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Higher Population Densities of the Abundant Specialist *Gyrophaena boleti* in Near Natural than Previously Clear-Cut Mature Forests

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Abstract

Boreal forests are home to thousands of species, many of which are dependent on dead wood. In Norway, more than half of the known species live in the forest. Modern forestry in Norway has altered the characteristics of forests, creating homogenous forest stands of even aged trees with low volume and diversity of deadwood, risking the habitat of saproxylic organisms. In this study, I investigated the saproxylic beetle *Gyrophaena boleti* (L.) in previously clear-cut and near natural forests in South-eastern Norway by window traps and individual counts on the underside of *Fomitopsis pinicola* (Fr.) Karst. fruit bodies. A higher number of *G. boleti* was trapped in the near natural forests compared to the previously clear-cut forests. The difference could be explained by a higher volume of deadwood in early decay stages, facilitating for more *F. pinicola* which is the main habitat for *G. boleti*. There was no significant difference in the density of *G. boleti* on the hymenium of *F. pinicola* between the two forest types. However, as fruit bodies of *F. pinicola* occurred in higher numbers and were larger sized in the near natural forests, estimated population densities of *G. boleti* were higher in the near natural forests. This study shows that the abundance of even common forest species such as *G. boleti* can be reduced as a result of clear-cutting compared to near natural forests.

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1. Introduction

The boreal forests make up about one third of the total area of forest in the world, and are home to and support several thousands of species of organisms (Gauthier et al., 2015; Jacobsen et al., 2020). In Norway, forests make up about 37 % of the total mainland area (Svensson et al., 2023; Thorsnæs, 2023), and of the 44 00 known species in Norway, 60% of them live in the forest (Bartlett et al., 2020). Most of the biodiversity in forests is made up by fungi and invertebrates (Stokland et al., 2012). As much as 48% of the red listed species in Norway depend on forest, most of which are also dominated by fungi or insects (The Norwegian Biodiversity Information Centre, 2021). This makes the boreal forests in Norway, especially considering fungi and insects, important for conservation of biodiversity.

Svensson et al. (2023) reported that only about 2% of the forests in Norway are categorized as old growth forests, i.e. forests with no or few traces of management. Managed forests often contain less dead wood, both in volume and in diversity of decay stage than unmanaged forests (Jacobsen et al., 2020; Stokland et al., 2012; Svensson et al., 2023). Many of the species found in forests, including fungi, insects, mammals and birds, depend on a wide variety of dead wood (Jacobsen et al., 2020; Storaunet et al., 2005). When clear-cutting forests was introduced as the dominating harvesting method after 1950 (Stokland et al., 2012; Storaunet & Rolstad, 2020; Tomter & Dalen, 2014), the habitat properties of many forests were altered (Kuuluvainen, 2009). During clear-cutting, 95-98% of the tree volume is removed (Stokland et al., 2012), making clear-cutting negatively affect forest characteristics such as species diversity even decades and centuries later, especially affecting species requiring continuous habitat availability through features such as deadwood resources (Eckelt et al., 2018; Aakala et al., 2009). Forests that have not been exposed to clear-cutting and where management activities are no longer occurring, called “naturskog” in Norwegian, near natural forests in English, make up one third of the productive forest area in Norway (Storaunet & Rolstad, 2020). On a general basis, the near natural forests contain a high volume of deadwood, have variation in tree age classes, and have high structural heterogeneity promoting high species diversity (Jacobsen et al., 2020; Seibold et al., 2015; Storaunet et al., 2005). These forests can provide habitat comparable to old-growth forests for many species (Jacobsen et al., 2020). However, the majority of forests in Norway today are not protected by conservation policies, placing them in a vulnerable position (Sverdrup-Thygeson, Søgaard, et al., 2014).

Fungi play an important role in the forest by decomposing deadwood and contributing to the cycling and availability of nutrients (Birkemoe et al., 2018; Boddy & Jones, 2008; Hoppe et al., 2016). Most wood-decaying fungi belong to the phylum Basidiomycota. They are known as "true" wood-decaying fungi, and when it comes to mass loss during wood decay, they are believed to be the most important taxa (Birkemoe et al., 2018; Lunde, Boddy, et al., 2023; Stokland et al., 2012). *Fomitopsis pinicola* is a common keystone wood-decaying fungus (Lunde, Boddy, et al., 2023; Økland & Hågvar, 1994), belonging to the brown-rot fungi, known to be the principal wood decomposers in boreal forests (Gramss, 2020; Stokland et al., 2012). *F. pinicola* appears in both managed and unmanaged forests (Økland & Hågvar, 1994), and on both coniferous and broadleaved trees (Stokland et al., 2012). In addition to being an important decomposer, *F. pinicola* plays an important role in the life of many saproxylic insects (Birkemoe et al., 2018). *Gyrophaena boleti* is a common saproxylic beetle found in both managed and near natural forests, a specialist living on *F. pinicola* (Hågvar, 2018; Hågvar & Økland, 1997). *G. boleti* is one of the first species to arrive on fresh fruit bodies (Staniec et al., 2016), and is dependent on the hymenium of *F. pinicola* throughout its life cycle (Hågvar & Økland, 1997; Staniec et al., 2016). It is one of the few known insects to breed inside living fruit bodies of *F. pinicola* (Hågvar & Økland, 1997; Staniec et al., 2016). Because of their dependence on older forests and deadwood, saproxylic beetles are often used as indicator species of the naturalness of forests (Eckelt et al., 2018). Even though both fungi and saproxylic beetles are the subject of several studies, knowledge of the importance of their interactions is lacking (Birkemoe et al., 2018).

A global decline in biodiversity has been reported for most taxa, both in terms of richness and abundance (Johnson et al., 2017). One of the main stressors for this decline is habitat loss, especially deforestation (Wagner, 2020; Wagner et al., 2021). In forests, studies have also shown that altering stand characteristics such as deadwood volume, size and decay stage of deadwood, has affected both red-listed species and the overall saproxylic beetle composition (Burner et al., 2022). Most studies of insect declines focus on endangered or charismatic species (Seibold et al., 2015; Wagner et al., 2021), however also abundant species are experiencing declines (Wagner et al., 2021). In addition, a steeper rate of decline has been reported for specialized than generalist insects (Wagner et al., 2021). As a common specialist, *G. boleti* can then still be interesting to study because ecosystem services often depend on abundant species (Wagner et al., 2021).

Population studies can give insight into the species dispersal, reflecting how populations are able to cope with habitat fragmentation (Ranius, 2006). When making population estimates, the aim should be absolute population estimates, referring to the number of individuals per unit of area (also called population density) (Samways et al., 2010; Southwood & Henderson, 2000). One of the approaches is to sample a unit of habitat; investigating the population intensity where the number of individuals per unit of habitat is estimated, then estimating the number of habitats in the area (Southwood & Henderson, 2000). The number of habitats can then be converted into number of units per unit surface area of soil (most often per square metre or hectare) (Pimentel, 1961; Southwood & Henderson, 2000).

When investigating insect populations, one should be aware that their activity and habitat use is influenced by time of the day, season, weather and life stage, and when comparing communities between different sites one should aim to minimise the variation in these conditions (Halbritter et al., 2020). Often, collection methods such as traps is the only option and these issues of variance in time and space make it difficult to relate numbers to sampling area (Halbritter et al., 2020; Sverdrup-Thygeson & Birkemoe, 2009). These challenges, together with the very high number of species, have contributed to the low number of studies focusing on actual population densities of insects (Wagner et al., 2021).

In this masters' project, I investigated whether modern forestry in Norway affects the number of *G. boleti* by comparing previously clear-cut forests and near natural forests. I have used traditional trapping methods and counted the number of animals per habitat patch to compare actual population densities to trap catches. In addition, I have estimated population densities of *G. boleti* based on the number of *G. boleti* per fruit body and the total number of fruit bodies available in the forests. I predicted that we would trap and observe larger numbers of *G. boleti* in forests that are near natural than in the previously clear-cut, because the volume of deadwood is higher, leading to more fruit bodies of *F. pinicola*.

2. Materials and methods

2.1. Study area

This thesis is part of the EcoForest project researching the long-term effects of modern forestry, both regarding biodiversity in the soil and dead wood, and how carbon storage is affected. The project is in collaboration with the University of Oslo (UiO), the Norwegian University of Life Sciences (NMBU), the Norwegian Institute of Bioeconomy Research (NIBIO), and Norwegian Institute for Nature Research (NINA), and is financed by the Norwegian Research Council (EcoForest, n.d.).

All the sites included in this thesis were chosen by the EcoForest team. They were all located in the boreal zone of forest in Norway and selected to be spruce (*Picea abies* (L.) H. Karst) dominated with bilberry (*Vaccinium myrtillus* L.) vegetation on the ground. At each site, a forest stand clear-cut in the 1950s or earlier and a near natural forest were selected in close vicinity of each other. The forest pairs were chosen to be comparable, with the same exposure, vegetation type, slope and soil characteristics. The sites visited in this study are all forest areas located in South-eastern Norway. A total of 10 sites were selected (Figure 1). The altitudes ranged from 190 to 697 metres above sea level.

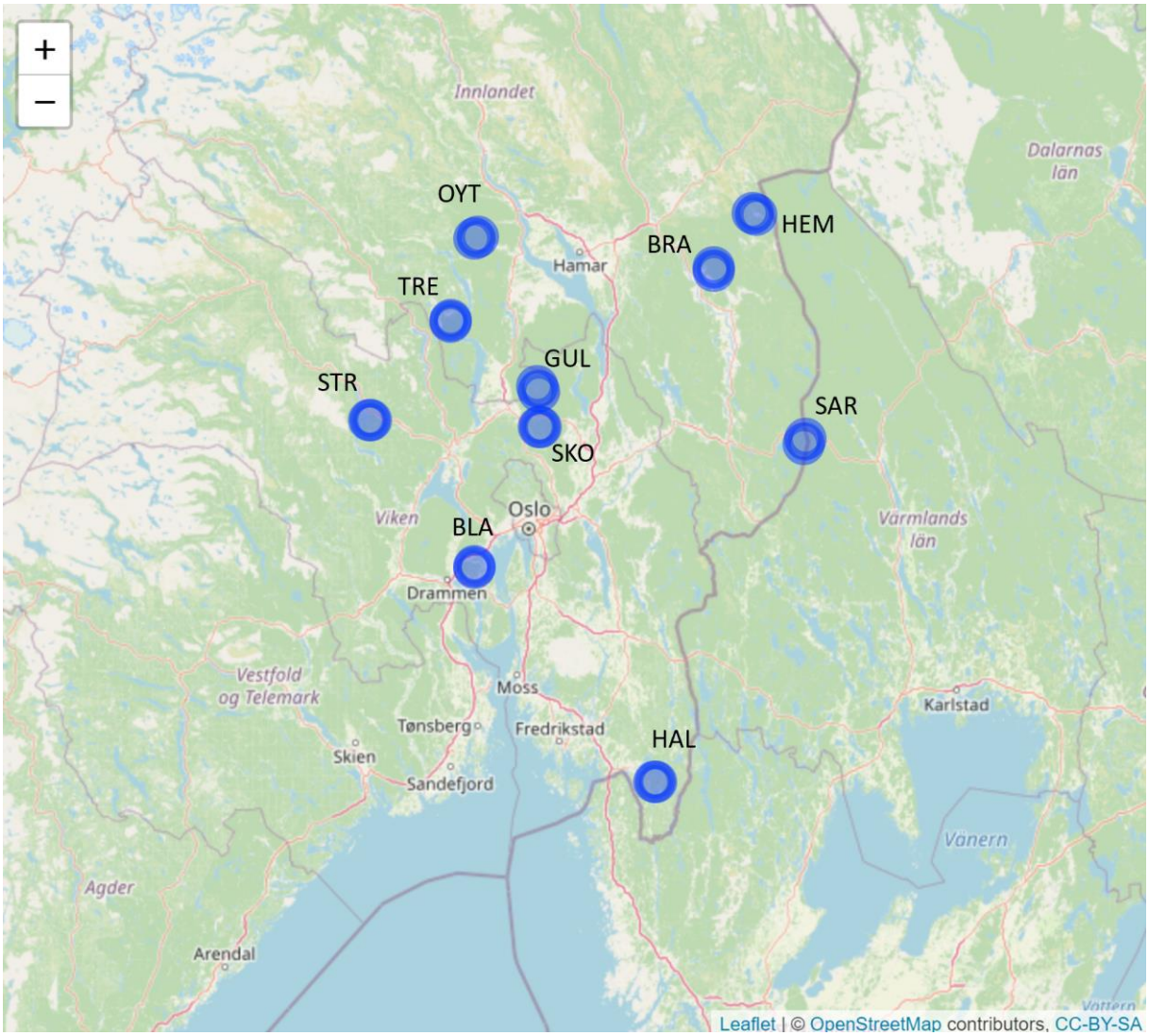

Figure 1. Map of South-eastern Norway showing the sites included in the study, created using the R-package "leaflet" (Cheng et al., 2022). Each dot represents one site with two forests, totalling up to 20 forests.

