



Contrasting population dynamics of Goodyera repens and Alectoria sarmentosa in managed boreal forests: A multi-scale assessment

Johannes Nord

Independent project • 60 credits

Master's thesis

Swedish University of Agricultural Sciences, SLU

Faculty of Forest Sciences • Department of Ecology

Uppsala 2026

Contrasting population dynamics of *Goodyera repens* and *Alectoria sarmentosa* in managed boreal forests: A multi-scale assessment

Kontrasterande populationsdynamik hos Goodyera repens och Alectoria sarmentosa i brukad borealskog: En utvärdering på flera skalor

Johannes Nord

Supervisor: Joachim Strengbom, Swedish University of Agricultural Sciences, Department of Ecology

Examiner: Alistair Auffret, Swedish University of Agricultural Sciences, Department of Ecology

Credits: 60 credits

Level: Advanced level, A2E

Course title: Master's thesis in Biology - Ecology

Course code: EX0900

Course coordinating dept: Department of Aquatic Sciences and Assessment

Place of publication: Uppsala

Year of publication: 2026

Keywords: *Goodyera repens*, *Alectoria sarmentosa*, Boreal forest, Forest continuity, Shelterwood logging, Multi-scale assessment.

Swedish University of Agricultural Sciences

Faculty of Forest Sciences

Department of Ecology

Abstract

This study investigates how modern silvicultural management methods such as clear-cutting affects the population dynamics of two different specialized species: the epiphytic lichen *Alectoria sarmentosa* and the terrestrial orchid *Goodyera repens*. Using a multi spatial scale approach (landscape, within-stand, and local plot occurrence levels), this study assesses how these species populations change over a 12-year period in stands regenerated after clearcutting (young stands) and in old stands that have likely never been clear-cut. This part of the study was conducted in Hälsingland. In a separate study, I examined the short-term response of *G. repens* to shelterwood logging and clear-cutting in comparison to unharvested reference. This component of the study was conducted in experimental logging sites in Uppland.

Results from the 12-year long inventory in Hälsingland showed contrasting, spatial-scale dependent population trends for the two assessed species. For *G. repens*, the assessed populations maintained completely unchanged at a minimal occurrence across all spatial scales in the young production forests (47-57 years old). In the old forests (>85 years old), there was a significant decline at both the within-stand level and local plot level. For *A. sarmentosa*, a significant increase was observed across all three spatial scales in the young production forests and in the old forests, there were no observed significant changes. Regarding the experiment in Uppland examining the effects of clear-cutting and shelterwood logging on *G. repens*, clear-cutting led to a significantly higher net loss of individuals compared to the unlogged reference areas. Shelterwood logging ended up in an intermediate position, not being significantly different from either the unlogged reference or the clear cutting.

This study concludes that a “one size fits all” standardized management in forestry is insufficient for properly protecting these specialized species. In order to ensure the survival of both species, *G. repens* classified as vulnerable and *A. sarmentosa* classified as near threatened, a more diverse forest strategy model is needed. This strategy needs to prioritize the preservation of enhanced connectivity in the landscape, old growth continuity forests and extended harvesting rotation periods.

Keywords: *Goodyera repens*, *Alectoria sarmentosa*, Boreal forest, Forest continuity, Shelterwood logging, Multi-scale assessment.

Sammanfattning

Denna studie undersöker hur moderna skogsbruksmetoder såsom kalhygge påverkar populationsdynamiken hos två olika specialiserade arter: den trädlevande laven *Alectoria sarmentosa* och den marklevande orkidén *Goodyera repens*. Genom att använda en flerskalig undersökning (landskaps-, inom bestånd- och lokal nivå), undersökte jag hur dessa arters populationer förändras över en 12 årsperiod i yngre skogar samt äldre skogar som troligen aldrig blivit nedhuggna. Denna del av studien genomfördes i Hälsingland. I en separat del av studien så undersöktes den kortsiktiga påverkan på *G. repens* efter skärmhygge och kalhygge jämfört med en orörd referensyta. Denna delen av studien genomfördes i experimentella hyggesområden i Uppland.

Resultaten från inventeringen i Hälsingland avslöjade olika, skalberoende populationstrender för de undersökta arterna. *G. repens* hade en oförändrad, minimal population inom alla tre skalor i de unga skogarna (47-57 år). I de gamla skogarna (>85 år) upptäcktes en signifikant minskning inom skogarna samt de lokala ytorna. *A. sarmentosa* visade en signifikant ökning inom alla tre skalor i de unga skogarna. I de gamla skogarna upptäcktes inga signifikanta förändringar. För experimentet i Uppland där effekterna från kalhygge och skärmhygge på *G. repens* undersöktes så uppmättes en signifikant högre nettoförlust inom kalhygget jämfört med de orörda referensytorna. Skärmhygget hamnade på en mitt-emellan position och var inte signifikant skild från varken kalhygget eller referensytorna.

Denna studie har som slutsats att ett likformigt standardiserat skogsbruk är otillräckligt för att på ett ordentligt sätt skydda dessa specialiserade arter. För att kunna försäkra sig om överlevnaden för båda arterna (som nu båda klassas som sårbara) måste en mer diversifierad skogsbruksmodell användas. Denna strategi behöver prioritera bevarandet av konnektiviteten i landskapet, gammal kontinuitetsskog samt förlängda rotationstider för hygget.

Table of contents

Abstract	3
Sammanfattning	4
List of tables	6
List of figures	7
Abbreviations	9
1. Introduction	10
1.1 Biodiversity	10
1.2 Boreal Forest Ecology and Structural Complexity	10
1.3 Impact of forest management, local, structural and microclimatic shifts	11
1.4 Landscape-scale amplification: fragmentation, edge effects, and time	12
1.5 Study species as ecological indicators	13
1.6 Research questions and aims	14
2. Method	16
2.1 Study area	16
2.2 Influence of forest stand age and density on species populations	16
2.3 Impacts of shelterwood logging and clear-cutting on <i>G. repens</i>	17
3. Data analysis	19
3.1 <i>G. repens</i> and <i>A. sarmentosa</i> in Hälsingland	19
3.2 Basal area of trees	19
3.3 Species Occurrence in relation to landscape occurrences	20
3.4 Slope aspect analysis	21
3.5 Effect of harvest method on <i>G. repens</i> in Uppland	21
3.6 Canopy cover	22
4. Results	23
4.1 Population trends in <i>G. repens</i>	23
4.2 Population trends in <i>A. sarmentosa</i>	23
4.3 Correlation with landscape frequency (Public findings)	27
4.3.1 Relationship between public findings and change over time	27
4.3.2 Relationship between public findings and current occurrence	27
4.4 Influence of forest density	29
4.5 Change in occurrence in relation to topographic directional aspect of the ground	29
4.6 Effect of management treatments on <i>G. repens</i>	29
4.7 Canopy openness relationship to change in occurrence of <i>G. repens</i>	32
4.7.1 Canopy openness relationship to recruitment and mortality	34
5. Discussion	36
5.1 Change in occurrence of <i>A. sarmentosa</i>	36
5.2 Topographic influence	36
5.3 The role of forest density for <i>A. sarmentosa</i>	37
5.4 Change in occurrence for <i>G. repens</i>	38
5.5 The role of forest density for <i>G. repens</i>	40
5.6 Short-term Effects of Harvest Methods on <i>G. repens</i>	40
5.7 Management Implications for Boreal Conservation	41
5.8 Conclusion	43
6. References	45
Popular science summary	50

List of tables

Table 1. Baseline (2013) and present (2025) occurrence patterns of <i>G. repens</i> and <i>A. sarmentosa</i> across young production forests (47–57 years old) and late-successional old forests (>85 years old) in Hälsingland, Sweden. Values represent the actual biological occurrence quantified during the 2013 and 2025 inventories across three distinct spatial resolutions: stand-level occurrence, within-stand occurrence, and local plot occurrence, represented as the percent of occupied plots. Young forests: (stand level (n=10 stands), within stand level (n=100 plots), and local plot level (n=400 subplots) and old forests: (stand level (n=6 stands), within stand level (n=60 plots) and local plot (n=240 subplots)).	25
Table 2. P-values from one-sample t-tests comparing the mean change in occurrence against zero for <i>G. repens</i> and <i>A. sarmentosa</i> . Tests were conducted separately for young and old forests across three spatial resolutions (stand level, within stand level and local plot level).	26
Table 3. Results from Welch's two-sample t-tests comparing the mean change in occurrence between young and old forests for <i>G. repens</i> and <i>A. sarmentosa</i> across three spatial resolutions (stand level, within stand level and local plot level).	26
Table 4. Table showing the correlation between public findings and change in occurrence of <i>G. repens</i> and <i>A. sarmentosa</i> summary of all results from the analysis for stand level, within stand level and local plot level. (Not based on forest age). The focus is on whether the relationship between the number of findings in the surrounding area and the change in the forest stand is significant ($p < 0.05$).	27
Table 5. Table showing correlation between public findings and change of occurrence of <i>G. repens</i> and <i>A. sarmentosa</i> (based on forest age) from the analysis for stand level, within stand level and local plot level. The focus is on whether the relationship between the number of findings in the surrounding area and the change in the forest stand is significant ($p < 0.05$). NA values had zero variance. <i>G. repens</i> in young forest were excluded in this table as there were no changes in these cases.	28
Table 6. Table showing the summary of correlation analysis between the number of reported surrounding findings and the current species occurrence level (post-2025 measurement). Significance level: ($p < 0.05$).	28
Table 7. Summary of linear regression analyses for the relationship between the change in occurrence of <i>G. repens</i> and <i>A. sarmentosa</i> and the total basal area (m ² /ha) of trees within stand occurrence in old and young forests. The table includes forest age, intercept (k), estimate (m), coefficient of determination (R ²), and p-value.	29

List of figures

- Figure 1. Schematic representation of the hierarchical sampling design used to assess the occurrence of *G. repens* and *A. sarmentosa* at different spatial resolutions. Stand level represents the overall forest stand (Stand level occurrence). Within stand level shows the distribution of sampling points within the stand (Occurrence within a stand). Local plot level illustrates the local occurrence, where each sampling point was further divided into four quadrants (Q1–Q4). 17
- Figure 2. Change in the occurrence of *G. repens* between the two inventory periods (2013 - 2015) across three spatial resolutions. Decline between the two inventory occasions are indicated by values below zero. Distribution of change is displayed by the boxplots with the horizontal line representing the median, the enclosing box represents the interquartile range (25th to 75th percentiles) and the whiskers extend to extreme data points within 1.5 times the interquartile range. Outliers are shown as points outside the whiskers. One-sample t-tests confirmed that the decline in old forests was statistically significant at within stand level ($p = 0.009$) and local plot level ($p = 0.021$), but not at stand level ($p = 0.175$). Occurrence in young forests remained completely stable across all resolutions ($p = 1.0$). 24
- Figure 3. Change in the occurrence of *A. sarmentosa* between the two inventory periods across three spatial resolutions. Decline between the two inventory occasions are indicated by values below zero. Distribution of change is shown with the boxplots with the line representing the median, the enclosing box represents the interquartile range (25th to 75th percentiles) and the whiskers extend to extreme data points within 1.5 times the interquartile range. Outliers are shown as points outside the whiskers. The red dashed line represents a value of zero change. One-sample t-tests showed a highly significant increase in occurrence in young forests across all resolutions: stand level ($p = 0.001$), within stand level ($p < 0.001$), and local plot level ($p < 0.001$). Occurrence in old forests showed no significant deviation from zero at any resolution (stand level: no change; within stand level: $p = 0.872$; local plot level: $p = 0.222$). 25
- Figure 4. Effect of different forest management treatments (Clear-cut, shelterwood, and unlogged reference) on the change in occurrence of the orchid *G. repens*. Change in occurrence is defined as difference in individuals between the two sampling periods, i.e. survival and losses of marked individuals and new additional individuals. The thick horizontal line represents the median, the box indicates the interquartile range (25th–75th percentiles), and the vertical whiskers extend to the minimum and maximum values within 1.5 times the interquartile range. Data points outside this range are plotted as outliers. Statistical comparisons were performed using a one-way ANOVA followed by Tukey's HSD post-hoc test. Significant differences ($p < 0.05$) are displayed with specific p-values, while non-significant differences are denoted as "ns". Sample size=78. 30
- Figure 5. Effect of different forest management treatments (Clear-cut, shelterwood, and unlogged reference) on the recruitment of new individuals of the orchid *G. repens*. Change in occurrence is defined as difference in individuals between the two sampling periods, i.e. survival and losses of marked individuals and new additional individuals. The thick horizontal line represents the median, the box indicates the interquartile range (25th–75th percentiles), and the vertical whiskers extend to the minimum and maximum values within 1.5 times the interquartile range. Data points outside this range are plotted as outliers. Statistical comparisons were performed using a one-way ANOVA followed by Tukey's HSD post-hoc test. Significant differences ($p < 0.05$) are displayed with

specific p-values, while non-significant differences are denoted as "ns". Sample size=78.....	31
Figure 6. The number of <i>G. repens</i> individuals lost (mortality or disappearance) per plot across different forest management treatments. Lost individuals are defined as marked individuals that were lost (died) between the two sampling periods. Boxplots represent the median and interquartile range. No significant differences in the absolute number of lost individuals were found between treatments (Kruskal-Wallis test, $\chi^2_{22}=4.36$, $p=0.113$).	32
Figure 7. Change in <i>G. repens</i> in relation to canopy openness. Each point represents one site. The analysis showed a weak negative, but statistically non-significant, correlation between canopy openness and the change in <i>G. repens</i> occurrence (Spearman's $\rho = -0.16$, $p = 0.159$). There was a weak, but non-significant relationship between change in occurrence of <i>G. repens</i> and canopy openness.	33
Figure 8. Relationship between changes in canopy openness and changes in <i>G. repens</i> occurrence across study sites. Each point represents one site. Results from a linear regression test shows a weak, non-significant association between the variables ($\beta=-3,053$, $p=0,386$, $R^2=0,01$)......	34
Figure 9. Change in <i>G. repens</i> individuals in relation to change in canopy cover. Data shows the number of new <i>G. repens</i> individuals established in relation to net change in canopy cover in the different forest management treatments. Linear regression analysis showed no statistically significant relationship between the change in solar radiation and the establishment of new individuals ($F_{1,68}=0.3719$, $p=0.544$, $R^2=0.005$). The estimated slope was -0.6595 , indicating a weak, non-significant decrease in recruitment with decreasing canopy cover.	35
Figure 10. Figure illustrating the correlation between the change in canopy cover and the number of <i>G. repens</i> individuals lost from the sampling plots. Linear regression analysis showed no statistically significant relationship between the change in solar radiation and the number of lost individuals ($F_{1,68}=1.119$, $p=0.294$, $R^2=0.016$). The estimated slope was 3.383 , suggesting a weak, non-significant increase in the loss of individuals with decreasing canopy cover.	35

