only done in one site, general conclusions should be made carefully. We have avoided to draw any conclusions on effects on beetle populations at a larger scale than the local stand. However, we argue that the experiment was appropriate for evaluating the long-term effect of gap-cutting since the stand is a good representation of a fertile mixed oak/Norway spruce forest typically found in southern Sweden. There is a possibility that the oaks we studied responded quickly because of high site fertility, enabling the trees to fill the gaps faster than oaks would have done on a poorer site. Therefore, more studies conducted on less fertile sites are needed. No other study has addressed this question with an experimental design similar to ours and long-term studies on ecological succession are relatively rare. A space-for-time substitution (chronosequence) is often used, which is handy, but has several disadvantages compared to long-term studies and may even lead to incorrect conclusions (Walker et al., 2010).

CONCLUSIONS

Healthy oaks provide dead branches and hollow wood for a longer time than suppressed dying oaks, and if well managed, a high proportion of the dead wood will be sun-exposed and serve as a valuable habitat for saproxylic beetles. Thus, it is important to maintain and conserve oaks through several rotations in commercial plantations. Forest management practices, for instance thinning, can create favourable conditions for retained trees and species associated with them. Even only moderate release (MR), removing a few trees growing underneath the oak crown, can sustain biological values within the stand. It is important to consider not only the overall quantity of dead wood but also the quantity of sun-exposed dead wood in conservation measures directed towards saproxylic oak beetles. We suggest to avoid planting crop trees beneath retained oaks when regenerating conifer forests and to proceed with conservation management during subsequent thinning by removing regeneration under the oak crown. We emphasize the benefits of monitoring the retained oak to maintain tree vitality, habitat quality and insolation.

ACKNOWLEDGMENTS

We thank the staff at Asa Experimental Forest and Research Station for their help with stand data collection. Bengt Andersson and Hans-Erik Wanntorp carried out beetle identification. Victor Delorme helped with the fieldwork and drawing the trees. We also thank Maria Koch Widerberg for helping with gathering and explaining the data.

FUNDING INFORMATION

This work was financed by the research programme FRAS—Future Silviculture in Southern Sweden. The project is a collaboration between the Swedish University of Agriculture Science (SLU), Linnaeus University, and Skogforsk (the Forestry Research Institute of Sweden). This work was also supported by the Tranemåla (Erik och Ebba Larssons Thure Rignells) foundation and the Extensus foundation.

CONFLICT OF INTEREST

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

DATA AVAILABILITY STATEMENT

Data available on request from the authors

ORCID

Delphine Lariviere https://orcid.org/0000-0002-1415-3476

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting Information

How to cite this article: Lariviere, D., Holmström, E., Petersson, L., Djupström, L. & Weslien, J. (2023) Ten years after: Release cutting around old oaks still affects oak vitality and saproxylic beetles in a Norway spruce stand. *Agricultural and Forest Entomology*, 25(3), 416–426. Available from: https://doi.org/10.1111/afe.12563