2.2. Study design

For the purpose of this thesis, I will be using the terms site, forest stand, transect and plot to describe the study design. "Site" refers to the forest pairs, for example Halden, with both a previously clear-cut (CC) and a near natural forest (NN). Forest stand refers to entire structures of forests, defined by natural forest edges, bounded by a lack or change of tree species. Each site then has two forest stands, one classified as near natural and the other as previously clear-cut. Each stand contains a 133.33x15 metre transect where dead wood was registered, and a 15x15 metre plot in which detailed soil measurements are carried out (Figure 2). In my study, I also counted number of *F. pinicola* fruit bodies in a 10-metre radius around each trap (Figure 3).

Most of the field work for this thesis was conducted around the plot, in the middle of the transect. We installed four IBL-2 window flight interception traps consisting of a clear pane with a "roof" to divert rainwater, and a bottle on the bottom to collect the sample (Figure 4) (Burner et al., 2022). The bottles contained a mixture of 70% propylene glycol and 30% water, and were placed just outside of the plot; one in the North, one in the East, one in the South, and one in the West, 10-15 metres apart. The traps were attached to a tree in each end and hung about 1.5 metres above the ground. A log decomposition experiment was carried out in close proximity to the traps (Figure 2).

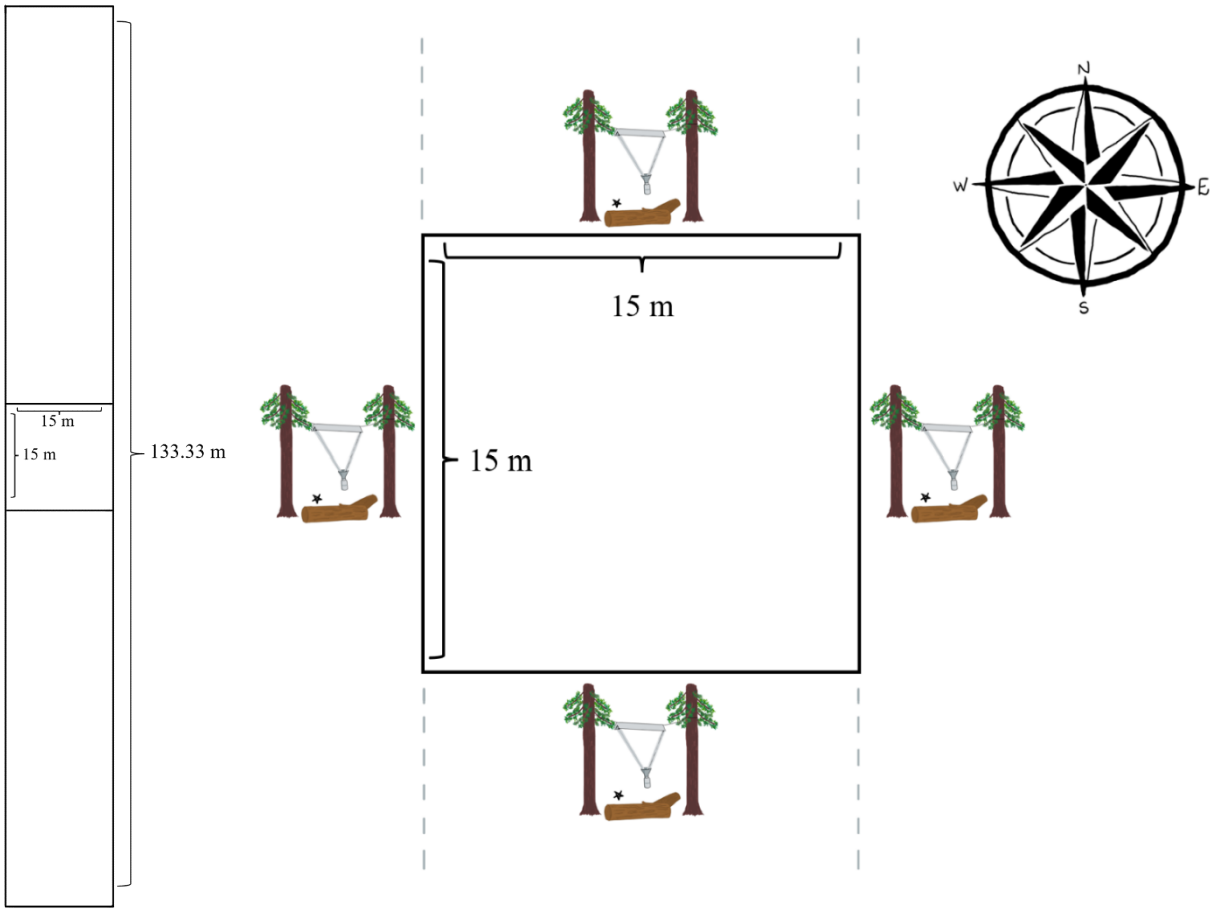

Figure 2. The study design. To the left, the transect of 133.33x15 metres. To the right, a closer look at the 15x15 metres plot, with the window traps placed on each side. The log decomposition experiment (marked with a black star) is also illustrated.

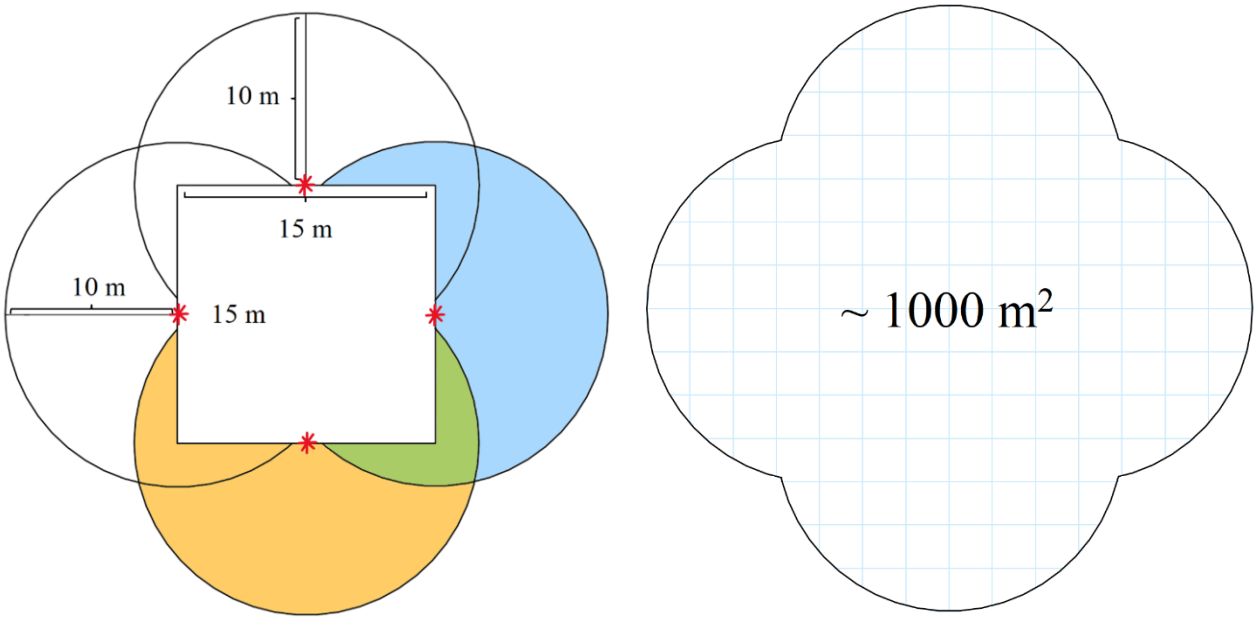

Figure 3. The area surrounding the 15x15 metre plot. The red stars on the left part represent the window traps, with the area in which *F. pinicola* fruit bodies were counted surrounding each trap.

Figure 4. An IBL-2 window trap produced by CHEMIPAN (Warsaw, Poland).

2.3. Study species

The main species in this thesis are *Fomitopsis pinicola* and *Gyrophaena boleti*.

F. pinicola is a polypore growing on dead or weakened wood (Stokland et al., 2012), found in all continents of the world except for Antarctica, and is common in both managed and natural forests (Hågvar & Økland, 1997; Staniec et al., 2016). It grows on both coniferous and deciduous trees, in Norway it is most commonly found on spruce (*Picea abies*) (Hågvar, 1999; Økland & Hågvar, 1994). Fungi, followed by bacteria and insects, are the most important decomposers in forests (Weslien et al., 2011), with *F. pinicola* being one of the most important decomposers of wood in boreal forests (Gramss, 2020).

Fungi such as *F. pinicola* play important roles for forest insects by providing food and living habitat for other species, and they play an important role in the biodiversity maintenance in fungicolous insect communities (Lipkow & Betz, 2005; Staniec et al., 2016). Many insect species are found to inhabit or visit the fruit bodies of *F. pinicola*, including red listed beetle species (Thunes et al., 2000). For the family of Staphylinidae, the relationship with fungi has played an important part in the evolution of the beetles, especially when it comes to morphology (Lipkow & Betz, 2005). A majority of the subfamilies are found in or on fungi, and they are among the first to arrive on fresh fruit bodies (Lipkow & Betz, 2005; Staniec et al., 2016).

The staphylinid *G. boleti* is a specialist living on the fruit bodies of *F. pinicola*, and depend on the hymenium both as larvae and adult. The beetle is described as obligatory saproxylic and exclusively mycophagous (Hågvar, 2018; Staniec et al., 2016), feeding on the spores and the hymenium of the fungi (Staniec et al., 2016). Because of this, *G. boleti* has a body shape well fitted for the narrow tubes of the hymenium, with shortened structures on the head and thorax, and well-adjusted setae and length of the urogomphi. *G. boleti* is a relatively small beetle, from 0.9 to 1.3 mm (Staniec et al., 2016). This makes the larvae small enough to enter the pores of *F. pinicola*, but the adult bodies are too wide. The adults are still able to enter with their head, making it possible for them to feed on the pore layer (Hågvar, 2018).