Abbreviations

ANOVA	Analysis of variance
HSD	Honest significant difference
Q-Q plots	Quantile-quantile plots
RGB	Red, green and blue (pixels for image analysis)

1. Introduction

1.1 Biodiversity

Biodiversity is a multi-dimensional concept which includes the variety of life across multiple organizational scales, stretching from the genetic diversity within certain populations to the broader structures of whole ecosystems (Noss 1990; IPBES 2019). Ecological resilience is completely dependent on the biological diversity that ensures an ecosystem's ability to adapt to environmental shifts which in turn allows them to continue to provide important ecosystem services (Gauthier et al. 2015; Mori et al. 2017). Biodiversity is however impossible to fully evaluate through a singular, static perspective. It instead relies on several different factors such as the physical structure of the environment and the different spatial scales at which species interact with this structure (Esseen et al. 1997; Noss 1990).

Structural diversity involves the physical arrangement, heterogeneity, and long-term continuity of spatial components within a habitat (Esseen et al. 1997; Noss 1990). The variation of the structure is important as it can provide a large number of niches for many types of specialized species (Winter & Möller 2008; Zhang et al. 2024). When anthropogenic disturbances simplify the complexity of these physical structures, the amount of specialized niches shrink, leading to big challenges for many species (Fedrowitz et al. 2014; Johansson et al. 2026; Östlund et al. 1997).

So, in order to properly understand the biodiversity in different environments, it is not enough to for example only look at the number of species. It is instead necessary to look at several aspects of the diversity and interactions across different spatial scales (Noss 1990). Population dynamics and ecosystem processes does not look the same across the entire landscape. A population can for example look stable on a landscape scale while decreasing locally (Kuussaari et al. 2009; Noss 1990), making multi scale assessments necessary for properly evaluating environmental changes (Lindenmayer & Franklin, 2002; Noss, 1990).

1.2 Boreal Forest Ecology and Structural Complexity

The boreal forest is an environment that covers a large area of the northern hemisphere and plays an important role in the global carbon cycling system and climate regulation (Bradshaw et al. 2009; Gauthier et al. 2015). In the boreal forest's natural, undisturbed state, the species communities are shaped by different disturbance regimes such as wildfires, windthrows and insect outbreaks. This generates a complex environment that contains successional stages across the landscape (Esseen et al. 1997; Kuuluvainen 2002).

At the stand level, complexity is characterized by an uneven age distribution of the trees, multi-layered tree canopies, and a continuous existence of decaying woody debris that gives these forests a diverse environment that includes a big array of microhabitats (Esseen et al. 1997). This heterogeneity of structures provides a large number of ecological niches that can support different food webs and symbiosis, such as canopy epiphytes and soil fungi networks (Esseen et al. 1996; Těšitelová et al. 2022). An important part when maintaining this ecological complexity is that it contributes to continuity of habitats. Forest continuity is defined as the uninterrupted presence of the canopy cover over a long period of time without large scale anthropogenic disturbances (Nordén et al. 2014; Rolstad et al. 2002). This stability over a long temporal scale allows environmentally sensitive species with restricted dispersal to persist as they can maintain stable populations, e.g. due to the stable microclimate that old growth forests provides (Nordén et al. 2014; Zhang et al. 2024).

1.3 Impact of forest management, local, structural and microclimatic shifts

In Fennoscandia, modern silviculture is mainly characterized by an intensive management that is dominated by clear-cutting, leading to the fundamental altering of the natural dynamics offered by older growth forest stands (Johnsson 2014; Esseen et al. 1997; Östlund et al. 1997). When harvesting of a mature forest has been conducted, the immediate and most drastic change is the removal of the trees. This leads to the direct reduction of both forest density and canopy cover, leading to a shift from a shaded, multi layered environment to a sun exposed and in later stages, an even aged forest stand. This also leads to the elimination of many of the aforementioned habitat structures that provide a critical microclimate that many species rely on (Esseen et al. 1996; Esseen et al. 1997).

So, beyond the direct loss of the physical structures of the forests, the reduction in canopy cover and forest density also leads to a disruption in the local microclimate. The microclimate is dependent on the physical structures of the forest in order to maintain a buffering capacity that moderates the temperature fluctuations and maintain a high and stable humidity (De Frenne et al. 2019; Zellweger et al. 2020). Once the trees are removed, this buffering effect is essentially lost, leading to higher temperature fluctuations, more wind exposure and reduced humidity (Esseen et al. 1997; Zhang et al. 2024).

In addition to the structure of the forest, the physical topography of the local landscape also plays a role in affecting these microclimates, in particular the directional slope of the ground (Hylander 2005). Slopes that are north facing receive lesser amounts of solar radiation and can thereby potentially retain a higher amount of humidity compared to south facing slopes (Zhang et al. 2024). The intensive forest harvesting might however be too much of a disturbance that the topographical aspect will not be enough to save the concerned microclimate in such a degree that sensitive species can survive (Koelemeijer et al., 2022;

Schmalholz & Hylander 2011; Zhang et al. 2024). Therefore, it is of importance to understand the interaction between factors such as the forest density, topographical aspect and canopy cover and their ability to affect the persistence of sensitive species.

One way to mitigate the negative ecological impacts of the conventional clear-cutting method, is to apply alternative silvicultural methods that promote tree continuity and emulate the structural complexity generated by natural disturbances (Gustafsson et al. 2012; Kuuluvainen et al. 2021). Shelterwood logging, a method that involves the gradual removal of mature trees in the forest stands in partial harvests, leaving a portion of mature trees that can allow new trees to grow under the shelter of the older trees is one such method. A main goal of this method is to maintain the microclimate buffer by not removing all trees at once. So by preserving a portion of mature trees, the effects of solar radiation and wind can be mitigated compared to the case of clear-cutting (De Frenne et al. 2019; Zhang et al. 2024). The greater buffering of the microclimate, compared to clear cuts, is hypothesized to “life boat” species over the harvesting phase, thereby promoting biodiversity (Fedrowitz et al. 2014; Johnson 2014; Rudolphi et al. 2014). The canopy cover that is needed to secure this function is however poorly understood (Craig & Macdonald 2009; Fedrowitz et al. 2014).

1.4 Landscape-scale amplification: fragmentation, edge effects, and time

The ecological consequences of the clear-cutting harvest method is difficult to understand if we only observe the isolated harvested stands. The surrounding landscape is an important factor that affects the biological interactions between different areas (Gustafsson et al. 2025; Kouki et al. 2001). On a larger landscape scale, clear-cutting can lead to fragmentation, as it disrupts larger areas of well-connected forests into smaller fragments (Essen et al. 1997; Kouki et al. 2001). Fragmentation leads to increased edge effects, where the microclimate gets negatively affected by the increased exposure to wind and solar radiation (Esseen et al. 1997; Zhang et al. 2024).

Beside increasing the edge effects, a fragmented landscape will also influence the possibility of recolonisation after disturbance. Species with limited or slow dispersal capability will be most affected by such fragmentation. Several studies highlight the importance of the presence of nearby dispersal sources in the form of neighboring populations within the surrounding landscape (Dettki et al. 2000; Gustafsson et al. 2025). These nearby populations can act as a continuous source of seeds or propagules that makes it possible for species to spread within the landscape (Gustafsson et al. 2025). If the landscape lacks these dispersal sources as a result of fragmentation, local recolonization becomes slow (Dettki et al. 2000; Johansson et al. 2026). Another issue that sensitive species have is that as modern silvicultural harvest rotation time periods are around 80 -100 years, the time window for sensitive specialized species can become too narrow to recolonize a recovering forest stand (Johansson et al. 2026; Johnson 2014).

In the event of fragmentation in the landscape, ecological responses are often not instant and could potentially lead to an “extinction debt”. This is a phenomenon where isolated populations slowly decline and eventually reach the local extinction of the species within areas that no longer are connected to the broader landscape (Hanski 2000; Kuussaari et al. 2009; Johansson et al. 2026).

1.5 Study species as ecological indicators

In order to empirically assess the pressuring factors of the degrading microclimate, fragmentation of the landscape and the temporal constraints, this study utilized two different sensitive and specialized indicator species. The terrestrial orchid *Goodyera repens* (L.) R. Br. and the epiphytic lichen *Alectoria sarmentosa* (Ach.) Ach. As both of these species has shown a high sensitivity to disturbances and are associated with late successional forests, they serve as good ecological proxies that can be used to monitor the forest continuity and habitat stability (Esseen et al. 1996; Johansson et al. 2026).

Goodyera repens is a small sized, evergreen orchid which has a circumpolar distribution, commonly known as creeping lady’s tresses. It spans the hemiboreal and boreal zones of North America, Asia and Europe (Johansson et al. 2026). In Sweden, it is associated with late successional forests that has complex structural features and high habitat heterogeneity (Johnson 2014; Widenfalk and Weslien 2009). The presence of *G. repens* is strongly linked to forest conditions that provide well shaded, closed canopy environments, which helps maintain the stable, humid and cool microclimate (Johansson et al. 2026).

According to Johansson et al. 2026, data from the Swedish National Forest Inventory indicate an alarming decline in *G. repens* over the past three decades. Between the years of 1993 and 2022, the orchid population went through a major decline in Swedish forests. Its occurrence probability dropped from 1.9% during the years of 1993-1997 to 0.6% in 2018-2022. This means that *G. repens* underwent a total population decline of 66%, a highly significant negative trend. Understanding *G. repens* short term survival following shelterwood logging as well as its long term ability to recolonize an area after clear-cutting is therefore of high importance.

Alectoria sarmentosa is an epiphytic lichen that is commonly known as witch’s hair. It is mainly found in boreal montane environments (Esseen 2016). The lichen is also associated with late successional forests, where it grows on the branches of older trees. In particular, the Norway spruce (*Picea abies*) (Dettki 1998; Esseen et al., 2022). The lichen thrives in environments where the humidity is high and the local microclimate is stable (Ellis 2012). It has a high sensitivity to air pollution and the effects of silvicultural practices, making it a good indicator of habitat stability and forest continuity (Dettki 1998; Esseen et al. 2022).

The vulnerability and distribution of *A. sarmentosa* is greatly affected by the mechanics of dispersal for the species. It mainly spreads and reproduces by vegetative fragmentation, which is a process where smaller pieces of the thallus

break off and get transported away with wind, snow or animals (Dettki 1998). The fragmented pieces are however, relatively heavy, leading to the dispersal distance by fragmentation is limited (Dettki 2000). The restricted capacity of dispersal can explain why the species are dependent on older, undisturbed forests. When the habitat gets disturbed by for example clear-cutting, *A. sarmentosa* faces big challenges when trying to colonize new areas (Dettki 2000; Esseen et al 2022). *Alectoria sarmentosa* therefore acts as a very good proxy for evaluating whether managed production landscapes can facilitate dispersal as well as the ability of species like this to recolonize an area after clear-cutting.

As both of these species likely are limited by their slow dispersal, one can assume that their recolonization patterns after a disturbance will be different depending on what spatial scale of which we observe them (Dettki 1998; Johansson et al. 2026). One can therefore anticipate that the number of young forests that harbour populations of these species will increase with time after a disturbance, and one can also expect that the occurrences (or abundance) of the species within a forest increases with time since disturbance. In forests where these species are already established, we would expect to see them increase in occurrence as they should be able- to continue their expansion internally once established.

By assessing how these species develop over time in forests of that are regenerated after clearcutting (young forests) and older forest that likely never been exposed to clearcutting as well as evaluating alternative forest managing methods such as shelterwood logging's ability to mitigate the negative effects on these species, we can obtain a better understanding of how to manage our forests in the future.

1.6 Research questions and aims

In my thesis, I address the following questions. How do occurrences of *G. repens* and *A. sarmentosa* develop over a 12-year period, and does the development of occurrence differ between young forests regenerated after clear-cutting and older forests that likely never have been clear-felled. How does the change differ among spatial scales (landscape, within-stand and patch size) and between young and old forests?

My hypotheses related to these questions are:

H1: The occurrence at all measured spatial scales (landscape, within-stand, and patch size) of *G. repens* and *A. sarmentosa* will show a significant increase over the time period of 12 years, both in young (47-57 years old) and in old (>82 years old) forests.

An additional aim was to evaluate whether shelterwood logging improves the short-term (one-year) survival of *G. repens* following logging compared with conventional clear-cutting

I hypothesised that (H2) the survival of *G. repens* will have a less negative decline of individuals after shelterwood logging compared to clear-cutting. I do not expect any significant change in the unlogged reference area.