The adult individuals of *G. boleti* are active from May to September, with certain studies reporting the highest number of individuals in May (Staniec et al., 2016), while others have reported peaks of *G. boleti* on *F. pinicola* from April to June (Lunde, Ferkingstad, et al., 2023).

2.4. Data collection

Data was collected during spring and summer of 2022, from May 9th to July 11th.

After deploying the traps the first time, the traps were emptied, and the samples collected every two weeks, resulting in four sampling periods. The samples were collected in the same order of activation to reduce variance in sampling time. Content from all traps were stored in marked containers and kept in the freezer at -20 degrees Celsius until further processing. Due to limited time, we were not able to sort one of the sampling periods, resulting in the data for this thesis only to include three periods.

From May 9th to June 23rd, Ine-Susanne Hopland Methlie photographed the hymenium *F. pinicola* fruit bodies found in the forest stands of each site. They were taken using a standardized method including a backdrop, ruler, and a visible identification tag (Figure 5). In total, Hopland Methlie photographed 181 sporocarps of *F. pinicola*.

Figure 5. One of the photographs provided by Ine-Susanne Hopland Methlie of the hymenium of *F. pinicola*. We can see *G. boleti* as black dots on the underside of the hymenium.

In addition to the photographs, Hopland Methlie provided metadata including temperature, coordinates and altitude where the photos were taken, and the substrates where the fruit bodies were found.

The occurrence of *F. pinicola* was registered around the window traps from June 6th to June 27th. The number of dead trees with fruit bodies of *F. pinicola*, and the number of *F. pinicola* fruit bodies on each piece of dead wood was registered. Every fruit body within a radius of about 10 metres of each window trap was registered. Unfortunately, I did not have a

measuring tape available, and the measures of the area are therefore approximate. The estimates were made by stepping up the distance to the nearest trap. The radius of 10 metres was chosen to ensure that the entire area around the plot and traps were included without too much overlapping. Due to restrictions from walking inside the main 15x15 plot, only the fruit bodies seen from the edges of the plot are registered.

Data on deadwood was collected by several people in the EcoForest team. They registered all deadwood in the 133.33x15 metre transect with a minimum diameter of 5 cm (at breast height or at base), and a minimum length or height of 130 cm. For each piece of deadwood, they recorded the tree species, tree type, special type, diameter, length/height, decay class, bark cover, epiphyte cover and ground contact. Only diameter, length/height, decay class and whether it was snags, stumps or downed deadwood, were used to make calculations in this thesis. I included all dead wood, both snags, downed and standing deadwood, registered on both spruce and birch. The decay classes ranged from I to V, where decay class I was fresh dead wood, and decay class V was completely decomposed. In this thesis, the main focus is on deadwood in decay class I and II, i.e. the early stages of decomposition.

2.5. Data processing

Together with two other master students on the EcoForest project, Ragnhild Ranstorp Karlstad and Ingvild Skjelle Fimreite, Milda Norkute and Petr Kozel, we sorted the content from the window traps into two categories: “beetles” and “other arthropods”. The contents were then put in vials with 85% ethanol. A total of 240 samples were sorted, after leaving out one sampling period because of limited time. The beetles were then sent to expert Sindre Ligaard who determined the species.

The photographs received from Hopland Methlie were analysed in OneNote (Microsoft, 2023b); the number of *G. boleti* on each hymenium was counted using touch screen and a touch pen. In addition, the photographs were used to calculate the area of the hymenium. To do this, ImageJ 1.53 T (Rasband, 1997-2018) was used. The information about the number of individuals and the area of each hymenium was added to an Excel sheet (Microsoft, 2023a), where calculations of the number of *G. boleti* per square centimetre hymenium in the previously clear-cut and near natural forests were made.

To quantify the volume of deadwood, the volume of each piece of dead wood was calculated using formulas for the volume of a cone. We used two formulas for; 1) pieces where the top diameter was of a significant size (downed dead wood), and 2) where the end of the tree piece came to a point, or we did not have data about the diameter at the top (snags and stumps) (Figure 6). The lengths of the pieces were registered in metres, and the diameters were registered in centimetres, with the final volume given in cubic metres (m^3). The calculations were made in Excel (Microsoft, 2023a).

1) $Volume = \frac{1}{3} * 3.14 * (h * 100) * \frac{\left(\frac{Dtop}{2}\right)^2 + \left(\frac{Dtop}{2} * \frac{Dbase}{2}\right) + \left(\frac{Dbase}{2}\right)^2}{1000\,000}$

2) $Volume = \frac{1}{3} * 3.14 * (h * 100) * \frac{\left(\frac{D}{2}\right)^2}{1000\,000}$

Figure 6. Formulas for calculating volume of deadwood. h = height/length, Dtop = diameter of the top of the piece of deadwood, Dbase = diameter of the base, and D = diameter registered for snags and stumps (Store norske leksikon, 2022).

Both the total volume of deadwood and the volume of deadwood in decay class I and II were measured. Fruit bodies of *F. pinicola* grow on deadwood in decay class I and II, so the measured volumes for those decay classes are combined into one group in this study.

I estimated the population density of *G. boleti* by taking the calculated density of *G. boleti* on *F. pinicola*, multiplying it with the separately estimated mean hymenium area of *F. pinicola* in near natural and previously clear-cut forests, and multiplying it the number of fruit bodies per 1000 m^2 in each forest, using the formula:

$$Population\ density = G.boleti_{density} * mean_{area} * nF.pinicola$$

Figure 7. Formula for estimating the population density of *G. boleti* in each forest. $G.boleti_{density}$ is the calculated mean number of individuals of *G. boleti* per cm^2 hymenium of *F. pinicola*. $mean_{area}$ is the mean area of the hymenium of *F. pinicola* calculated for each forest type. nF.pinicola is the number of *F. pinicola* registered in the 1000 m^2 area of each forest.

2.6. Statistical analysis

All data was further analysed using RStudio (RStudio team, 2022). The raw data was loaded into RStudio using the "read_excel" function from the R-package "readxl" (Wickham & Bryan, 2023). All plots were generated using the "ggplot" function from the R-package "ggplot2" (Wickham, 2016), and all tables were made using the function "sjPlot" from the R-package "sjplot" (Lüdecke, 2022).

To investigate the differences between the two forest types, I used a t-test in RStudio. A threshold of $\alpha = 0.05$ for statistical significance was used throughout the thesis.

When analysing *G. boleti* caught in window traps, I used ANOVA analysis to investigate the relationship between the number of *G. boleti* caught and the sampling period. The t-test in RStudio was used to investigate the relationship between the number of individuals of *G. boleti* caught in the flight interception traps and the forest type. When looking into which variables influence the number of *G. boleti* caught in traps, I used significant variables after performing t-test and ANOVA analysis (Appendix; Table A1) to select which predictor variables to include in the model. The correlation coefficients between several of the variables were investigated by calculating the Pearson's product-moment correlation coefficients using the function "cor.test" in RStudio (Appendix; Table A2). A threshold of $|r| = 0.7$ was used in order to avoid including strongly correlated variables in the same model (Dormann et al., 2013).

To determine the factors influencing the number of individuals of *G. boleti* caught in the flight interception traps, I first investigated the data for over- and underdispersion by using the function "dispersiontest" from the R-package "AER" (Kleiber & Zeileis, 2008). I then used the function "glmer.nb" from the package "lme4" (Bates et al., 2015) to build models suited for overdispersed data; negative binomial generalized linear models (GLM). Site was included as a random effect in all models to account for among-sites variation. To find the best fitted model, I investigated the summary and the Akaike Information Criterion (AIC). The built in function AIC() in RStudio calculates the AIC using the formula:

$$AIC = -2\,log-likelihood + kn_{par}$$

Figure 8. Formula for calculating the AIC of a model. k = 2 for the usual AIC, and n_{par} represents the number of parameters in the fitted model (DataCamp, 2023).

To investigate whether there was a significant difference in area of the hymenium of *F. pinicola* between previously clear-cut and near natural forests, I used the t-test in RStudio.

The same test was used to investigate if there was a significant difference between the number of individuals of *G. boleti* counted per cm^2 hymenium in the previously clear-cut and near natural forests. The Pearson's product-moment correlation coefficient for the number of *G. boleti* counted related to the area of the hymenium was calculated, and the relationship was visualized with a scatter plot and regression line. Thresholds chosen considered $|r| \leq 0.35$ as weak correlations, $0.36 \leq |r| \leq 0.67$ as moderate correlations, and $|r| \geq 0.68$ as strong correlations (Taylor, 1990). Two outliers with high numbers of *G. boleti* on one hymenium were removed before analysing.

ANOVA analysis was used to investigate the significance of variables explaining the number of *G. boleti* counted on the hymenium of *F. pinicola*. I then fitted several linear mixed models (LMMs), using the "lmer" function from the R-package "lme4" (Bates et al., 2015) with density of *G. boleti* on the hymenium as the log-transformed response variable. Site was again included as a random effect in all models to account for among-sites variation. Using the R-package "lmerTest", the p-values were calculated by Satterthwaite's method for calculating p-values (Kuznetsova et al., 2017). To choose which model had the best fit, I once more investigated the summary and the AIC of the models.

Using the built in t-test in RStudio, I investigated the difference between the estimated populations in the previously clear-cut and near natural forests. Furthermore, I used a Poisson regression model (GLM) to investigate the relationship between the number of individuals of *G. boleti* caught in traps and the estimated population density in each forest.

3. Results

3.1. *Fomitopsis pinicola* and its dead wood habitat in near natural versus previously clear-cut forests

The near natural forests had a significantly higher volume of deadwood in decay class I and II (t-test, t = -5.8576, df = 123,17 $p < 0.001$) (Figure 9), in addition to a higher number of *F. pinicola* fruit bodies surrounding the traps (t-test, t = -5.8454, df= 185.88, $p < 0.001$) (Figure 10).