2. Method

2.1 Study area

This study was conducted in two different regions in Sweden. The initial part was conducted in the region of Hälsingland in Mid-central Sweden. Data collection occurred in 2025 between September 2 and 16, around the city of Ljusdal (approx. 62°02'06"N, 15°55'04"E). This area is located within the middle boreal zone of Sweden. Scots pine (*P. sylvestris* L.) and Norway spruce (*P. abies* (L.) Karst.) are the dominating tree species in this area. The climate around Ljusdal is characterized by an annual precipitation of 550 mm - 650 mm (SMHI). The mean temperature is around -7°C in January and 16°C in July.

The second part of this study consisted of a short term assessment of the response of *G. repens* to different harvest methods. This data was collected in September 16-25, 2025 in Uppland in south-central Sweden. I compared my data with data collected in October-November 2024, before the harvest treatments were made. The climate of this region is characterized by an annual precipitation of approximately 550–600 mm and an average temperature of around -3 to -5 °C in January and 17–18 °C in July (SMHI). This area is also characterized by a domination of Scots pine and Norway spruce.

2.2 Influence of forest stand age and density on species populations

To investigate the influence of forest age on *G. repens* and *A. sarmentosa*, the presence across two distinct forest age classes: 47-57, and >82 years was analysed. 10 stands were selected for the younger forests and 6 stands were selected for the older forests. These forest stands were part of a previous assessment conducted in 2013 (Johnsson 2014) where 36 forest stands were assessed for the occurrence of *G. repens* and *A. sarmentosa*. This assessment was conducted across three different spatial scales which was replicated in this study (Figure 1). All sites were dominated by Norway spruce with *Vaccinium*-type ground cover, characterized by mesic soil and intermediate productivity. While the younger age class originated from clear-cutting, the oldest stands likely had a history of selective logging, resulting in a multi-cohort structure. Within each stand, ten circular plots ($r=2$ m for *G. repens* and $r=5$ m for *A. sarmentosa*) were surveyed at minimum intervals of 50 meters. The reason for the difference in plot sizes for each species was that *G. repens* and *A. sarmentosa* have different growing patterns, *G. repens* growing tightly on the ground while *A. sarmentosa* grows more spread out on the trees. Rather than counting individuals, cover/abundance was estimated by recording the presence of the species within

four quadrants per plot. For *G. repens* this measure was used as an estimate of clonal size. For *A. sarmentosa* it was used as an estimate of local occurrence. This setup was the same as the 2013 assessment.

In order to assess the forest density of the stands, the basal area (m^2/ha) was measured from the center of each measuring site using a relascope (factor = 1). Basal area was separately recorded for Scots pine and Norway spruce, while all deciduous trees were merged and treated as one category. The spatial scale of observed trends were evaluated by measuring the change of occurrence at three different resolution levels:

Stand level: Stand scale occurrence, indicating how commonly distributed the species is in the landscape.

Within stand level: Within stand occurrence, indicating how widespread the species is within forest stands

Local plot level: Within plot occurrence, indicating how abundant the species is locally within the plot.

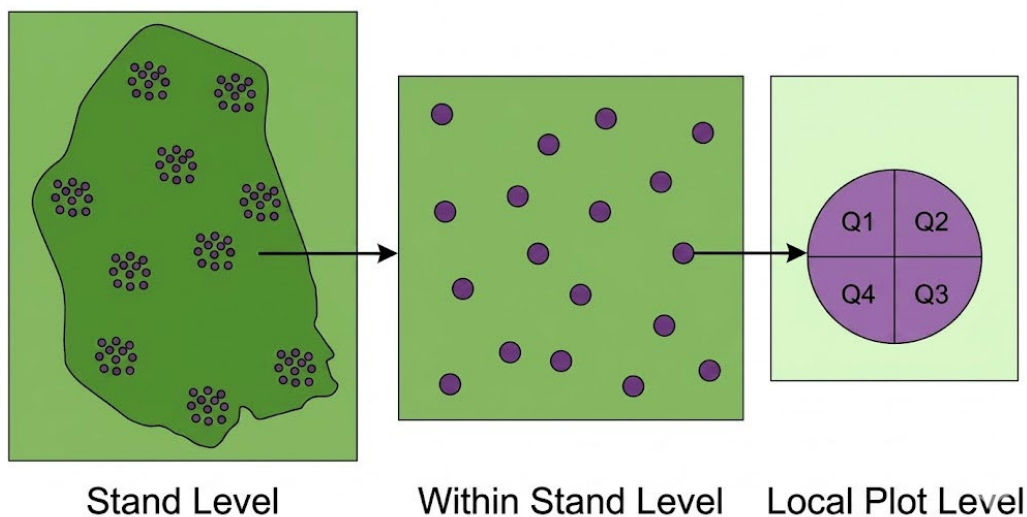


Figure 1. Schematic representation of the hierarchical sampling design used to assess the occurrence of *G. repens* and *A. sarmentosa* at different spatial resolutions. Stand level represents the overall forest stand (Stand level occurrence). Within stand level shows the distribution of sampling points within the stand (Occurrence within a stand). Local plot level illustrates the local occurrence, where each sampling point was further divided into four quadrants (Q1–Q4).

2.3 Impacts of shelterwood logging and clear-cutting on *G. repens*

The second part of this study consisted of a detailed assessment of *G. repens* in relation to different harvest methods. This part of the study was conducted in the

region of Uppland and utilized an experiment addressing biodiversity effects from different harvesting methods.

Shelterwood logging is a harvest method that involves removing parts of the mature forest canopy. In the study plots, the harvester volume was around 50-55% which meant a removal of approximately 110-170 m³ per hectare. This method was contrasted against traditional clear-cutting where approximately 95% of the standing tree volume is harvested and the remaining trees are left as environmental concern to fulfil the forestry act and meet certification schemes such as FSC.

Three different geographic sites were assessed to represent the different management methods:

- **Fäboberget:** A site containing three distinct treatment plots: a clear-felled area, a shelterwood logged area, and an undisturbed reference area (60.079328, 17.133666).
- **Laksjön:** A site featuring a single clear-felled plot (60.098139, 17.136703).
- **Råksjön:** A site including both a clear-felled area and a shelterwood logged area (60.046046, 17.077795).

For my study I utilized permanent 0.5 × 0.5m plots established prior to the harvesting operations. Each plot was permanently marked in the field with vertically placed plastic rods at the corners to ensure precise relocation. Prior to logging, in November 2024, all individuals of *G. repens* within each plot were recorded and tagged with unique, numbered plastic tags attached to the stem using metal wire. For the purpose of this study, each individual leaf rosette was considered a single individual. In September 16-25, 2025, the plots were resurveyed after the treatments had been conducted to estimate survival and mortality of marked plants and record new individuals.

3. Data analysis

3.1 *G. repens* and *A. sarmentosa* in Hälsingland

To analyse the changes in occurrence of *G. repens* and *A. sarmentosa*, data from 2013 was compared to inventory data from 2025. The data was compared between three spatial scales representing stand level occurrence, within stand level occurrence, and local plot level occurrence (Figure 1). The species were inventoried in two different forest age categories, young (47-57 years) and old (>85 years).

When assessing if trends in occurrences differed between forests of different ages, linear mixed-effects models were conducted for each spatial resolution and species. The model that was used included 'Forest Age* (Young and Old) and 'Time* (Before and After) as factors, with 'Site ID' as a random effect in order to account for paired data. The main statistical result of interest was the interaction between 'Time' and 'Forest Age' which indicates whether change over time is significantly different between the two inventories. Separate models were executed for each species across three distinct spatial resolutions: stand level occurrence, within stand occurrence, and local plot occurrence (Figure 1).

In order to further investigate the results within each category, the net change in occurrence (calculated as the value in 2025 minus the value in 2013) was calculated for each individual site. Two follow-up analyses were performed afterwards: One-sample t-tests were used to determine whether the mean net change within a specific forest age class significantly deviated from zero (to indicate any statistical increase or decline). Welch's two-sample t-tests were applied to directly compare the mean net change between young and old forests, ensuring robust results even in the presence of potentially unequal variances between the two groups.

Normality and homoscedasticity of the model residuals were visually assessed using Quantile-Quantile (Q-Q) plots and residuals-versus-fitted plots prior to final statistical evaluation. Statistical significance for all tests was defined at $\alpha=0.05$.

3.2 Basal area of trees

In order to test whether the changes in occurrence *G. repens* and *A. sarmentosa* (calculated as the net change in the within stand spatial scale between 2013 and 2025 (Figure 1)) were driven by the forest density and the composition of tree species, a number of linear regression analyses were performed. The current (2025) total basal area (m^2/ha) of all trees as well as the separate basal area for spruce, pine and deciduous trees were measured at each sampling point at the within stand spatial scale and used as structural proxies for the forest density and light availability (higher values indicating denser forests and less light

availability). In order to evaluate the potentially differing ecological responses across the different successional stages, the data was also stratified into the two forest ages: young and old.

The analysis of change in occurrence for *G.repens* and *A.sarmentosa* between 2013 and 2025 was conducted by using linear regression models. This was done in two different steps. The first step was a multiple linear regression including all three tree species categories as predictors to assess their relative importance and combined effects. The second step was a simple linear regression that fitted univariate models for each tree species and for the total basal area separately. This was done to specify specific species relationships and to create regression equations ($y=\beta_0+\beta_1x$) for visualization. These models were utilized to isolate specific species-specific relationships and generate regression equations for visualization and determination of the coefficients of determination (R^2).

3.3 Species Occurrence in relation to landscape occurrences

To test whether current occurrences (2025) and changes in occurrence over time (difference between 2013 and 2025 inventories) were related to the occurrences of the species in the surrounding landscape, I combined data from the inventories with publicly available records of landscape-level occurrences for both *G. repens* and *A. sarmentosa*. The publicly available records consist of citizen-science observations reported and were obtained from Artportalen (<https://www.artportalen.se/>). Here I used observations reported between 2013 and 2025 within 1.5 km after placing a circle in QGIS (version 3.42.1-Münster) with the same radius over the central position of each forest surveyed in my study and then counting all records of the two species that were reported in that area. I chose a radius of 1.5 km because this was the maximum radius that could be used without creating overlap among the landscapes surrounding the sites that included in my study.

The model included the variable change in occurrence for each species between 2013 and 2025, the current occurrence (2025) and the public findings of the two species within a 1,5 km radius during the same time period (2013 - 2025). To determine whether the influence of the surrounding landscape differed between the two forest age classes, separate analyses were conducted for young and old stands.

Two primary correlation analyses were performed using Pearson's product-moment correlation coefficient (r). This parametric test was selected to assess the strength and direction of the linear relationship between the variables, utilizing the continuous nature of both the finding frequency and occurrence data. Analysis for change tested if the change in occurrence of *G. repens* and *A. sarmentosa* correlated with the frequency of reported findings in the surrounding 1,5 km radius. A second analysis tested if the frequency of reported findings in the surrounding 1,5 km radius correlated with the current occurrence of *G. repens* and *A. sarmentosa* (in 2025).

3.4 Slope aspect analysis

To investigate whether slope aspect/direction influences species occurrences, the relationship between aspect and the change in occurrence was analyzed for both *G. repens* and *A. sarmentosa*. The response variable defined for this analysis was the change in occurrence between 2013 and 2025. The explanatory variable, 'Aspect', was derived from topographic data (elevation data, Grid 2+, Lantmäteriet) using QGIS (version 3.42.1-Münster) and categorized into three groups: "North", "South", and "Other" (East and West). To detect potential age-specific patterns, the tests were performed both on the entire dataset and stratified by forest age (Old Forests and Young Forests).

The north facing slopes included an interval of 315° and 15°, while south facing slopes were between 135° and 225°. The "other" category did accept for representing west- and east facing slopes, also included points that were located on flat terrain. To be considered as flat terrain, the slope had to be less than 2°.

To test for differences in the change of occurrence for *G. repens* and *A. sarmentosa* between the three different aspect groups, a Kruskal-Wallis H-test was conducted. Statistical significance was defined at $\alpha=0.05$.

3.5 Effect of harvest method on *G. repens* in Uppland

To clarify how choice of silvicultural practice influences the short-term survival of *G. repens*, I compared change in occurrence of the species over two years in stands that were exposed to clearcutting, shelterwood logging or left intact (reference).

Analysis of variance (ANOVA) was used to analyze the effect of the different forest management methods (clear cut, shelterwood-logging and untouched reference) on the net change in occurrence for *G. repens*. Residuals vs fitted plots and Q-Q plots were used prior to the analysis in order to visually verify normality and homogeneity of variance of the data. In cases where a significant treatment effect ($p<0.05$) was found, a post-hoc test (Tukey's honest significant difference) was used to identify significant differences among the different harvest methods.

The data for both recruitment and mortality consisted of discrete data counts that was characterized by a large number of zeroes. This meant that the data had skewed distributions and could not be considered to have normality. The data did therefore not meet the requirements for parametric testing. Instead, a non-parametric Kruskal-Wallis rank sum test was used to assess the differences of mortality and recruitment (separately) between the methods.

In order to visualize the results, boxplots were created showing the median and the interquartile range. Mortality was presented with negative values. Statistical tests were all two-tailed with a significance level of $\alpha=0.05$.

3.6 Canopy cover

In the experiment assessing effects of different harvest methods in Uppland, the canopy cover was assessed by using upward-looking hemispherical photographs from the ground level using a circular fisheye lens at each sampling point. Pixel level RGB values were extracted for each image and circular masking was used in order to only include the relevant circular part of the images. The radius of the circular mask was manually defined and adjusted in order to ensure that the black areas outside the image were removed.