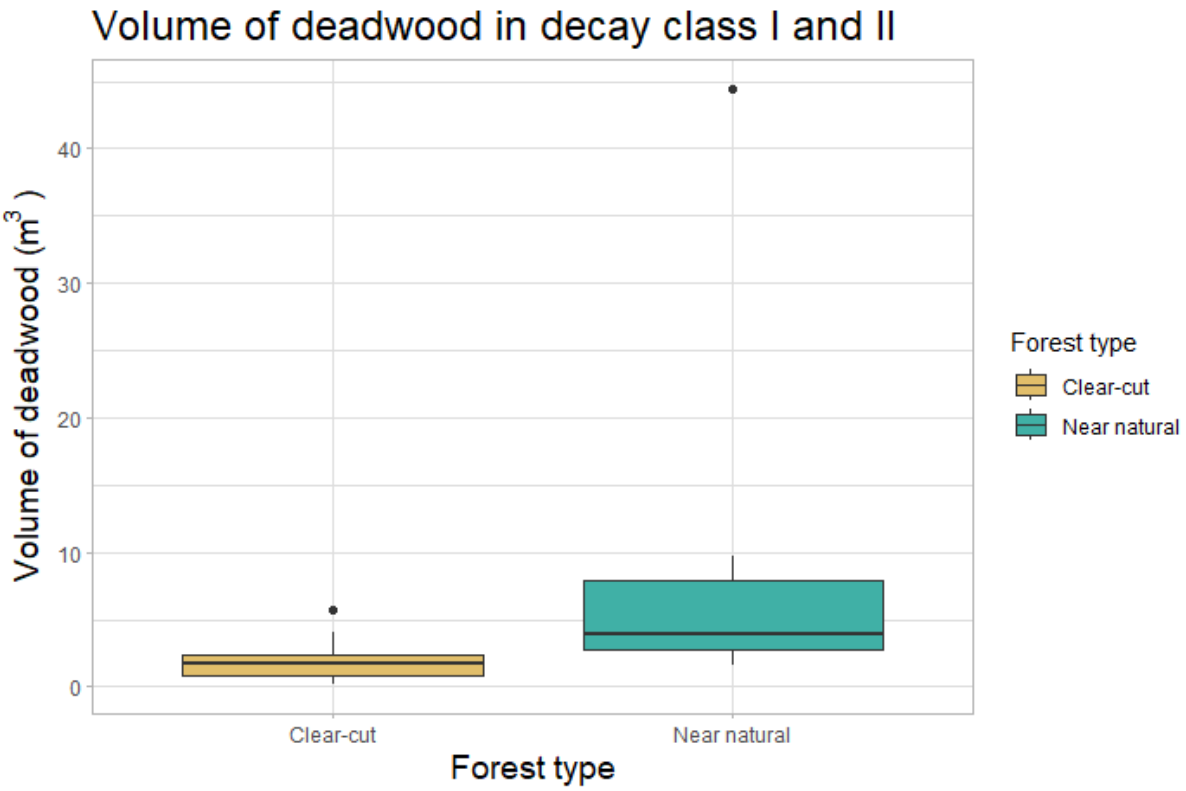

Figure 9. Boxplot showing the volume of deadwood in decay class I and II in previously clear-cut and near natural forests in South-eastern Norway. The median, the 70th and 90th percentile are illustrated in the boxplot.

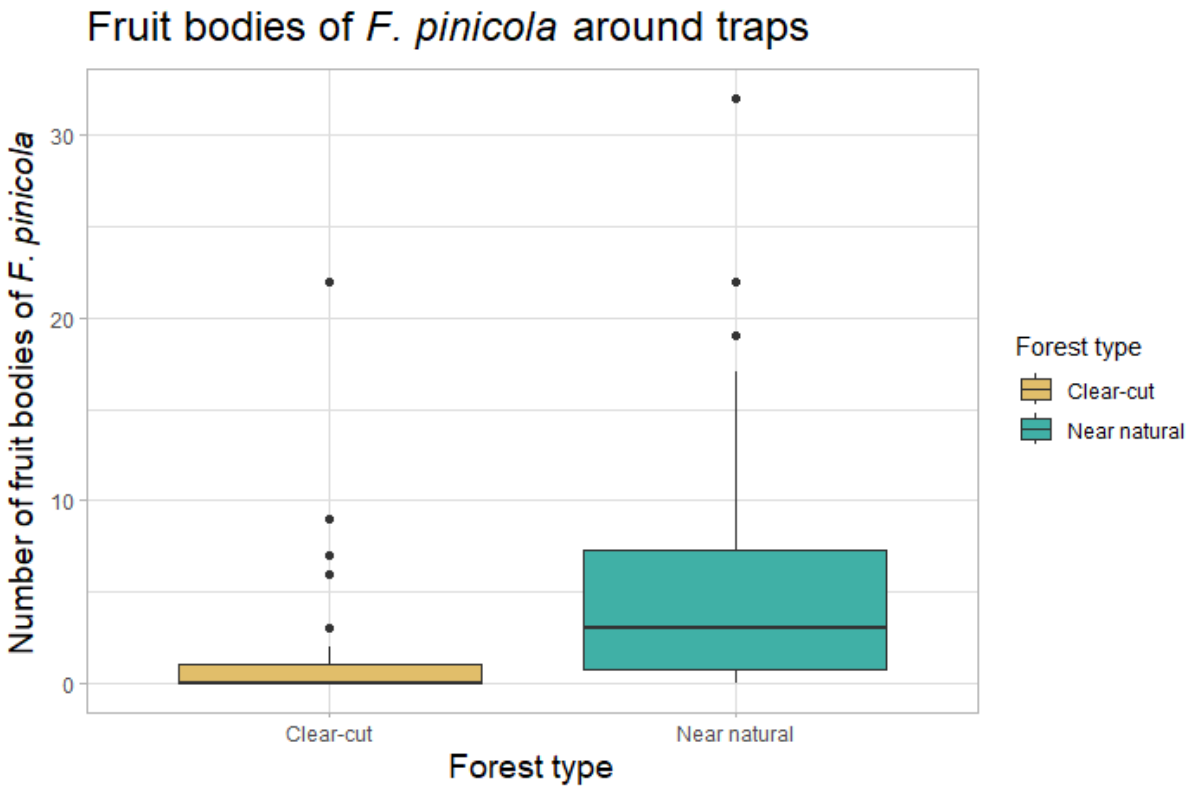

Figure 10. Boxplot showing the number of *F. pinicola* fruit bodies around the traps in previously clear-cut and near natural forests in South-eastern Norway. The median, the 70th and 90th percentile are illustrated in the boxplot.

3.2. *G. boleti* in near natural and previously clear-cut forests estimated by window traps

In total, 138 individuals of *G. boleti* were caught in the flight interception traps over the weeks included where the traps were active (Figure 11). Most of the individuals were caught in the first two sampling periods, but the difference between the three periods was only close to significant (ANOVA, Df = 1, Sum Sq = 8.7, F-value = 3.476, p = 0.064).

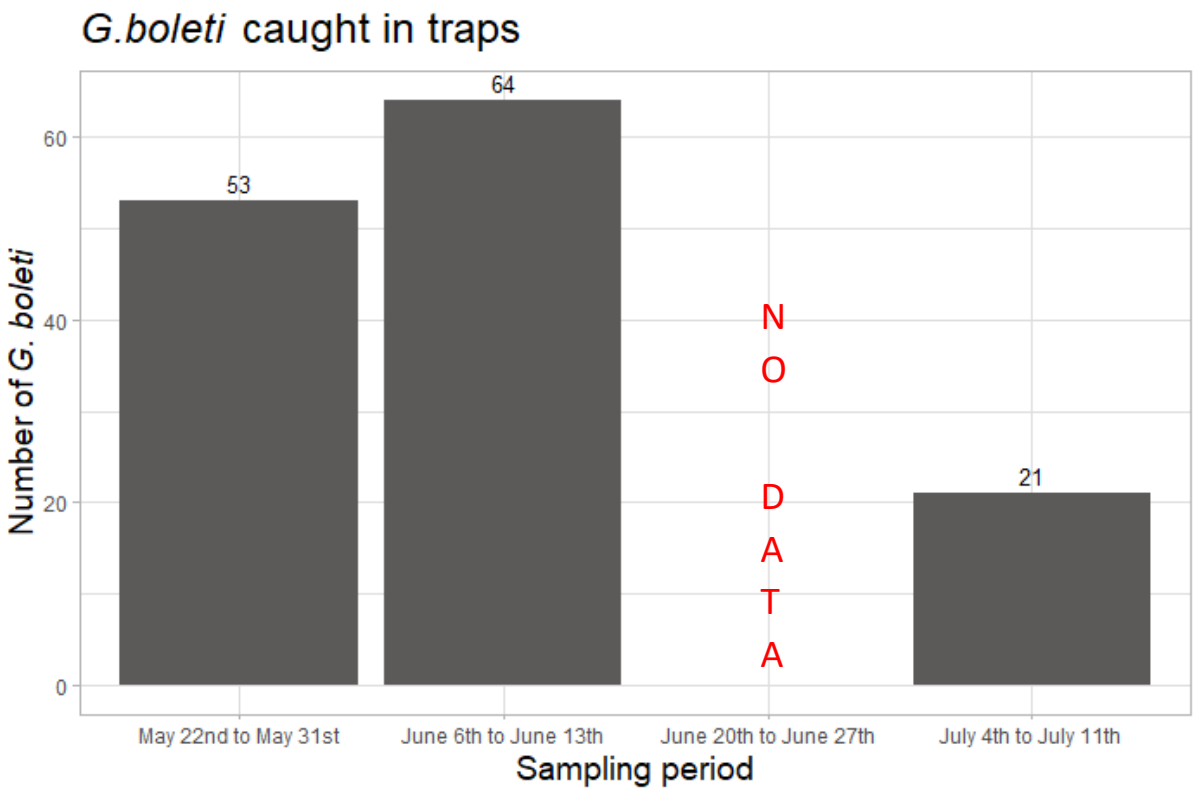

Figure 11. Number of individuals of *G. boleti* caught in flight intercept traps in each sampling period. In total, 138 individuals of *G. boleti* were caught and registered. Samples from June 20th to June 27th (sampling period 3) was not included in this study.

There was a significant difference between the number of *G. boleti* trapped in the flight intercept traps in near natural and previously clear-cut forests (t-test, t = -3.055, df = 140.93, p = 0.003) (Figure 12).

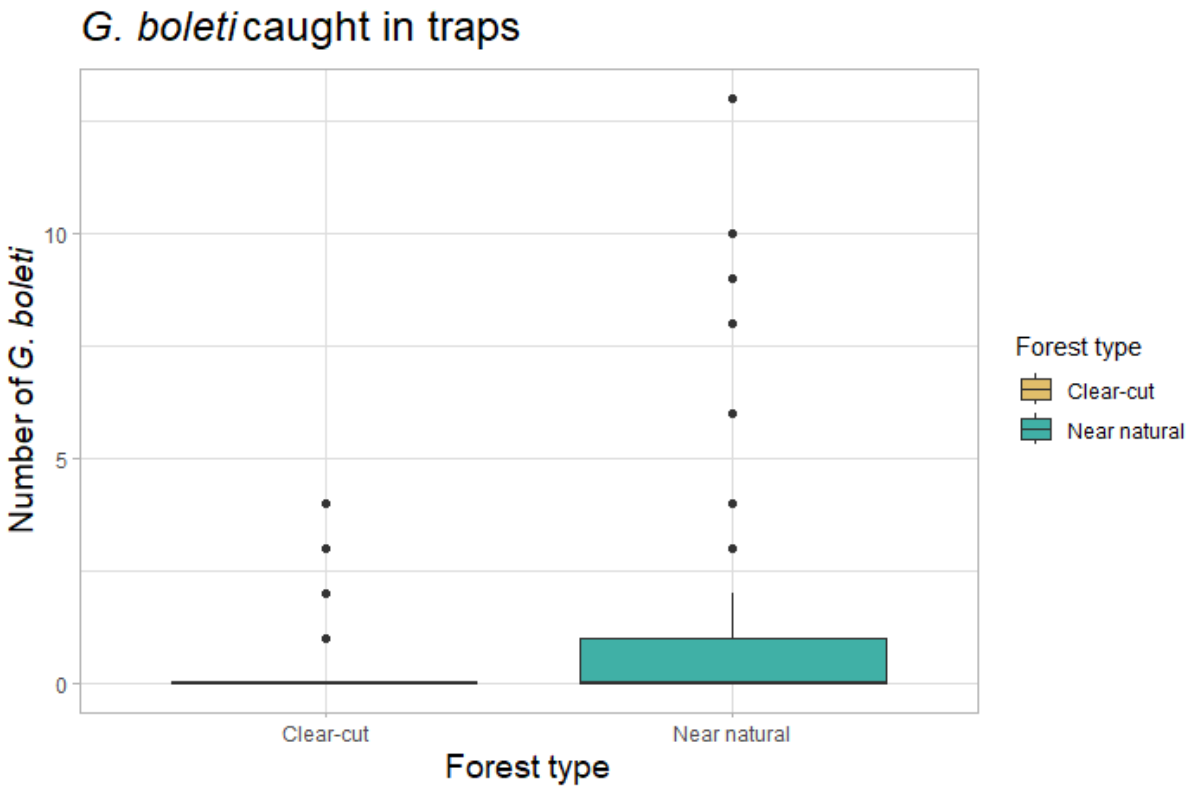

Figure 12. Boxplot showing the number of *G. boleti* caught in traps in previously clear-cut and near natural forests in South-eastern Norway. The median, the 70th and 90th percentile are illustrated in the boxplot.

Number of trees with *F. pinicola*, number of fruit bodies of *F. pinicola*, total volume deadwood, volume of deadwood in decay class I and II, and site were also shown as significant and possible predictors for the number of *G. boleti* caught in traps (Appendix; Table A1). Trees with *F. pinicola* and number of *F. pinicola* registered, as well as total volume deadwood and volume of deadwood in decay class I and II, were strongly correlated (Appendix; Table A2). Thus, of them, only number of fruit bodies of *F. pinicola* and volume of deadwood in decay class I and II were included in the models as they were considered most ecologically relevant. After fitting several GLMs, the model with the lowest AIC only had forest type, number of fruit bodies of *F. pinicola* and volume of deadwood as predictor variables, but deadwood volume was the only significant predictor for *G. boleti* (Table 1). The number of *G. boleti* increased with increased volume of deadwood (Table 1, Figure 13).

Table 1. Output from negative binomial generalized linear model (GLM) with number of *G. boleti* caught in flight interception traps as response variable, explained by the predictors given. Site was included as a random variable to account for among-sites variation. AIC = 399.933.

Predictors	*Estimate*	*SE*	*Z*	*Pr(>|z|)*
(Intercept)	-1.778	0.303	-5.870	**< 0.001**
Forest type near natural	0.145	0.306	0.473	0.636
Number of *F. pinicola*	0.033	0.020	1.652	0.0985
Volume deadwood decay class I or II (m^3)	0.066	0.016	3.995	**< 0.001**

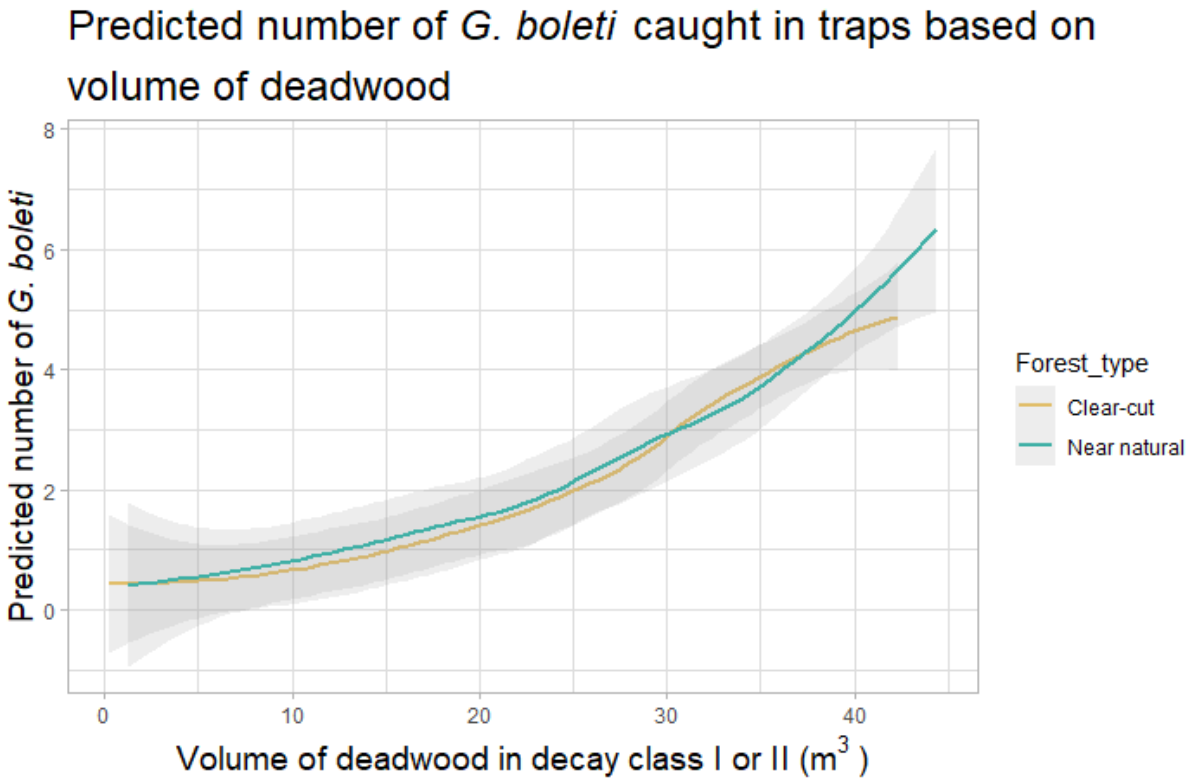

Figure 13. Predicted regression lines plotted for the number of *G. boleti* caught in traps based on the volume of deadwood in decay class I and II in the transect of the two forest types. 95% confidence intervals are plotted in light grey.

3.3. What determines the density of *G. boleti* on the hymenium layer of *F. pinicola*?

In total, the area of 180 hymenium layers of *F. pinicola* were measured and the number of *G. boleti* counted. The sizes of the hymenia were smaller in previously clear-cut than near natural forests (t-test, t = -2.686, df = 166.49, p = 0.008) (Table 2, Figure 14).

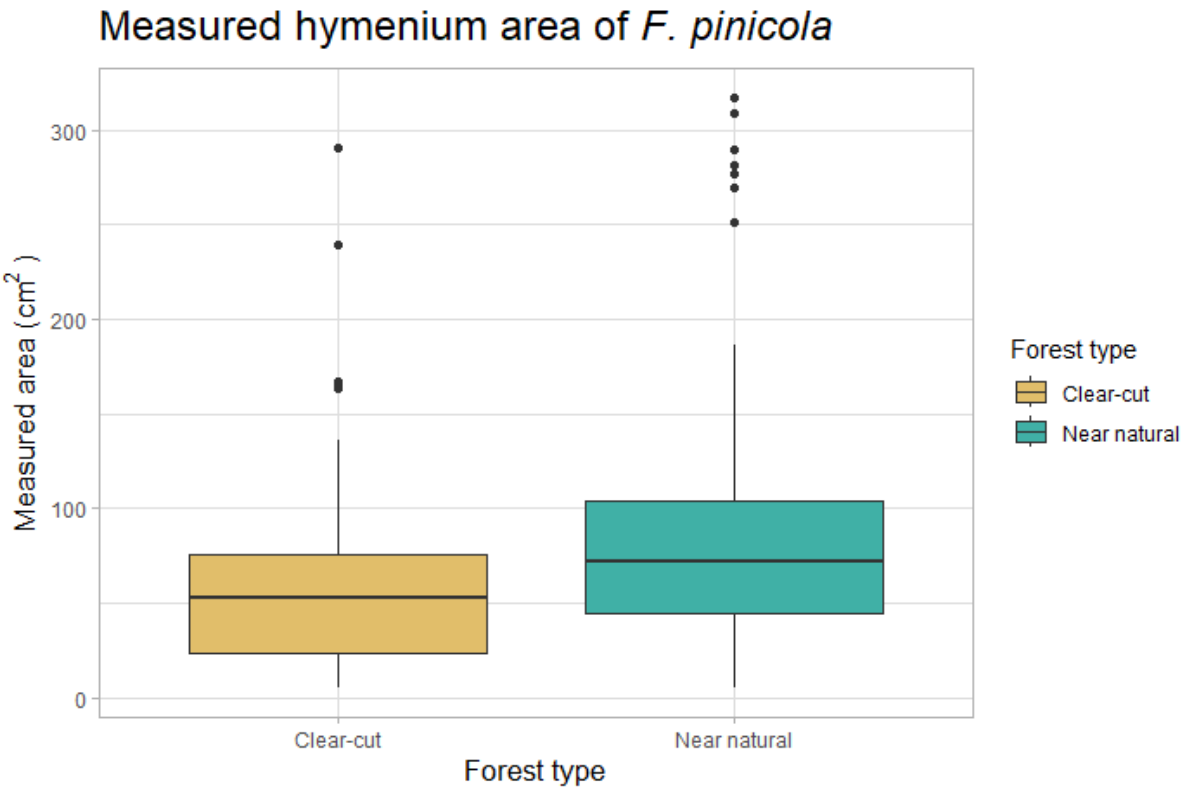

Figure 14. Box plot showing hymenium area of *F. pinicola* fruit bodies in previously clear-cut and near natural forests in South-eastern Norway. The median, the 70th and 90th percentile are illustrated.

There was a moderate positive correlation between the number of *G. boleti* counted on the hymenium and the area of the hymenium (Pearson's product-moment correlation, t = 5.218, df = 165, r = 0.383, p < 0.001) (Figure 15). This was calculated after removing two outliers of fruit bodies with relatively high numbers of *G. boleti*; one from Halden CC with a number of 946 individuals, and the other from Tretjerna NN with 722 individuals.

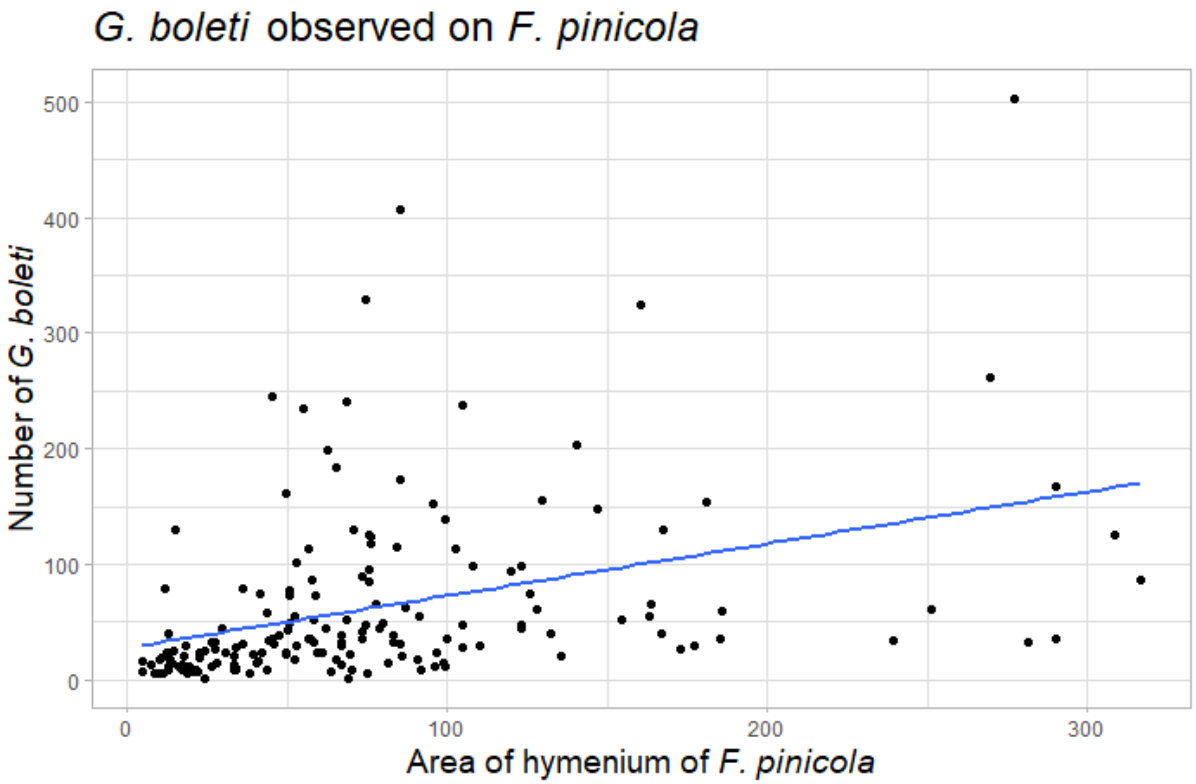

Figure 15. Scatter plot with *G. boleti* counted plotted against hymenium area of *F. pinicola* fruit bodies.