Pixels classified as sky were identified using a rule-based classification that combined color- and brightness thresholds. Pixels were classified as sky when blue channel values exceeded both red and green channel values and overall brightness exceeded a defined threshold. Low saturated and bright pixels were identified as clouds. The canopy openness was calculated as the ratio of sky pixels against the total number of pixels within the circular mask. The calculation was made for images representing each site before and after the treatments (photos taken in October 2024 and September 2025). The change in canopy openness was calculated as the difference in canopy cover between pre-treatment and post-treatment. Positive values indicate an increase in occurrence following treatment, whereas negative values indicate a decrease.

To assess whether changes in canopy openness were associated with changes in *G. repens* occurrence, both non-parametric and parametric approaches were applied to test associations between the change in canopy openness and the change in *G. repens* occurrence. When data after visual inspection of (Q-Q) plots and residuals versus fitted values could not be assumed to fulfil the assumptions for parametric approaches, a Spearman's rank correlation test was used to examine the association. In other cases linear regression analysis was applied.

A sensitivity analysis was also conducted to test the robustness of the regression results. This was done by conducting the linear regression test without an extreme negative value (outlier). The results from this test were then compared to the original test with the extreme value included in order to assess whether this single data point affected the result to be significant/ not significant.

All statistical analyses were performed using R statistical software version 4.4.1 (R Core Team, 2024). Data processing and visualization of the results were conducted using the tidyverse suite of packages (Wickham et al., 2019).

4. Results

4.1 Population trends in *G. repens*

The assessment of the inventories conducted between 2013 and 2025 showed big differences in the population dynamics between *G. repens* depending on the forest age and the evaluated spatial scale (Figure 1). Regarding the younger forest stands (47-57 years) regenerated after clearcutting, the populations stayed stable over the 12-year period across all three spatial scales. (mean net change = 0.00, $p=1.0$; Table 2). The landscape context of the orchid was however very scarce also in the first inventory in 2013, meaning that *G. repens* has not been able to colonize a greater share of young stands since then. There was a 10% occurrence at the stand level, the within-stand occurrence was 1% and the local patch occupancy was as low as 0.025% (Table 1).

In contrast to the young forest, the old forest stands (>85 years old) showed a significant decline in the within stand level as well as the local plot level. This means that there was a clear reduction in occurrence for *G. repens* within the forest stands. At the within stand level, old forests experienced a significant average loss of 2.33 occupied plots per forest stand (mean change = -2.33, $p=0.009$; Table 2). At the local plot level, I also observed a significant decline in occurrence as the orchid disappeared from an average of 6.33 local plots per forest stand (mean change = -6.33, $p=0.021$; Table 2).

Although the landscape level occupancy level changed from 100% in 2013 to 67% in 2025 (Table 1) the change was not significant ($p=0.175$). This indicates that the orchid has managed to persist in the broader landscape but is declining internally within stands. Welch's two-sample t-tests robustly confirmed that this fine- and intermediate-scale deterioration in old forests was significantly different from the absolute stability observed in the young production forests (within stand level: $p=0.007$; local plot level: $p=0.021$; Table 3).

4.2 Population trends in *A. sarmentosa*

The assessment of the inventories conducted between 2013 and 2025 for *A. sarmentosa* showed an ability to recolonize younger stands regenerated after clearcutting as well as to remain stable in the older forest stands. The lichen showed a significant increase across all three spatial scales in the younger forests. At the stand level in younger forests, the lichen went from occupying 30% of the stands to 100% (mean net change = +0.70, $p=0.001$; Table 2), colonizing 70% of the young forest landscapes where it was entirely absent 12 years ago. At the within stand level, the lichen went from occupying 7% of the plots in 2013 to 80% in 2025 (mean net change = +7.30, $p<0.001$; Table 2), expanding its presence significantly within the forest stands. At the local plot level in younger forests, I also saw a significant increase, going from occupying only 0.018% of the local plots in 2013 to 50.5% in 2025 (mean net change = +19.50, $p<0.001$;

Table 2). In contrast, in the older forests I found no significant change in occurrence in any of the three assessed spatial scales (Table 3).

Welch's two-sample t-tests strongly confirmed that the robust recolonization surge quantified in the young production stands was statistically and fundamentally different from the stagnant dynamics of the older, continuous forests across all three spatial resolutions (stand level: $p=0.001$; within stand level: $p<0.001$; local plot level: $p=0.002$; Table 3).

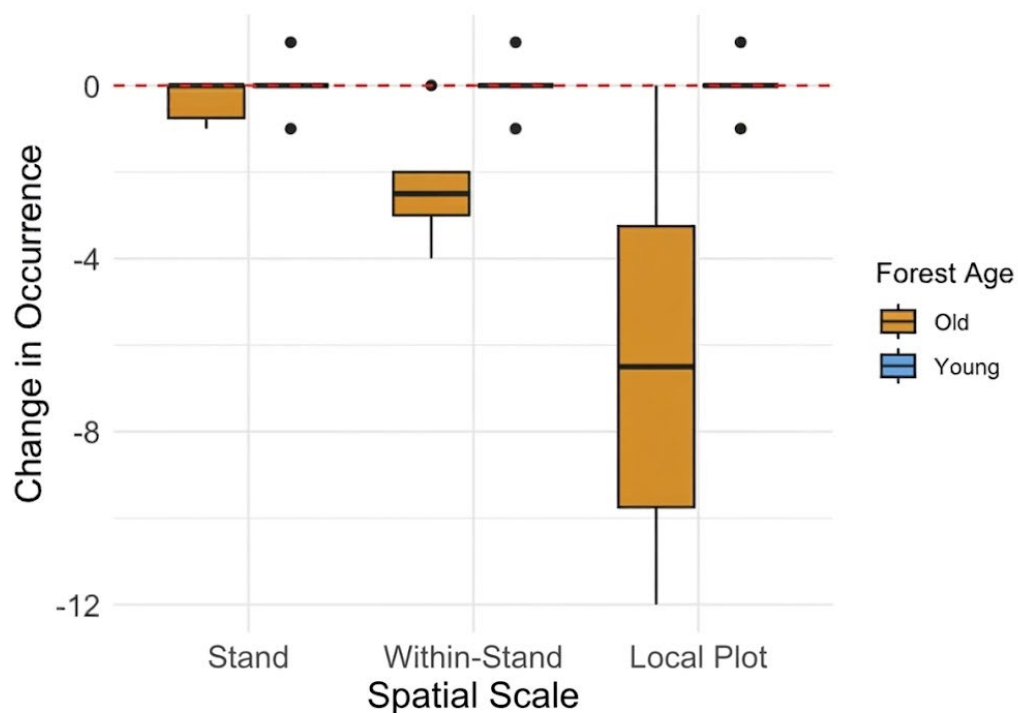


Figure 2. Change in the occurrence of *G. repens* between the two inventory periods (2013 - 2015) across three spatial resolutions. Decline between the two inventory occasions are indicated by values below zero. Distribution of change is displayed by the boxplots with the horizontal line representing the median, the enclosing box represents the interquartile range (25th to 75th percentiles and the whiskers extend to extreme data points within 1.5 times the interquartile range. Outliers are shown as points outside the whiskers. One-sample t-tests confirmed that the decline in old forests was statistically significant at within stand level ($p = 0.009$) and local plot level ($p = 0.021$), but not at stand level ($p = 0.175$). Occurrence in young forests remained completely stable across all resolutions ($p = 1.0$).

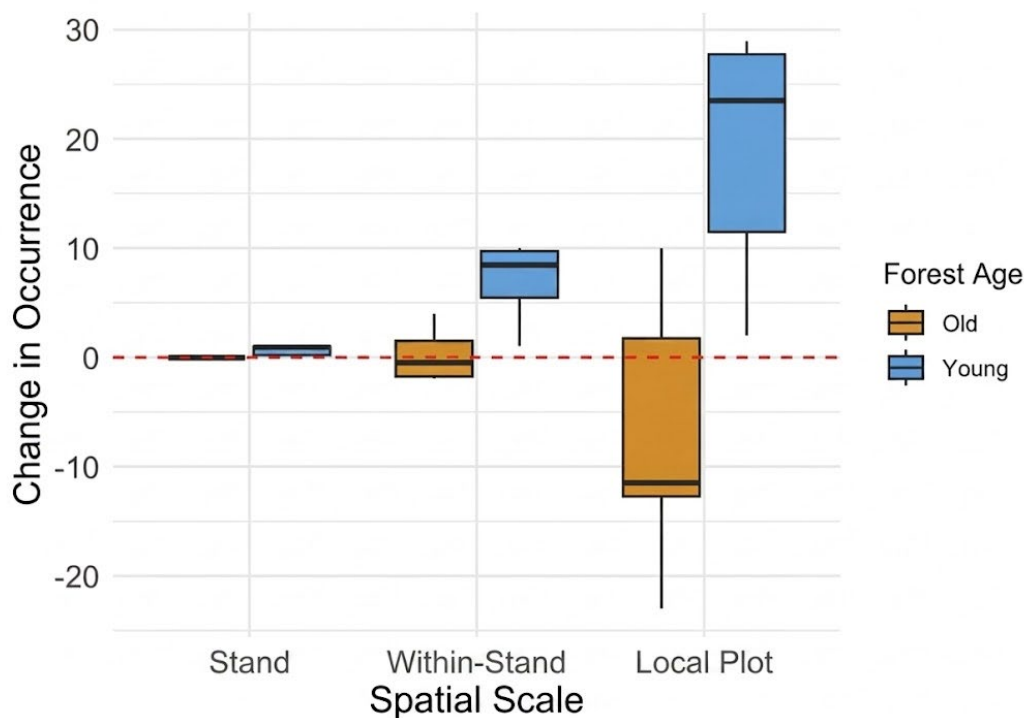


Figure 3. Change in the occurrence of *A. sarmentosa* between the two inventory periods across three spatial resolutions. Decline between the two inventory occasions are indicated by values below zero. Distribution of change is shown with the boxplots with the line representing the median, the enclosing box represents the interquartile range (25th to 75th percentiles) and the whiskers extend to extreme data points within 1.5 times the interquartile range. Outliers are shown as points outside the whiskers. The red dashed line represents a value of zero change. One-sample t-tests showed a highly significant increase in occurrence in young forests across all resolutions: stand level ($p = 0.001$), within stand level ($p < 0.001$), and local plot level ($p < 0.001$). Occurrence in old forests showed no significant deviation from zero at any resolution (stand level: no change; within stand level: $p = 0.872$; local plot level: $p = 0.222$).

Table 1. Baseline (2013) and present (2025) occurrence patterns of *G. repens* and *A. sarmentosa* across young production forests (47–57 years old) and late-successional old forests (>85 years old) in Hälsingland, Sweden. Values represent the actual biological occurrence quantified during the 2013 and 2025 inventories across three distinct spatial resolutions: stand-level occurrence, within-stand occurrence, and local plot occurrence, represented as the percent of occupied plots. Young forests: (stand level ($n=10$ stands), within stand level ($n=100$ plots), and local plot level ($n=400$ subplots) and old forests: (stand level ($n=6$ stands), within stand level ($n=60$ plots) and local plot ($n=240$ subplots)).

Species and spatial scale	Young forests 2013	Young forests 2025	Old forests 2013	Old forests 2025
<i>G. repens</i>				
Stand	10%	10%	100%	67%
Within stand	1%	1%	34%	10%

Local plot	0.025%	0,025%	18%	2,5%
<i>A. sarmentosa</i>				
Stand	30%	100%	100%	100%
Within stand	7%	80%	85%	86.7%
Local plot	0.018%	50.5%	68%	50%

Table 2. P-values from one-sample t-tests comparing the mean change in occurrence against zero for *G. repens* and *A. sarmentosa*. Tests were conducted separately for young and old forests across three spatial resolutions (stand level, within stand level and local plot level).

Species	Age	Stand level	Within stand level	Local plot level
<i>G. repens</i>	Young	NS (p=1.0)	NS (p=1.0)	NS (p=1.0)
<i>G. repens</i>	Old	NS (p=0.17)	Sig (p=0.009)	Sig (p=0.021)
<i>A. sarmentosa</i>	Young	Sig (p=0.001)	Sig (p<0.001)	Sig (p<0.001)
<i>A. sarmentosa</i>	Old	NS (NaN*)	NS (p=0.87)	NS (p=0.22)

Table 3. Results from Welch's two-sample t-tests comparing the mean change in occurrence between young and old forests for *G. repens* and *A. sarmentosa* across three spatial resolutions (stand level, within stand level and local plot level).

Species	Resolution level	Mean change (young)	Mean change (old)	t-value	df	p-value
<i>G. repens</i>	Stand	0.00	-0.33	-1.29	9.88	0.226
<i>G. repens</i>	Within stand	0.00	-2.33	-4.04	5.72	0.007
<i>G. repens</i>	Local plot	0.00	-6.33	-3.31	5.06	0.021
<i>A. sarmentosa</i>	Stand	0.70	0.00	-4.58	9.00	0.001
<i>A. sarmentosa</i>	Within stand	7.30	0.17	-5.18	12.75	<0.001
<i>A. sarmentosa</i>	Local plot	19.50	-7.17	-4.37	9.12	0.002

While the occurrence of *G. repens* in young forests did not change over time (mean change = 0), the occurrence in old forests showed decline. One-sample t-tests confirmed that this decline in old forests was statistically significant at both

within stand level (mean change = -2.33, $t(5) = -4.18$, $p = 0.009$) and local plot level (mean change = -6.33, $t(5) = -3.32$, $p = 0.021$).

When assessing forest stands (6) that had been clear-cut approximately 6-10 years after the first inventory made in 2013, no individuals of *G. repens* were found. A total of 6 clear-cut stands were assessed and they were clear cut approximately 6-10 years ago. No individuals of *A. sarmentosa* were found either as there were no trees large enough for them to grow after the area was clear-cut.

4.3 Correlation with landscape frequency (Public findings)

4.3.1 Relationship between public findings and change over time

A correlation analysis showed a significant negative correlation between the change of occurrence and the public findings of *G. repens* both within stand level ($r = -0.527$, $p = 0.044$) and local plot level ($r = -0.594$, $p = 0.019$) (Table 4). A significant negative correlation was also found for *A. sarmentosa* at the local plot level ($r = -0.532$, $p = 0.041$; Table 4), indicating that forest stands located in landscapes with more reported findings experienced a bigger decline in the local occurrences of both species.

When stratifying the data by forest age, no significant correlations were observed between the changes in occurrence and public findings, for neither young or old forests (Table 5).

4.3.2 Relationship between public findings and current occurrence

A correlation test between the current species occurrence in all three spatial resolution levels and reported public findings showed no significant correlation for any of the two assessed species (Table 6).

Table 4. Table showing the correlation between public findings and change in occurrence of G. repens and A. sarmentosa summary of all results from the analysis for stand level, within stand level and local plot level. (Not based on forest age). The focus is on whether the relationship between the number of findings in the surrounding area and the change in the forest stand is significant ($p < 0.05$).

Species	Resolution level	Correlation (r)	p-value
<i>A. sarmentosa</i>	Stand	-0.398	0.142
<i>A. sarmentosa</i>	Within stand	-0.470	0.077
<i>A. sarmentosa</i>	Local plot	-0.532	0.041
<i>G. repens</i>	Stand	-0.142	0.615

<i>G. repens</i>	Within stand	-0.527	0.044
<i>G. repens</i>	Local plot	-0.594	0.019

Table 5. Table showing correlation between public findings and change of occurrence of *G. repens* and *A. sarmentosa* (based on forest age) from the analysis for stand level, within stand level and local plot level. The focus is on whether the relationship between the number of findings in the surrounding area and the change in the forest stand is significant ($p < 0.05$). NA values had zero variance. *G. repens* in young forest were excluded in this table as there were no changes in these cases.

Species	Forest age	Resolution level	Corr. (r)	p-value
<i>G. repens</i>	Old	Local plot	-0.307	0.615
<i>G. repens</i>	Old	Within stand	-0.115	0.854
<i>G. repens</i>	Old	Stand	NA	NA
<i>A. sarmentosa</i>	Young	Local plot	-0.203	0.574
<i>A. sarmentosa</i>	Young	Within stand	-0.235	0.513
<i>A. sarmentosa</i>	Young	Stand	-0.400	0.252

Table 6. Table showing the summary of correlation analysis between the number of reported surrounding findings and the current species occurrence level (post-2025 measurement). Significance level: ($p < 0.05$)

Species	Forest type	Resolution Level	Corr. (r)	p-value
<i>G. repens</i>	Old	Local plot	0.752	0.143
<i>G. repens</i>	Old	Within stand	0.752	0.143
<i>G. repens</i>	Old	Stand	NA	NA
<i>A. sarmentosa</i>	Old	Local plot	0.255	0.679
<i>A. sarmentosa</i>	Old	Within stand	-0.049	0.938
<i>A. sarmentosa</i>	Old	Stand	NA	NA
<i>A. sarmentosa</i>	Young	Local plot	-0.173	0.633
<i>A. sarmentosa</i>	Young	Within stand	-0.135	0.710
<i>A. sarmentosa</i>	Young	Stand	NA	NA

4.4 Influence of forest density

Linear regression models were utilized to analyze the relationship between the change in occurrence (based on within stand occurrence) of both *G. repens* and *A. sarmentosa* and the total basal area of trees (BA) as proxy for forest stand density. No significant relationships were detected for any of the two species in either old or young forests (Table 7).

Table 7. Summary of linear regression analyses for the relationship between the change in occurrence of *G. repens* and *A. sarmentosa* and the total basal area (m²/ha) of trees within stand occurrence in old and young forests. The table includes forest age, intercept (k), estimate (m), coefficient of determination (R²), and p-value.

Species	Forest age	Intercept (k)	Estimate (m)	R ²	p-value
<i>G. repens</i>	Old	-0.616	0.014	0.043	0.101
<i>G. repens</i>	Young	0.030	-0.001	0.003	0.578
<i>A. sarmentosa</i>	Old	-0.341	0.014	0.055	0.064
<i>A. sarmentosa</i>	Young	0.716	0.0002	<0.001	0.982

4.5 Change in occurrence in relation to topographic directional aspect of the ground

The change of *G. repens* occurrence over time was not significantly related to the topographic directional aspect of the ground (Kruskall-Wallis test: p=0.523, n=94). Further, there were no significant differences found when stratifying the data by the forest age. Young: (not tested as there were no change) and old: (p=0.533, n=44).

The change of *A. sarmentosa* occurrence over time was not significantly related to the topographic directional aspect of the ground (Kruskall-Wallis test: p=0.054, n=94). There also were no significant differences found when stratifying the data by the forest age. Young forests: (p=0.626, n=50) and old forests: (p=0.076, n=44).

4.6 Effect of management treatments on *G. repens*

A one-way ANOVA showed that the choice of silvicultural practice had a significant influence on the short-term change in occurrence of *G. repens* ($F_{2,75} = 3.31$, p=0.042). According to a Tukey HSD post-hoc test, there was a significant difference in the net change of individuals between the unlogged reference area and the clear-cut stands (p=0.037), where clear-cut areas had lost more individuals (Figure 6). The shelterwood treatment did, however, not differ significantly from either the unlogged reference area or the clear-cut areas (Figure 6). When examining potential differences between treatments regarding recruitment of new

individuals (Kruskal-Wallis test, $\chi^2_2=5.05$, $p=0.080$) as well as the number of lost individuals (Kruskal-Wallis test, $\chi^2_2=4.36$, $p=0.113$), no significant differences were found (Figure 7, Figure 8).

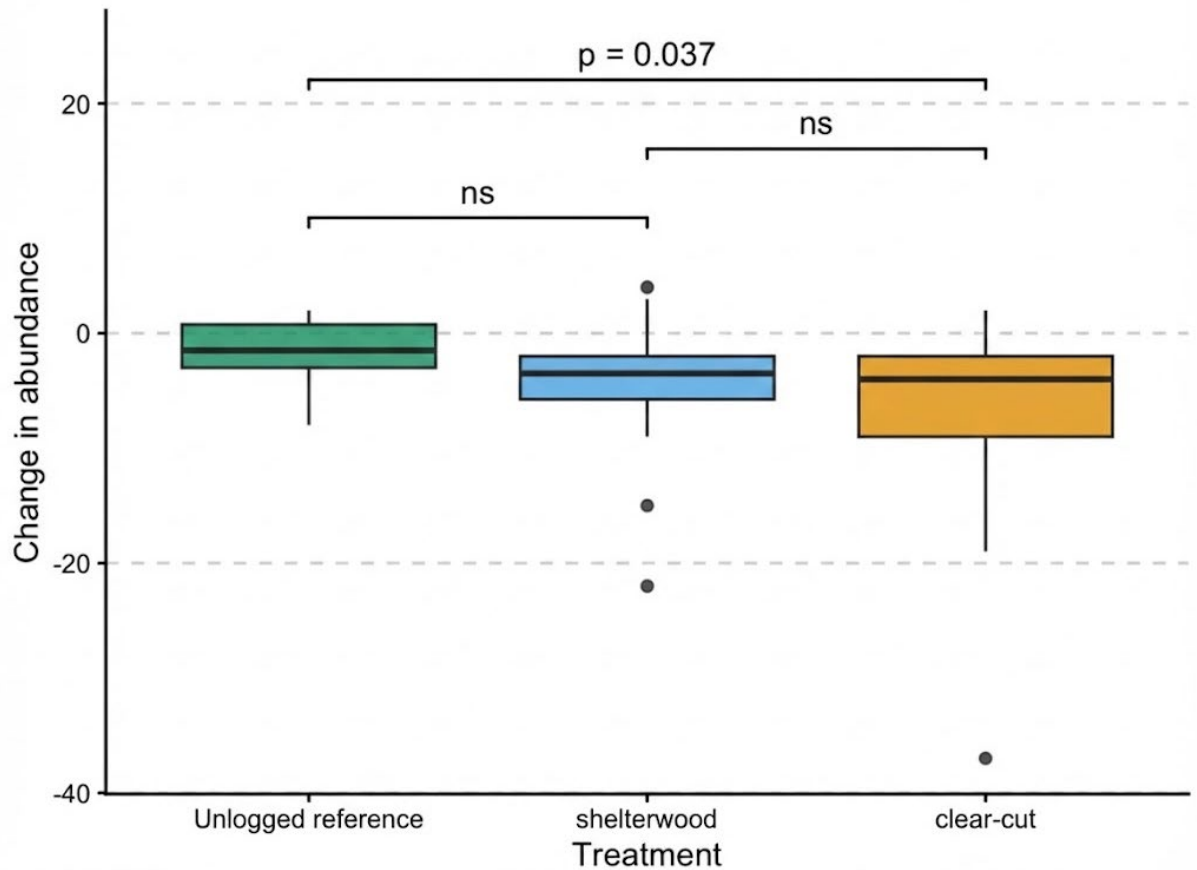


Figure 4. Effect of different forest management treatments (Clear-cut, shelterwood, and unlogged reference) on the change in occurrence of the orchid *G. repens*. Change in occurrence is defined as difference in individuals between the two sampling periods, i.e. survival and losses of marked individuals and new additional individuals. The thick horizontal line represents the median, the box indicates the interquartile range (25th–75th percentiles), and the vertical whiskers extend to the minimum and maximum values within 1.5 times the interquartile range. Data points outside this range are plotted as outliers. Statistical comparisons were performed using a one-way ANOVA followed by Tukey's HSD post-hoc test. Significant differences ($p < 0.05$) are displayed with specific p -values, while non-significant differences are denoted as "ns". Sample size=78.

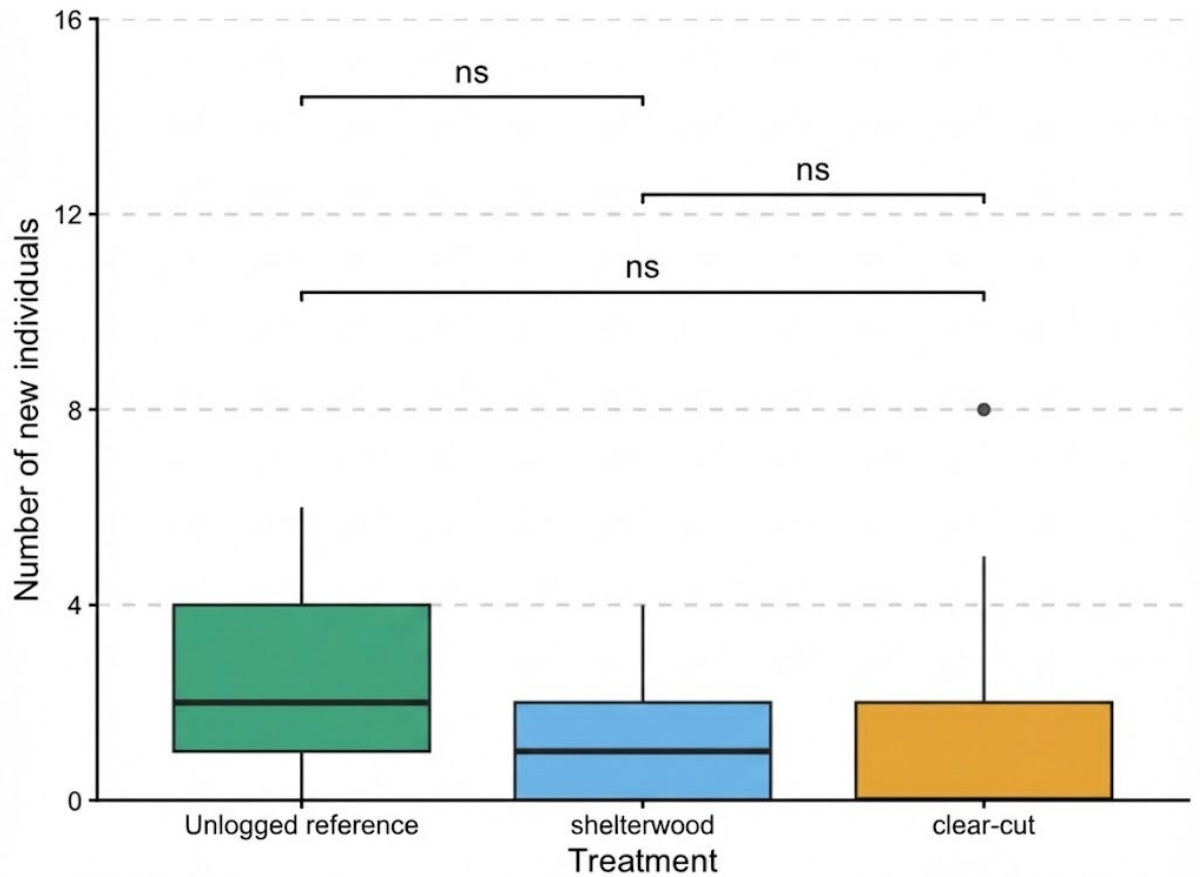


Figure 5. Effect of different forest management treatments (Clear-cut, shelterwood, and unlogged reference) on the recruitment of new individuals of the orchid *G. repens*. Change in occurrence is defined as difference in individuals between the two sampling periods, i.e. survival and losses of marked individuals and new additional individuals. The thick horizontal line represents the median, the box indicates the interquartile range (25th–75th percentiles), and the vertical whiskers extend to the minimum and maximum values within 1.5 times the interquartile range. Data points outside this range are plotted as outliers. Statistical comparisons were performed using a one-way ANOVA followed by Tukey's HSD post-hoc test. Significant differences ($p < 0.05$) are displayed with specific p -values, while non-significant differences are denoted as "ns". Sample size=78.