Density of *G. boleti* on the hymenium did not differ between the previously clear-cut and the near natural forests (t-test, t = -0.99812, df = 166.93, p = 0.320) (Table 2, Figure 16).

Table 2. Mean calculations of hymenium layer area on *F. pinicola* and number of *G. boleti* per area hymenium for previously clear-cut and near natural forests in South-eastern Norway.

Forest type	*Hymenium area of F. pinicola (cm²)*	*G. boleti/cm² hymenium of F. pinicola*
Clear-cut	62.68	1.00
Near natural	88.21	1.23
Total	77.48	1.13

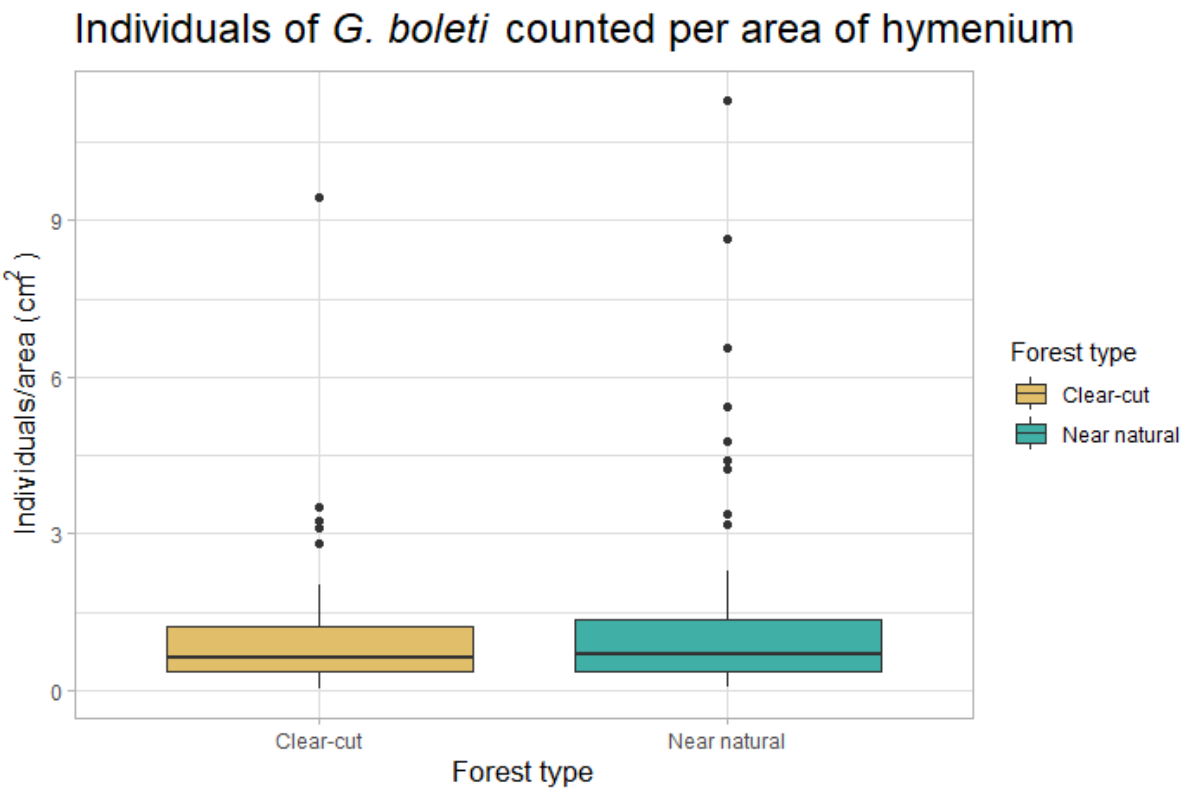

Figure 16. Boxplot showing the density of *G. boleti* on the hymenium of *F. pinicola* in previously clear-cut and near natural forests in South-eastern of Norway. The median, the 70th and 90th percentile are illustrated in the boxplot.

When analysing through single-variable models, no predictor variable had a significant effect on the density of *G. boleti* on the hymenium (Appendix; Table A3). The variables were still included when attempting to fit a model to see if the combination of them would result in a different outcome. After fitting a linear mixed model with the individuals per cm^2 as the response variables, I found that the model with the lowest AIC only had forest type as a predictive variable. The effect was however not significant (p = 0.356) (Table 2).

Table 3. Output from linear mixed-effect model (LMM) with density of *G. boleti* on hymenium as the log-transformed response variable, and forest type and site as predictive variables. Site was included as a random variable to account for among-sites variation. AIC = 501.697.

	Estimate	*SE*	*Df*	*t-value*	*Pr(>|t|)*
(Intercept)	-0.500	0.134	30.490	-3.707	**< 0.001**
Forest type Near natural	0.149	0.161	166.283	0.926	0.356

3.4. Population density estimates of *G. boleti* in forests

All populations densities were estimated (Appendix; Table A4, Figure 17) for approximately 1000 m^2 (Figure 3). For four of the areas sampled (Halden clear-cut, Halden near natural, Hemberget clear-cut and Øytjern clear-cut), no fruit bodies of *F. pinicola* were found within this area.

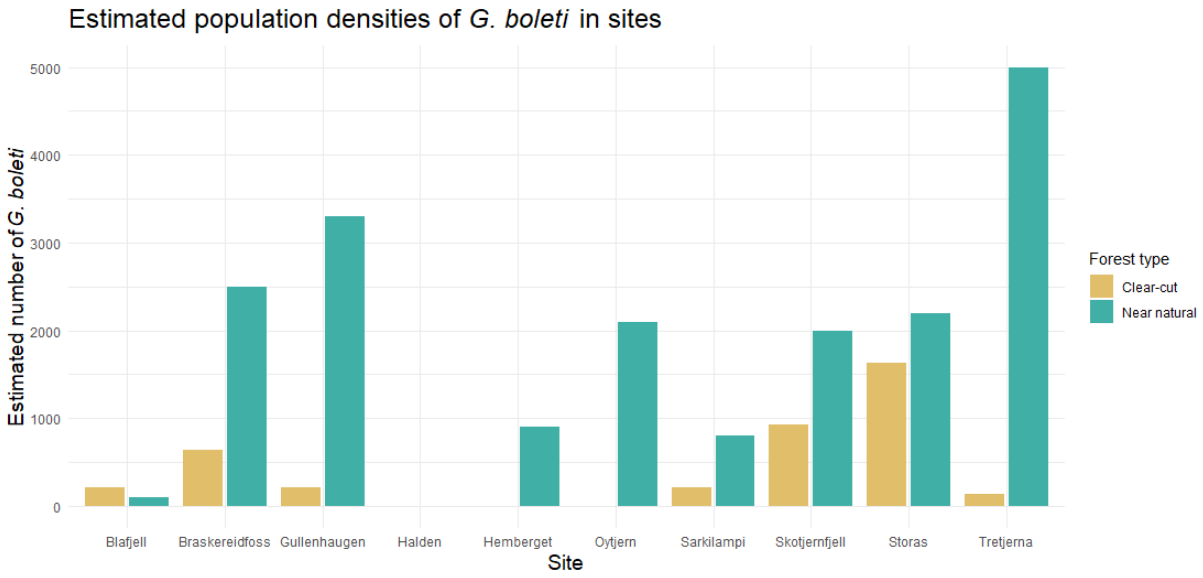

Figure 17. Barplot showing the estimated population densities per 1000 m^2 in each forest. This is based on the mean area of the hymenium layer of *F. pinicola* measured for the two forest types (62.28 cm^2 for CC and 88.21 cm^2 for NN), and the estimated number of individuals per square centimetre of hymenium (1.13 individuals per cm^2). No fruit bodies were found within the area in Halden CC, Halden NN, Hemberget CC and Øytjern CC).

There was a significant difference between the estimated population densities in the previously clear-cut and near natural forests (t-test, t = -2.912, df = 11.106, p = 0.014) (Figure 18) with a median of 213 beetles of *G. boleti* in previously clear-cut forests versus 2048 in near natural forests. Thus, the estimated population densities were on average 9.6 times higher in the near natural than the previously clear-cut forests.

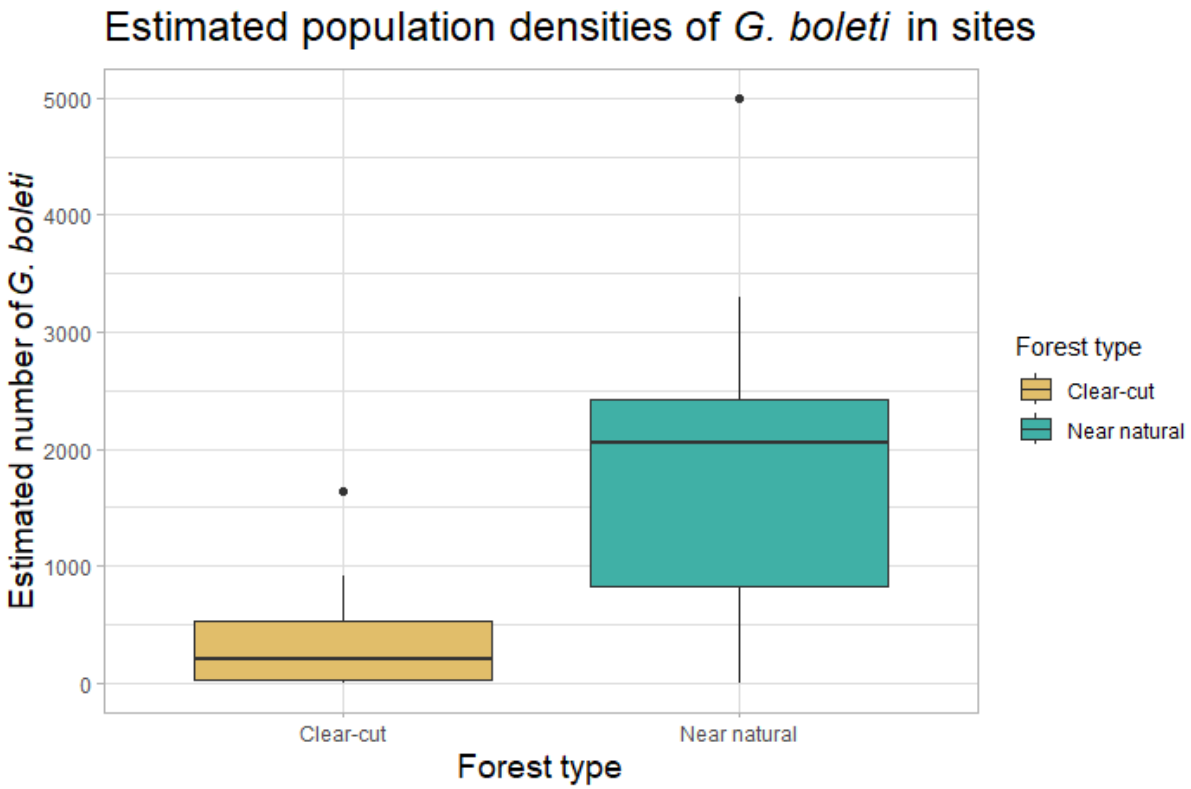

Figure 18. Boxplot showing the estimated populations densities per 1000 m^2 of *G. boleti* in previously clear-cut and near natural forests in South-eastern Norway. The median, the 70th and 90th percentile are illustrated.