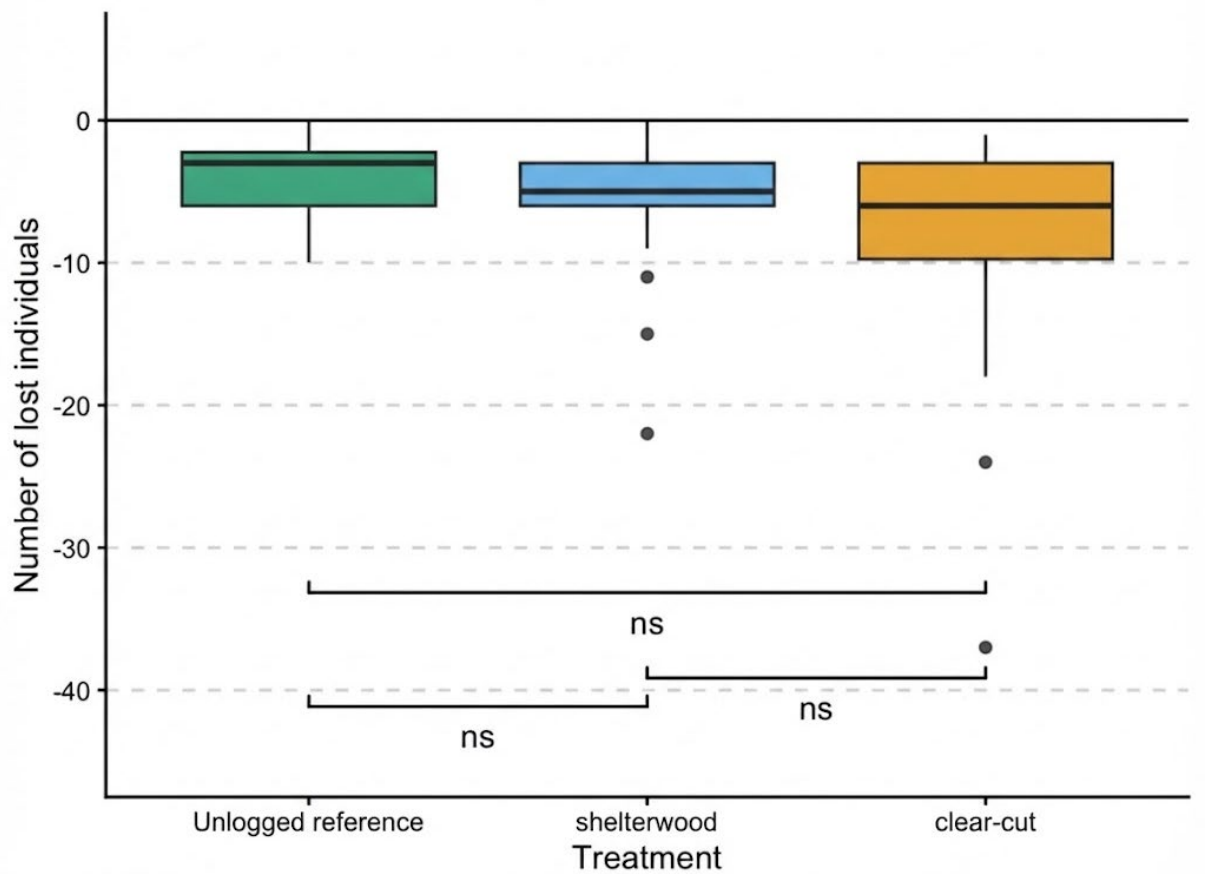


Figure 6. The number of *G. repens* individuals lost (mortality or disappearance) per plot across different forest management treatments. Lost individuals are defined as marked individuals that were lost (died) between the two sampling periods. Boxplots represent the median and interquartile range. No significant differences in the absolute number of lost individuals were found between treatments (Kruskal-Wallis test, $\chi^2_2=4.36$, $p=0.113$).

4.7 Canopy openness relationship to change in occurrence of *G. repens*

A Spearman's rank correlation test showed that there was no significant correlation between the current (2025) canopy openness and the change of occurrence of *G. repens* (ρ or $r_s=0.16$, $p=0.159$; Figure 9). A linear regression analysis also showed that there was no relationship between canopy openness and change of occurrence of *G. repens* ($\beta=-3.053$, $p=0.386$, $R^2=0.01$; Figure 10).

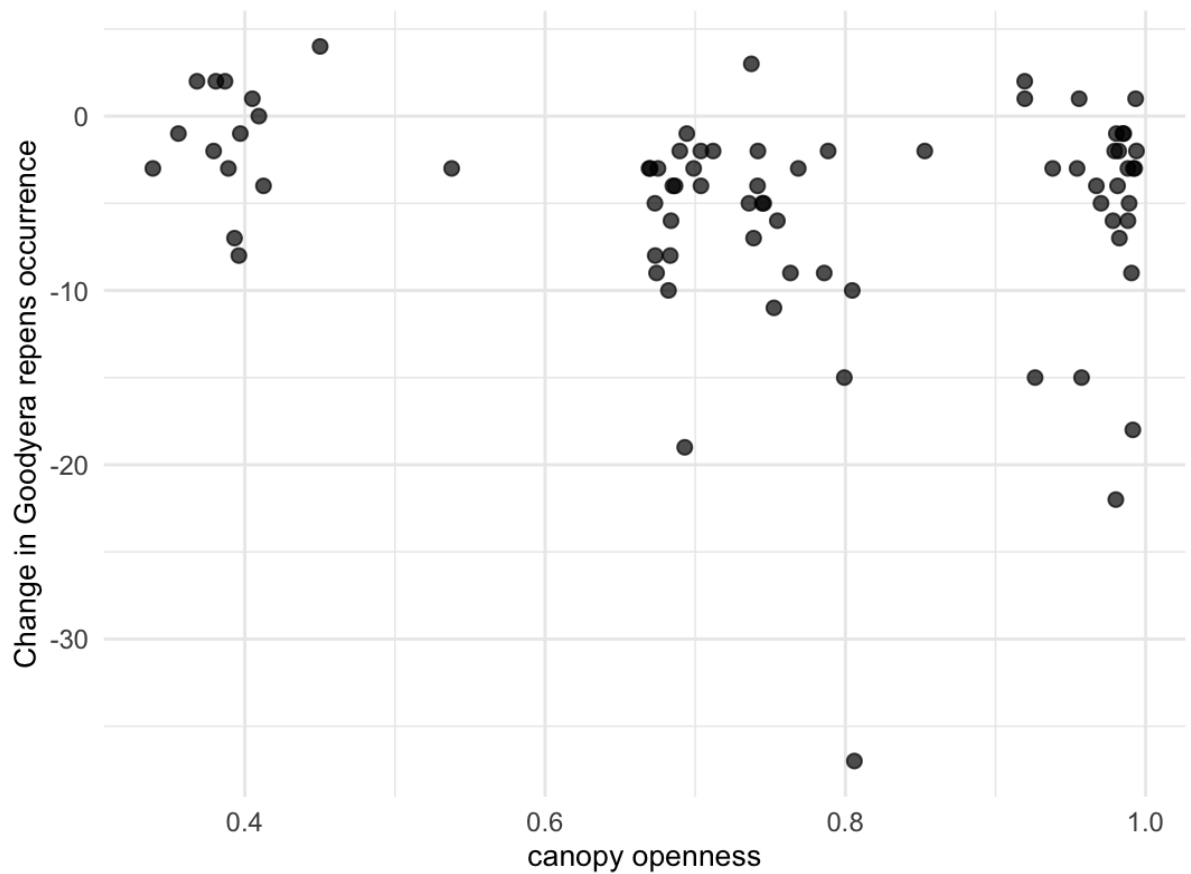


Figure 7. Change in *G. repens* in relation to canopy openness. Each point represents one site. The analysis showed a weak negative, but statistically non-significant, correlation between canopy openness and the change in *G. repens* occurrence (Spearman's $\rho = -0.16$, $p = 0.159$). There was a weak, but non-significant relationship between change in occurrence of *G. repens* and canopy openness.

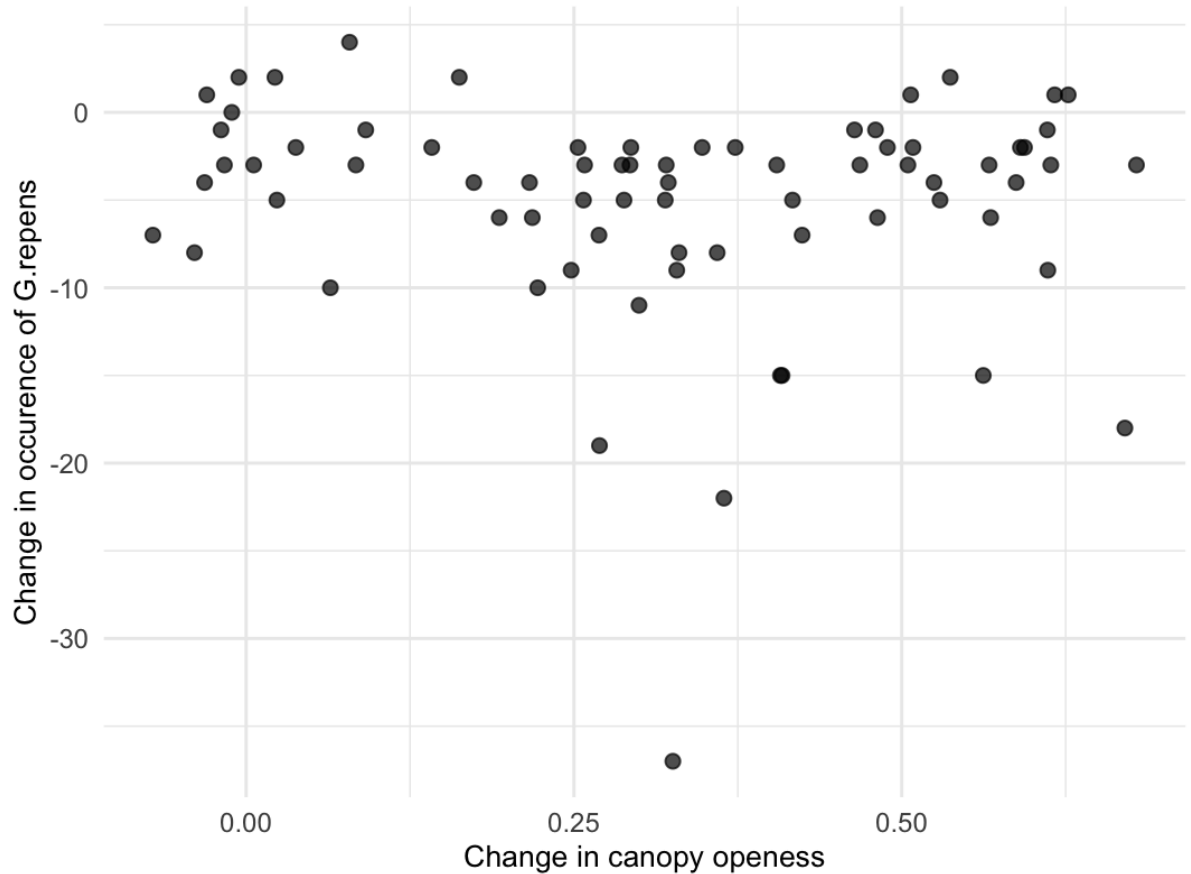


Figure 8. Relationship between changes in canopy openness and changes in *G. repens* occurrence across study sites. Each point represents one site. Results from a linear regression test shows a weak, non-significant association between the variables ($\beta = -3.053$, $p = 0.386$, $R^2 = 0.01$).

4.7.1 Canopy openness relationship to recruitment and mortality

Linear regression models were also used to test if there was a significant relationship between the change in canopy openness and the number of new individuals of *G. repens* between 2024 and 2025. The test revealed no statistical support for such a relationship ($F_{1,68} = 0.3719$, $p = 0.544$, $R^2 = 0.005$; Figure 11). There was also no significant relationship between the change in canopy openness and the number of lost individuals of *G. repens* ($F_{1,68} = 1.119$, $p = 0.294$, $R^2 = 0.016$; Figure 12)

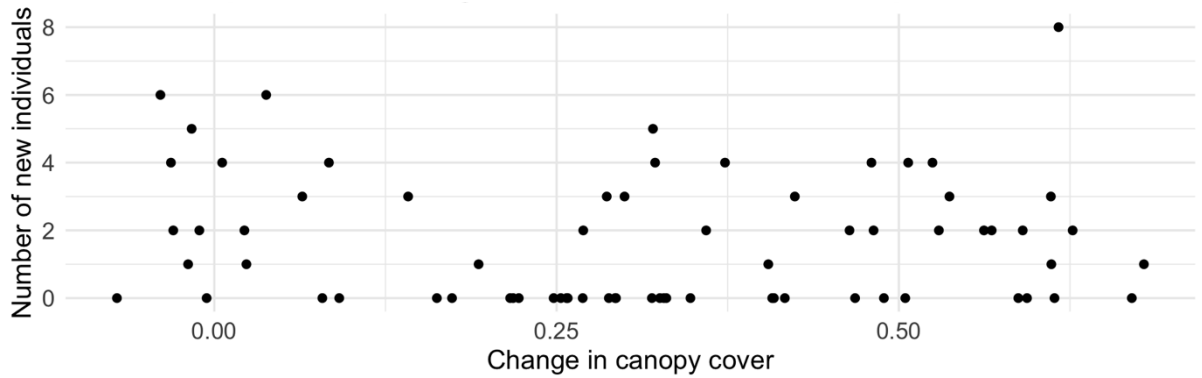


Figure 9. Change in *G. repens* individuals in relation to change in canopy cover. Data shows the number of new *G. repens* individuals established in relation to net change in canopy cover in the different forest management treatments. Linear regression analysis showed no statistically significant relationship between the change in solar radiation and the establishment of new individuals ($F_{1,68}=0.3719$, $p=0.544$, $R^2=0.005$). The estimated slope was -0.6595 , indicating a weak, non-significant decrease in recruitment with decreasing canopy cover.

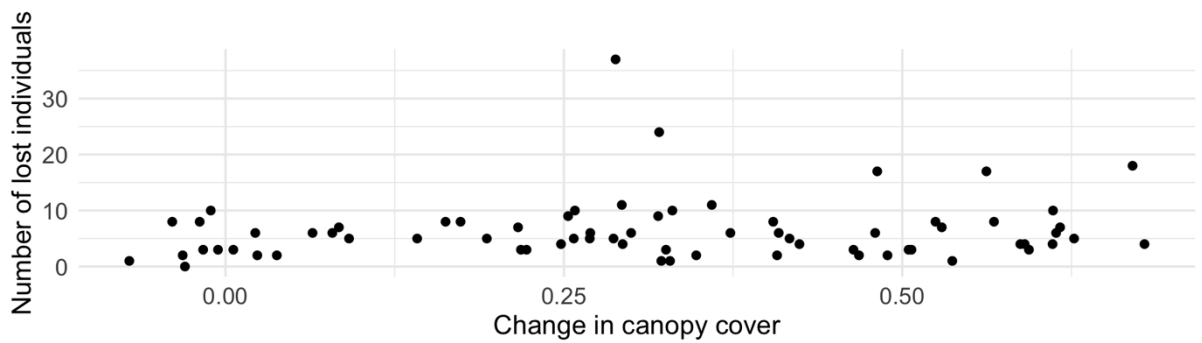


Figure 10. Figure illustrating the correlation between the change in canopy cover and the number of *G. repens* individuals lost from the sampling plots. Linear regression analysis showed no statistically significant relationship between the change in solar radiation and the number of lost individuals ($F_{1,68}=1.119$, $p=0.294$, $R^2=0.016$). The estimated slope was 3.383 , suggesting a weak, non-significant increase in the loss of individuals with decreasing canopy cover.

5. Discussion

5.1 Change in occurrence of *A. sarmentosa*

Alectoria. sarmentosa showed a significant increase in young forests between 2013 and 2025 across all three measured spatial scales. In 2025, *A. sarmentosa* was found in all young stands included in the survey (see Table 1, Figure 3). These findings suggest that young forests (47-57 years) have begun to develop enough structural complexity to allow for new establishment of *A. sarmentosa*. Lack of such structural complexity is suggested as an important reason why this lichen is missing from young forest stands regenerated after clear-cutting (Esseen et al. 1996; Dettki et al. 1998).

While these findings may appear to contrast with the reported 50% landscape-scale decline of pendulous lichens in Sweden (Esseen et al. 1996; Esseen et al. 2022), they likely reflect the specific ecological context of the Hälsingland study area. According to data observed on [Artportalen.se](https://artportalen.se), the Hälsingland area seems to contain a generally greater number of reported findings of *A. sarmentosa* compared to other parts of Sweden. This could explain why I see different results compared to other studies. The data from [Artportalen.se](https://artportalen.se) is however problematic as it is difficult to get a proper picture of the amount of *A. sarmentosa* in every area in Sweden.

This also indicates that the observed fast recolonization found in this study might be a result of a higher connectivity in this region compared to other regions, and that this particular landscape has density of dispersal sources high enough to compensate for the habitat losses that occur through the current rate of clear-cutting (Ellis 2012; Esseen et al. 2022). This result would indicate the importance of maintaining areas in terms of biodiversity so that they are not cut down immediately when reaching the minimum required age for harvesting, in order to let these specialized species return more effectively to managed production stands (Ellis 2012; Nordén et al. 2014; Esseen et al. 2022).

5.2 Topographic influence

The results regarding the topographic directional aspect of the ground showed no statistically significant association to the change of occurrence for *A. sarmentosa*, although the influence of topographical directional aspects was almost significant ($p=0.054$). The slope aspect should in theory be a critical factor for local microclimates. Slopes which are north-facing generally offer a higher level of moisture retention and lower temperatures compared to south-facing slopes that are more exposed to sunlight (Zhang et al. 2024; Chen et al. 1993). The fact that I did not find any statistical influence of the slope aspect suggests that larger scale anthropogenic disturbances from forestry may have such a large impact on the microclimates that it overshadows the effects of topography (Koelemeijer et al. 2022; Esseen et al. 1997; Zhang et al. 2024).

Additionally, to the directional aspect, other topographic factors such as the relative topographical position as well as the slope inclination could potentially play a role in the observed patterns (Hylander 2005; Ellis 2012). If the assessed stands had a low inclination, the difference in microclimate between north- and south-facing areas could be less prominent and more difficult to detect. The relative topographic position of a stand can also be a relevant factor. The assessed stand could either be situated on an exposed ridge, or in a sheltered valley, while still being north- or south facing, affecting the wind exposure and moisture accumulation (Ellis 2012). Additionally, variations in the local soil properties could also affect the water retention in the area (Ellis 2012; Tsiftsis et al. 2012), further affecting the local resilience of specialized species (Tsiftsis et al. 2012; Zhang et al. 2024).

The near significant positive result of *A. sarmentosa* having more individuals on north-facing slopes is however noteworthy from a conservation perspective. As an epiphytic lichen having its habitat above the ground, it is more exposed to the factors such as wind and solar radiation compared to ground living organisms (Esseen et al. 1997; Esseen et al. 2022). This could indicate that topographic differences could still have an effect on the lichen's ability to persist after an anthropogenic disturbance (Hylander 2005; Zhang et al. 2024).

A noteworthy limitation of the analytical approach in this study was the isolation of environmental factors in separate analyses. By examining the forest density and directional slope aspect independently, the analysis potentially oversimplifies the multi-dimensioned complexity of the microclimate buffering system (Hylander 2005; Koelemeijer et al. 2022). In a forest system, the environmental factors do not operate independently. They instead interact dynamically to affect the microclimate. For example, a higher forest density could potentially lessen the amount of solar radiation received by a south facing slope that would otherwise receive a higher amount of solar radiation while a more open canopy could amplify the stress on the same position (Zhang et al. 2024). So by not combining these variables into an interactive modeling approach, potentially interactive effects could not be found. Future studies should therefore approach the analysis with this in mind.

5.3 The role of forest density for *A. sarmentosa*

When analysing the correlation between the total basal area of trees and the occurrence of *A. sarmentosa*, no significant results were found (see Table 7). This pattern was the case for both young and old forests, although some results approached significant correlation, for example a near positive correlation for *A. sarmentosa* in old forests ($p=0.064$).

These results are noteworthy from an ecological perspective as the basal area of trees was used as a proxy in this study for the light availability, which in turn affects the microclimate (Zhang et al. 2024; Zhang et al. 2025). The higher forest density should in theory help maintain the high humidity and stable temperatures required by these specialized species (Zhang et al. 2024; Johansson et al. 2026).

The absence of a significant correlation may be interpreted through various factors. One possibility could be that the stability of the microclimate is only attained when the forest reaches some specific thresholds of the trees basal area (Zhang et al. 2024). Such threshold may be critical for the possibilities of a species to get established but values that are well below or above such threshold, may be of limited importance for explaining changes in occurrence over time. Another possibility that could explain the lack of a significant correlation between the basal area of trees and the occurrence of the assessed species is that the basal area of trees is too rough of a measurement to properly assess the variation in microclimate and light availability that determine the occurrence of the lichen. If so, this would mean that the relevant factors could not be measured to the required extent by the basal area alone.

5.4 Change in occurrence for *G. repens*

The significant decline of the populations of *G. repens* in older forests suggests that the species is sensitive to both direct and indirect factors and it also suggests that only the presence of older trees is not enough to sustain stable populations of *G. repens*.

The complete absence of *G. repens* individuals in the forest that had been clear-cut between the inventory in 2013 and the one in 2025 supports the conclusion that clear-cutting has large negative effects on the species. Seen in this context my result is in accordance with the earlier claims that *G. repens* is highly sensitive to the environmental change that clearcutting imposes (Johnson 2014; Johansson et al. 2026).

The results from the inventory in Hälsingland also revealed the near complete absence of recolonization in the young stands regenerated after clearcutting, where the occurrence remained as near zero through the 12-year long study period. This is a strong indication of *G. repens* high dependence on long forest continuity and would suggest that even half a century after clear-cutting, the forest has not regained the necessary structural attributes, such as stable microclimates that makes it possible for *G. repens* to recolonize (Cameron et al. 2006; Nordén et al. 2024; Těšitelová et al. 2022). As the modern silvicultural rotation periods in the region is about 80-100 years, *G. repens* might not get the time required for recolonization of these forest stands before they are logged again. This could eventually lead to the complete extinction of *G. repens* within managed forest stands which confirms the problematic situation for this species (Johnson 2014; Johansson et al. 2026).

The basal area of trees was used as a proxy in this study for the light availability which in turn affects the microclimate (Zhang et al. 2024; Zhang et al. 2025). The higher forest density should in theory help maintain the high humidity and stable temperatures required by these specialized species. (Zhang et al. 2024; Johansson et al. 2026). The absence of a significant correlation may be interpreted as further sign to the species being sensitive to a combination of drivers (Koelemeijer et al. 2022; Johansson et al. 2026).

One major factor that potentially could explain the significant decline of *G. repens* populations in older forests at both the within-stand and local occurrence levels, is the effects from edge effects originating from forest management in the surrounding landscape. When nearby forest stands are clear-cuts, the remaining forest stands get more exposure from wind, higher temperatures and lower humidity retention (Zhang et al. 2024; Zhang et al. 2025; Koelemeijer et al. 2022). *Goodyera repens* being a highly sensitive species, even relatively minor shifts in the local microclimate can exceed what the species can physiologically handle (Johansson et al. 2026).

In my study, I found no correlation between the changes in population and forest density which would indicate that higher forest density does not mean higher populations. While it is often assumed that denser and darker forests provide a stronger buffer effect (Zhang et al. 2024), the absence of a statistical correlation in this study suggests that there are other factors in play (Koelemeijer et al. 2022; Zhang et al. 2025). It could be that *G. repens* is more adapted to a semi open, or heterogeneous forest, rather than dense production stands that are common today (Esseen et al. 1997; Hedwall et al. 2019; Kyaschenko et al. 2022). If this is the case, and the orchid is more adapted to the structural heterogeneity and small-scale gap dynamics characteristic of natural old-growth forests, it could explain why no correlation was found between mere forest density and population changes (Esseen et al. 1997; Johansson et al. 2025; Johansson et al. 2026; Widenfalk & Weslien 2009).

Analysis regarding further environmental landscape context and factors showed results where no significant positive correlation between the number of reported sightings of the species and the change of occurrence was found (see Table 4). Other examined factors such as canopy openness, topographic directional aspect and the total basal area of trees showed no significant correlation with population changes, suggesting that the persistence of *G. repens* is affected by factors beyond the structure of the forest alone (see Figure 9, Table 7).

Furthermore, the results for *G. repens* could be an indication of “extinction debt” (Nordén et al. 2014; Johansson et al. 2026). The observed observations of declining populations in the older forests in the within-stand occurrence and local occurrence might mean that the areas have undergone fragmentation long ago and the trend we are seeing is a delayed response where smaller, isolated populations are slowly disappearing as they are no longer connected to a bigger network. The absence of a significant decline in the stand level does however make it impossible to say for certain that extinction debt is the observed phenomenon. If the observed trend is a result of extinction debt, conservation of these specialized species would require management that extends beyond the local habitats in order to account for large-scale habitat continuity (Ellis 2012; Nordén et al. 2014).

The lack of a significant positive correlation between reported sightings in the surrounding landscape and the declining populations of *G. repens* could further point to the effect of extinction debt. According to Artportalen.se, landscapes in

the assessed areas has historically been rich in *G. repens*. This could indicate that the fragmentation of these areas has been enough to trigger a “payment” of the extinction debt (Kuussaari et al. 2009; Johansson et al. 2026).

5.5 The role of forest density for *G. repens*

This study did not find any significant correlation between the basal area of trees and the population changes. Previous studies have shown that the probability of *G. repens* occurrence significantly increases in stands where the basal area of trees exceeds 30 m²/ha (Johansson et al. 2026). The assessed stand in this study had primarily basal areas below 30 m²/ha which is below this potential threshold, explaining why the statistical models might have failed to detect any significant correlation between species occurrence and basal area in my study.

While my study mainly focused on broader structural proxies such as the topographic aspects and the basal area of trees, other factors that were not assessed in this study might have a more prominent effect on the local environments of *G. repens* and *A. sarmentosa*. The lack of assessments of these factors might explain the lack of a significant correlation in forest density and topographic aspects (Esseen et al. 1996; Ellis 2012; Tsiftsis et al. 2012; Johansson et al. 2026).

Potential important factors which were not assessed in the Hälsingland inventory are the presence of specific microhabitats (Esseen et al. 1997; Winter & Möller 2008), vertical layering (Esseen et al. 1997; Ellis 2012) and the composition of tree species (Ellis 2012; Zhang et al. 2024) which all have documented significant effects on the habitat.