Linking population densities to the number of G. boleti caught in traps

The Poisson regression model showed a significantly positive relationship between the estimated population densities and the number of *G. boleti* caught in traps (Table 3). A positive relationship between the predicted number of *G. boleti* trapped based on the population estimates was visualized through a regression line (Figure 19). After removing the outlier Tretjerna NN from the dataset, the model still showed a positive relationship (Appendix; Table A5, Figure A1).

Table 4. Poisson regression model (GLM) with number of *G. boleti* caught in the flight interception traps as response variable predicted by the estimated population density in each forest. AIC = 123.810.

Predictors	*Estimate*	*SE*	*Z*	*Pr(>|z|)*
(Intercept)	0.583	0.166	3.517	**< 0.001**
Population size	0.0007	0.00005	14.443	**< 0.001**

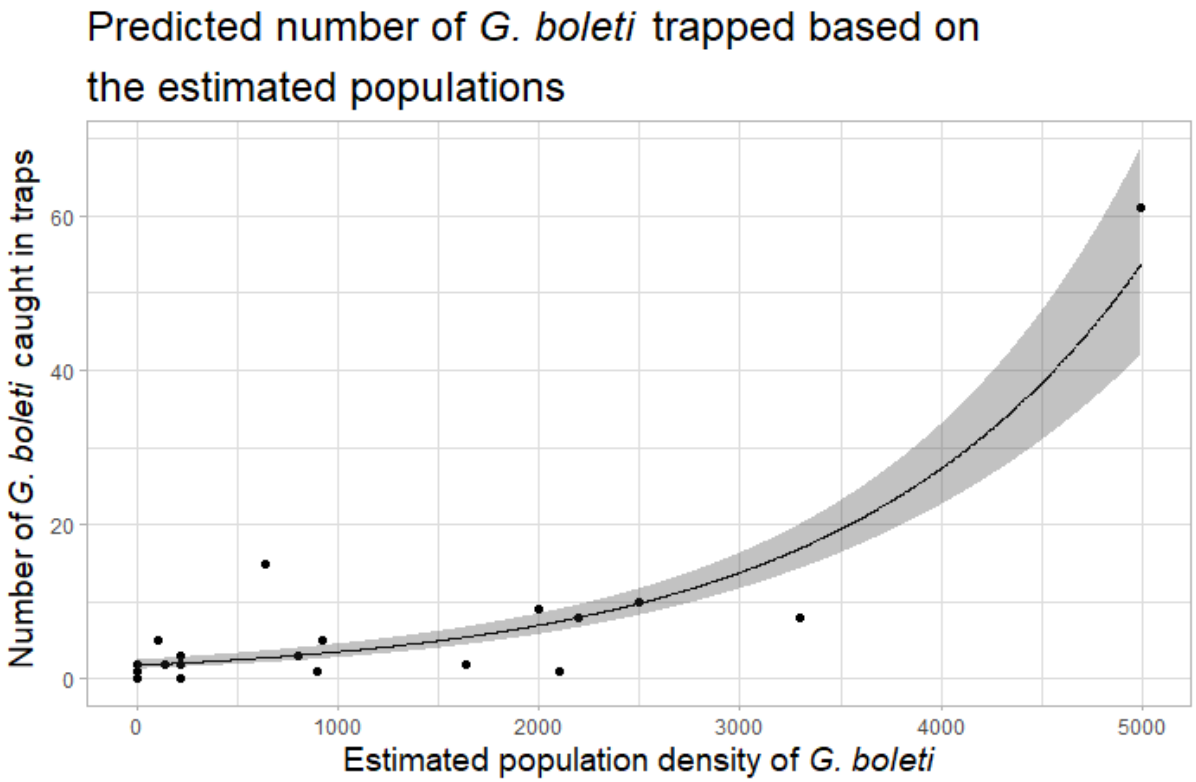

Figure 19. Regression line for the number of *G. boleti* caught in traps explained by the estimated population density in an area of 1000 m^2 in each forest. A 95% confidence interval is plotted in light grey. Points are estimated values based on observations.

4. Discussion

In the present study, I found that the number of *G. boleti* trapped was higher in the near natural than the previously clear-cut forests and that this pattern was most strongly driven by the amount of suitable deadwood for the host fungi *F. pinicola*. Number of *G. boleti* increased with area of hymenium, but the density of *G. boleti* on *F. pinicola* did not differ between near natural and previously clear-cut forests. The estimated population densities of *G. boleti* were 9.6 times higher in near natural forests than previously clear-cut, and the higher the population density, the higher the number of *G. boleti* was caught in the window trap.

Higher dead wood volume in near natural forests explain the higher catches of *G. boleti* relative to previously clear-cut forests

When investigating why a higher number of *G. boleti* was caught in near natural forest compared to previously clear-cut, it was revealed that it is not the forest type itself that is the reason behind the difference, but the difference in volume of deadwood in decay class I and II. A difference in the volume of deadwood was expected between the two forest types, although previous studies have shown that the difference is normally largest in regards to dead wood in later decay stages (Lish, 2022; Storaunet et al., 2005). Previously clear-cut forests could have been expected to having caught up or even exceeded near natural forests in volume of deadwood in early decay stages, a result found in certain studies (Storaunet et al., 2005). However, this was not the case in this study. One reason for these contrasting results could be differences in methodology when measuring the volume of deadwood, and in which pieces of deadwood were included regarding species and size.

Joelsson et al. (2018) found early-stage deadwood to be an important influence of early successional species. This is in line with the results from this study; being that *F. pinicola* grows on wood in early decay stages; the volume of dead wood in decay class I and II explains the observed significant difference in the occurrence of *F. pinicola* between the forest types. When including both volume of deadwood in decay class I and II, and the number of fruit bodies surrounding the window traps in the same model, number of *F. pinicola* was not significant. I assume this was because the volume of deadwood is more descriptive of the forest. In addition, there is a possibility that there were fruit bodies of *F. pinicola* I did not manage to register.

The number of *G. boleti* caught in traps is linked to fruit bodies of *F. pinicola*

G. boleti is most active during the time period covered by the first two samplings (Økland & Hågvar, 1994), which is reflected in the number of *G. boleti* caught. However, I would have expected the sampling period variable to be significant. A clear decline in *G. boleti* caught between sampling period 2 and 4 is observed, however I expect this difference would have been significant if period 3 had been included and more datapoints added.

Analysing as an isolated variable showed number of fruit bodies of *F. pinicola* as a significant predictor for the number of *G. boleti* caught in traps. Økland & Hågvar (1997) call this the "baiting effect"; the number of *G. boleti* captured depends on the density of *F. pinicola* fruit bodies close by. This could open up to questions about the flying habits of *G. boleti*. Based on results in this thesis, I would expect a higher number of *G. boleti* to be caught in traps with 10 surrounding fruit bodies of *F. pinicola* than traps surrounded by 3 fruit bodies, possibly indicating more flying activity and migration between proximal fruit bodies in areas with higher numbers of fruit bodies. This is also interesting to consider when investigating the dispersal range of *G. boleti*. The link between the fruit bodies in the 10-metre radius around traps and *G. boleti* caught in traps could suggest that *G. boleti* prefers to fly within close proximity of their current habitat when there is more habitat available. Interestingly, one and two individuals of *G. boleti* were caught in traps in Øytjern CC and Hemberget CC, respectively, where no fruit bodies of *F. pinicola* were registered in the 10-metre radius around the traps. This could indicate that they are capable of flying longer distances if required. The first saproxylic beetles to arrive on fresh dead wood have been shown to have longer dispersal ranges than other species, having registered ranges up to several kilometres (Komonen & Müller, 2018). In order to ensure survival at a landscape level, populations of saproxylic organisms have to be able to compensate local extinctions on logs and within forests stands by being able to repeatedly colonize (Jonsson et al., 2005). Being that fruit bodies of *F. pinicola* have been reported to live up to 18 years (Hågvar, 2008), I would suspect the need for recolonizing being less for *G. boleti* than for other saproxylic insects who depend on more volatile habitats. Studying dispersal and ranges of insects is challenging to do, and it is difficult to make assumptions without input from several studies and methods (Ranius, 2006). One weakness with this estimate is that limiting the forest area covered by captures through window traps is challenging (Sverdrup-Thygeson & Birkemoe, 2009), being reflected in the observations from Øytjern CC and Hemberget CC. Ideally, the number of fruit bodies variable could also be strengthened, by more accurate measures and by expanding the

area investigated. It would also be interesting to divide the occurrences of *F. pinicola* into distance classes by the distance from the closest window trap, to get a more nuanced image of their preferred flying distance.

The density of *G. boleti* on *F. pinicola* is determined by the hymenium layer

Based on Pimentel (1961), I would have expected the density of *G. boleti* on the hymenium of *F. pinicola* to be lower in near natural forests, due to more available habitat. This is also backed by Hågvar and Økland (1997) who reported higher density of individuals in areas with fewer fruit bodies. However, this was not the case in this study, as there was no difference in the density (individuals per cm^2 of hymenium) of *G. boleti* on *F. pinicola* in the previously clear-cut and the near natural forests even though a significantly higher amount of *F. pinicola* was registered in the near natural forests. Contrary to my predictions none of the variables showed as significant in the model explaining the density of *G. boleti* on *F. pinicola*, indicating that the capacity of *G. boleti* on the hymenium is not restricted by forest type, number of surrounding *F. pinicola*, or the volume of dead wood. Hågvar (2018) and Økland and Hågvar (1994) brought up water content/moisture of the hymenium as the most important factor limiting *G. boleti* on *F. pinicola*. Unfortunately, this was not a variable investigated in this study. Nevertheless, this can support the idea that hymenium-area related factors, such as water content, could be of importance for the density of *G. boleti* on the hymenium of *F. pinicola*. The fruit bodies were larger in near natural forests than previously clear-cut forests, and the number of individuals found on the hymenium increased with increasing area of the hymenium layer. This will lead to a higher number of *G. boleti* per fruit body in near natural forests, even if the density of *G. boleti* on the hymenium does not differ.

I would have expected the sampling week to be of significance and included as significant in the model explaining the density of *G. boleti*, because they were registered over the course of seven weeks. One explanation for the insignificance could be because the different sites have different times for peaks of activity. The colonization of the hymenium has been found to be well synchronized with sporulation of *F. pinicola* in May when the last snow has melted (Hågvar, 2018). The sporulation is then thought to be related to climatic conditions such as humidity, soil moisture, temperature and light (Hågvar, 2018; Haard & Kramer, 1970). Even though all sites in this study are located in South-eastern Norway, the conditions between the sites will naturally vary because of their differences in latitude and altitude, possibly making sporulation occur at different times. This could also be backed by the difference in reported

peaks for *G. boleti* on *F. pinicola*, e.g. by Staniec et al. (2016) and Lunde, Ferkingstad, et al. (2023).

Økland and Hågvar (1994) estimated that up to 160 individuals of *G. boleti* could live on the hymenium of *F. pinicola*. However, a more recent study by Hågvar found up to 400 individuals on one hymenium, while the highest number of *G. boleti* in this study was 946. These contrasting numbers could be caused by different sizes of *F. pinicola* being studied, which may vary a lot between forests, and which I have reason to believe is related to the number of *G. boleti* observed. Contrasting results could also be caused by differences in methodology used for counting or estimating the number of individuals. As for this study, separating beetles of *G. boleti* from random black dots on the hymenium was challenging in certain pictures, and represents a potential bias in the estimated numbers of individuals. In many cases, *G. boleti* also formed clusters which were difficult to count. However, all pictures in this study are counted under the same conditions, making them comparable within this dataset. One future solution to this challenge could be using computer programs to count individuals, possibly saving time and adding accuracy to the measurements (Halbritter et al., 2020). However, this would require far more time and different skills than what this thesis covers.

Higher population density gives more trapped *G. boleti*

Higher population densities were estimated for the near natural forests than the previously clear-cut forests. This can be linked to the earlier findings in this study of near natural forests having more dead wood in decay class I and II, facilitating for more fruit bodies of *F. pinicola*, again leading to higher numbers of *G. boleti*. In addition to more fruit bodies, the higher population densities in near natural forests can be linked to the findings of larger area of hymenium on *F. pinicola* compared to the previously clear-cut forests.

The regression line made explaining the number of *G. boleti* caught in traps by the estimated population densities shows a positive non-linear relationship. This non-linearity suggests that at higher densities, larger portions of the populations of *G. boleti* will be caught in traps. This could indicate more flying activity when populations of *G. boleti* are denser. A positive relationship between the density of populations and the rate of dispersal in species have been observed in several taxa's, including spiders, insects, mammals and birds (Travis et al., 1999). Studies have shown that population density can affect dispersal abilities, giving individuals in

denser populations characteristics better suited for dispersal (Lutscher, 2008). In this case, certain populations would be more severely affected by habitat fragmentation and habitat destruction.

Challenges when estimating population densities

This thesis presents a population density estimate for *G. boleti*, which is rarely done for saproxylic insects. I also show that the density estimate corresponds with the numbers caught in the traps which further indicate that using trap data for this species could be a good indicator of population densities. When estimating population densities, especially insect population densities, several challenges present themselves. The behaviour of insects is among other things dependent on ecological conditions (Halbritter et al., 2020). With each fruit body being photographed only once over a sampling period of several weeks, without being able to be flexible in relation to the weather conditions, limiting the variation of these ecological conditions is difficult.

The choice of unit is important when estimating populations. When investigating the populations of small abundant insects, such as *G. boleti*, the sampling unit should preferably be as small as possible (Southwood & Henderson, 2000). This is the basis for the choice of fruit body as unit of habitat, instead of dead trees with *F. pinicola*, even though spotting all fruit bodies may be challenging, increasing the possibility of errors. This is another thing to bear in mind when estimating population densities. The errors in the population estimates will normally be below the true value, because one cannot observe more individuals than the numbers present, but there is always a possibility of underestimating (Southwood & Henderson, 2000). The underestimation of total number of individuals may consequently be large when calculating through several steps, from the mean *G. boleti* per *F. pinicola* times *F. pinicola* in the habitat to estimate the population densities.

5. Conclusion

This study estimates that the population densities for the common species *G. boleti* is 9.6 times higher in near natural forests than previously clear-cut forests. Many species that depend on deadwood are far less common, and I would expect this effect to be applicable for these species even though we lack knowledge about their population densities.

The future of the forests depends on how we manage the forests today. If we choose to manage forests with a focus of protecting near natural forests, the more intensively managed forests today can give space for species dependent on the characteristics of near natural forests in the future (Storaunet & Rolstad, 2020). To do this, the natural disturbances in a forest need to be reflected in the management strategy (Kuuluvainen, 2009). We need knowledge about the forest characteristics, structure, diversity and dynamics at different scales (Kuuluvainen & Aakala, 2011). The management strategy should also reflect the species situated in the forest, highlighting the need for more knowledge about their dispersal and colonization (Sverdrup-Thygeson, Gustafsson, et al., 2014). More areas need to be protected for the future, and just as important, more consideration needs to be taken when choosing areas to be protected. As Sverdrup-Thygeson, Søgaard, et al. (2014) so nicely put it; "area coverage is not synonymous with conservation effectiveness".

New techniques for measuring insects are being developed, allowing for more accurate measurements and estimates in the future (Halbritter et al., 2020). Combining these methods in addition to the already existing studies will likely be of great value for the future of forest management, and for the future of our forests.

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7. Appendix

Table A1. Output from ANOVA analysis investigating the significance of predictor variables for the response variable number of *G. boleti* caught in window traps. Significant p-values are highlighted in bold.

Variable	*Df*	*Sum Sq*	*F value*	*Pr(>F)*
Trees with *F. pinicola*	1	44.700	19	**< 0.001**
Fruit bodies of *F. pinicola*	1	104.900	49.960	**< 0.001**
Period sampled	2	12.500	2.496	0.085
Placement	3	2.500	0.333	0.801
Total volume deadwood	1	254.400	172.800	**< 0.001**
Volume decay class 1 and 2	1	258.000	177.100	**< 0.001**
Site	9	131.100	7.078	**< 0.001**

Table A2. Pearson's product-moment correlation calculated between possible predictor variables for the number of *G. boleti* caught in window traps. Correlation coefficients deemed too strongly correlated are highlighted in bold.

Variables	*t*	*df*	*r*	*p*
Trees with *F. pinicola* ~ Fruit bodies of *F. pinicola*	27.961	238	**0.876**	< 0.001
Trees with *F. pinicola* ~ Total volume deadwood	4.327	238	0.270	< 0.001
Trees with *F. pinicola* ~ Volume deadwood decay class 1 and 2	4.140	238	0.260	< 0.001
Fruit bodies of *F. pinicola* ~ Total volume deadwood	8.311	238	0.474	< 0.001
Fruit bodies of *F. pinicola* ~ Volume deadwood decay class 1 and 2	8.284	238	0.473	< 0.001
Total volume deadwood ~ Volume deadwood decay class 1 and 2	117.730	238	**0.992**	< 0.001

Table A3. Output from ANOVA analysis investigating the significance of predictor variables for the response variable density of *G. boleti* observed on the hymenium of *F. pinicola*.

Variable	*Df*	*Sum Sq*	*F value*	*Pr(>F)*
Forest type	1	2.2	0.906	0.343
Site	9	34.3	1.641	0.108
Volume deadwood decay class 1 and 2	1	17.4	7.512	0.0068
Fruit bodies of *F. pinicola*	1	0.8	0.311	0.578
Week sampled	1	5.5	2.286	0.132

Table A4. Estimated population densities of *G. boleti* in an area of 1000 m^2 for all forests included in the study.

Estimated populations of *G. boleti*

Forest type	*Site*	*Estimated number of G. boleti*
Clear-cut	Halden	0
	Blafjell	212
	Gullenhaugen	212
	Hemberget	0
	Braskereidfoss	638
	Oytjern	0
	Sarkilampi	212
	Skotjernfjell	922
	Storas	1632
	Tretjerna	141
Near natural	Halden	0
	Blafjell	99
	Gullenhaugen	3296
	Hemberget	899
	Braskereidfoss	2497
	Oytjern	2097
	Sarkilampi	799
	Skotjernfjell	1997
	Storas	2197
	Tretjerna	4994

Table A5. Poisson regression model (GLM) with number of *G. boleti* caught in the flight interception traps as response variable predicted by the estimated population density in each forest. The outlier Tretjerna NN was removed before making the model. AIC = 111.690.

	Estimate	*SE*	*Z*	*Pr(>|z|)*
(Intercept)	0.894	0.192	4.641	< **0.001**
Population size	0.0004	0.0001	4.172	< **0.001**

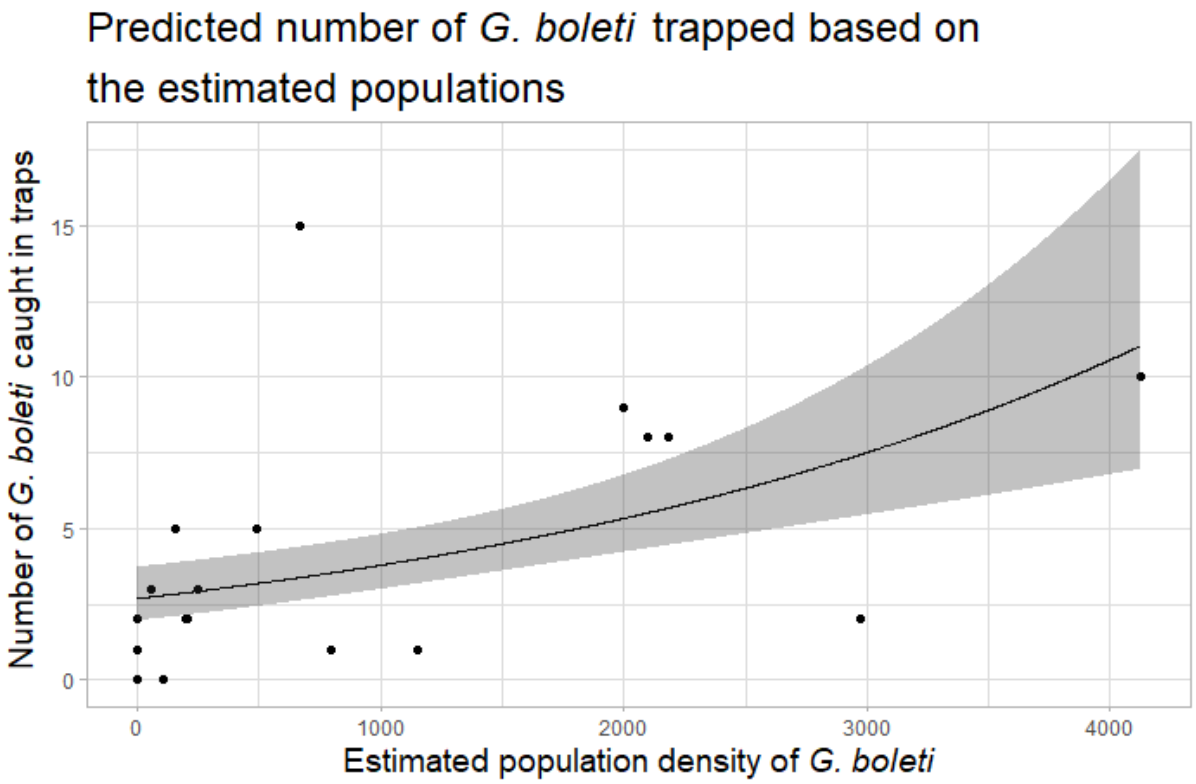

Figure A1. Plotted regression line for the number of *G. boleti* caught in traps explained by the estimated population density in an area of 1000 m^2 in each forest. A 95% confidence interval is plotted in light grey. Points are estimated values based on observations. The outlier Tretjerna NN was removed from the data before the predictions were made.

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