5.6 Short-term Effects of Harvest Methods on *G. repens*

My results showed that the changes in occurrence of *G. repens* after clear-cutting and shelterwood logging contrasted against unlogged reference forest. This gives some insight to whether shelterwood logging might be an alternative practice to mitigate negative effects from logging on sensitive species such as *G. repens*.

The Uppland experiment confirmed that the orchid is sensitive to the change in environmental conditions that forestry imposes. The short-term survival of *G. repens* was significantly affected by the choice of silvicultural treatment, where clear-cutting led to a significantly higher negative net change of individuals compared to the undisturbed unlogged reference areas (see Figure 6). The shelterwood method ended up as “middle ground” between the other two treatments, showing no significant difference from either of them. Regarding the recruitment and number of lost individuals, no significant difference was found between the treatments (see Figure 7 and 8). These results are in accordance with earlier studies highlighting that the species is sensitive to logging operations (Johnson 2014; Johansson et al. 2026).

The results from the experiment in Uppland helps give clarity in the impact of different silvicultural treatments on the short-term survival and persistence of *G. repens*. The results showed that the choice of silvicultural treatment had significant effects on the occurrence of the species within a timeframe of one year (see Figure 6).

The clearest difference was observed between clear-cut stands and the unlogged reference areas, where plots in clear-cut areas experienced a significantly higher loss of individuals compared to the unlogged reference areas (Figure 6). The change is however relatively small after just one year.

The results also showed that the shelterwood treated areas did not differ significantly from the clear-cut areas or the unlogged reference areas. This puts the shelterwood treatment in a sort of intermediate position, indicating that it could potentially offer some degree of protection by partly maintaining a more stable microclimate compared to clear-cutting (Fedrowitz et al. 2014; Zhang et al. 2024). The lack of a statistical difference may, however, still indicate that the partial harvest constitutes a large enough disturbance to exceed the resilience threshold for many individuals (Johnsson 2014; Johansson et al. 2026). Studies that follow the development over longer-time since logging is essential to clarify the potential benefit that application of shelterwood logging may have for species such as *G. repens*.

One surprising result from this study is the fact that no significant relationship between the change in canopy cover and the change in *G. repens* individuals was found (Figure 7 and 8). While the effect of removing trees significantly impacted the species survival, the degree of lost canopy cover above each measuring plot could not predict the number of lost individuals. This result suggests that the survivability of *G. repens* may be driven by other factors than just the amount of solar radiation. Such factors could, for example, be physical damage from the harvesting process, change in the soil moisture, or the disrupting effects on mycorrhizal networks which are important for the nutrient cycling of *G. repens* (Cameron et al., 2006). The variation in microclimate may also have been a factor in these results. I do not have any data to support it, but according to my personal observations, the survival appeared to be higher in deviating microhabitats, such as small depressions and on the north facing side of stones. This might indicate that the short-term survival is more dependent on small-scale variation in microclimatic conditions than the variation in tree canopy cover.

5.7 Management Implications for Boreal Conservation

Forest management in Fennoscandia has historically used a standardized silvicultural regime that is often described as a “one size fits all” approach to forestry (Esseen et al. 1997; Lundmark et al. 2013). This approach has industrial efficiency as a priority, leading to clear-cut areas on a landscape-scale, regardless of the local ecological variations (Östlund et al. 1997; Kuuluvainen et al. 2015). Such a generalized approach does however assume that all of the forest species will respond equally to such a disturbance (Granström 2001).

The results from this study does, however, challenge this assumption. The difference in response between the two assessed species indicates that a “one size fits all” approach to forest management might not be enough for protecting these kinds of specialized species (Kuuluvainen et al. 2021; Lindenmayer et al. 2006; Esseen et al. 2022). The results of this study show that *A. sarmentosa* and *G. repens* have contrasting population dynamics in the examined forests, where *G. repens* showed a significant decline in older forests and was totally lost after clear-cutting. In contrast, *A. sarmentosa* showed an ability to recolonize production stands regenerated after clearcutting. These contrasting responses suggest that a single standardized management strategy cannot address the needs of all species simultaneously (Felton et al. 2020; Esseen et al. 2022). A strict clear-cutting strategy destroys the continuity required by *G. repens* (2014; Johansson et al. 2026), while the survival of *A. sarmentosa* depends more on nearby dispersal sources and the landscape level connectivity rather than the specific harvest method (Ellis 2012; Esseen et al. 2022). Therefore, forest management should instead work towards a more diverse strategy that can combine the needs of several species by protecting older forests to ensure refuge for continuity sensitive species as well as planning to facilitate dispersal opportunities for colonizing species (Esseen et al. 2022; Johansson et al. 2026).

The urgency of a change in management is further highlighted by the silvicultural rotation ages creating a mismatch with *G. repens* slow recolonization rates (Johansson et al. 2026). Young production forests (47-57 years old) showed in this study a near zero occurrence for *G. repens*. This shows that even after half a century, the forest has not regained its required natural attributes for the re-establishment of *G. repens* such as stable microclimates and mycorrhizal networks (Cameron et al., 2006; Zhang et al., 2024; Johansson et al., 2026).

As forestry in this region implies a rotation period of 80-100 years, the window of re-establishment for *G. repens* between clearcuttings is quite narrow (Johansson 2014; Johansson et al. 2026). If the required time for the orchid to re-establish inside a forest exceeds the time of a standard forest treatment rotation, the orchid will effectively be excluded from such forests. Under a standardized “one size fits all” model of management that is dominated by clear-cutting, the local extinctions inside these forests will become permanent (Johansson et al. 2026). This means that maintaining areas of older forests becomes a biological necessity to prevent an eventual regional disappearance of species adapted to forest interior conditions (Ellis 2012; Nordén et al. 2014; Johansson et al. 2026).

The results from the experiment in Uppland suggests that alternate harvesting methods, such as shelterwood logging, can potentially play a role in mitigating the immediate biodiversity loss in boreal forests, in line with what earlier has been shown for retention forestry (Fedrowitz et al. 2014). Shelterwood logging still constitutes a degree of disturbance, but it did not result in significant drop in survival rate which was observed in the clear-cut areas. I cannot, however, say with certainty that shelterwood logged areas can work as a refuge for species like *G. repens*, as indicated by the fact that there were no significant differences

between shelterwood logging and clear-cutting. The results do, however, indicate that shelterwood logging offers some degree of buffering effect, potentially related to buffering of the microclimatic, in line with what previous studies has indicated for retention forestry (Fedrowitz et al. 2014; Zhang et al. 2024). Nevertheless, the most reliable strategy to prevent losses of this specialized species is to set aside the stand from forestry (Johansson et al. 2026).

The results regarding the correlation between species persistence and the frequency of records in the surrounding landscape being a significantly negative correlation emphasizes the need for a larger scale of management. Forest management should not be conducted in isolated patches that increase fragmentation and edge effects. Forest management should instead take connectivity between stands in account in order to ensure the dispersal of organisms like *A. sarmentosa* (Esseen et al. 1996; Dettki 1998; Esseen et al. 2022). In order to prevent local extinctions that can lead to larger regional extinctions, there is a need to maintain a network of mature forest patches (Esseen et al. 1997; Ellis 2012; Nordén et al. 2014; Johansson et al. 2026).

As *A. sarmentosa*'s ability to spread to new stands relies on the dispersal of its relatively heavy vegetative fragments, the distance between the different stands becomes highly relevant (Esseen et al. 1996; Dettki 1998). Even structurally suitable production stands can remain unoccupied if the physical spread of the species is hindered (Dettki et al. 2000; Nordén et al. 2014). The fact that *A. sarmentosa* had colonized so many of the young stands between the two survey periods likely means that the surrounding landscape is sufficiently well connected to ensure colonisation of young forest regenerated after clearcutting. This could also mean that the continued survival of the species is closely dependent on the connectivity of the region (Ellis 2012). This would mean that forest management needs to use methods that maintain a combination of structural complexity within the managed forest stands as well as safeguarding surrounding larger scale dispersal sources in order to help preserve some of these specialized species (Nordén et al. 2014; Esseen et al. 2022).

5.8 Conclusion

The inventory conducted in Hälsingland showed contrast for the two assessed species and across different forest ages. *G. repens* showed a significant decline in occurrence within older forests at both the within-stand and local occurrence, with the populations being low and stable in younger production forests. The decline was the most extreme at recently clear-cut areas (6-10 years ago) where the orchid was completely absent. In contrast, *A. sarmentosa* showed clear signs of expansion, by having a significant increase across all spatial scales in younger forests, while also maintaining a stable and high occurrence in older forests.

Regarding *G. repens*, the results from this study uncovered a possible “extinction debt” in older forests, which has been discussed by previous studies (Johansson et al. 2026). In younger forests (47-57 years old), the populations remained stable in contrast to older forests (>85 years old), where a significant decline was found.

This, in combination with their complete disappearance in clear-cut forest stands in Hälsingland highlights that the current forest management methods pose serious threats to the species long term survival and persistence (Johansson 2014; Johansson et al. 2026).

Regarding *A. sarmentosa*, the species showed a robust ability to recolonize and expand inside of younger, maturing production forests (47-57 years old). These results suggests that while *A. sarmentosa* seems to decline on a broader landscape scale (Esseen et al. 2022), populations within individual stand seems to recover as long as dispersal sources are available and if the environmental conditions are stable enough (Dettki 1998; Esseen et al. 2022).

The results from the experiment in Uppland showed that clear-cutting led to significantly higher losses of *G. repens* individuals when compared to the unlogged reference areas. The shelterwood logging treatment did not significantly differ from either of the two other treatments, leaving it at a middle position between them. While this treatment potentially could help mitigate microclimate damage (Fedrowitz et al. 2014; Zhang et al. 2024), the one-year time span of this experiment makes the results inconclusive for determining the long-term effects. So, while the results align with previous studies that found that forest specialists often need higher tree density to maintain a stable population (Löhmus & Kull 2011; Johansson et al. 2026), it underlines the need for longer term studies of the effects of shelterwood-logging.

My results are in accordance with other studies and underlying the importance of forest management needing to move away from standardized methods such as clear-cutting in order to favor a more diverse landscape (Esseen et al. 2022). Regarding *G. repens* and *A. sarmentosa*, a strategy which protects the older forests as well as enhancing the connectivity of the landscape is needed to help protect and preserve the populations (Johansson et al. 2026). As *G. repens* has shown to have a very slow recolonization rate, it is important to keep permanent areas clear from forestry which has a faster rotation cycle than what the orchid can handle (Johnson 2014; Johansson et al. 2026). As *A. sarmentosa* is dependent on its ability to spread through dispersal, it is important to uphold connectivity in the landscape to ensure the lichens' physical ability to spread (Dettki 1998; Esseen et al. 2022). So only by synchronizing silvicultural operations with these specialized species' special physical needs can the diversity of the boreal forests be secured for the future (Esseen et al. 1997; Esseen et al. 2022; Johansson et al. 2026).

6. References

- Bradshaw, C. J., Warkentin, I. G., & Sodhi, N. S. (2009). Urgent preservation of boreal carbon stocks and biodiversity. *Trends in Ecology & Evolution*, 24(10), 541–548. <https://doi.org/10.1016/j.tree.2009.03.019>
- Cameron DD, Leake JR, Read DJ. 2006. Mutualistic mycorrhiza in orchids: evidence from plant–fungus carbon and nitrogen transfers in the green-leaved terrestrial orchid *Goodyera repens*. *New Phytol.* 171:405–416. doi:10.1111/j.1469-8137.2006.01767.x.
- CBD (1992): Convention on Biological Diversity. (1992). *Article 2: Use of Terms*. United Nations.
- Chen et al. (1993) Chen, J., Franklin, J. F., & Spies, T. A. (1993). Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, 63(3-4), 219–237. [https://doi.org/10.1016/0168-1923\(93\)90061-L](https://doi.org/10.1016/0168-1923(93)90061-L)
- Colesie, C., Büdel, B., Hurry, V., & Green, T. G. A. (2018). Can Antarctic lichens acclimatize to changes in temperature? *Global Change Biology*, 24(3), 1123–1135. <https://doi.org/10.1111/gcb.13984>
- De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., ... & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5), 744–749.
- Dettki, H., Klintberg, P., & Esseen, P.-A. (2000). Are epiphytic lichens in young forests limited by local dispersal? *Ecoscience*, 7(3), 317–325. <https://doi.org/10.1080/11956860.2000.11682601>
- Dettki, H., Edman, M., Esseen, P. A., Hedenås, H., Jonsson, B. G., Kruys, N., ... & Renhorn, K. E. (1998). Screening for species potentially sensitive to habitat fragmentation. *Ecography*, 21(6), 649–652.
- Ellis, C. J. (2012). Lichen epiphyte diversity: A species, community and trait-based review. *Perspectives in Plant Ecology, Evolution and Systematics*, 14(2), 131–152. <https://doi.org/10.1016/j.ppees.2011.10.001>
- Esseen, P.-A., Ekström, M., Grafström, A., Jonsson, B. G., Palmqvist, K., Westerlund, B., & Ståhl, G. (2022). Multiple drivers of large-scale lichen decline in boreal forest canopies. *Global Change Biology*, 28, 3293–3309. <https://doi.org/10.1111/gcb.16128>
- Esseen, P.-A., Ekström, M., Westerlund, B., Palmqvist, K., Grafström, A., & Ståhl, G. (2016). Standardized forest inventories to monitor pendulous lichens in primary and managed boreal forests. *Fungal Ecology*, 22, 10–22. <https://doi.org/10.1016/j.funeco.2015.07.008>
- Esseen, P.-A., Ehnström, B., Ericson, L., & Sjöberg, K. (1997). Boreal Forests. *Ecological Bulletins*, (46), 16–47. <http://www.jstor.org/stable/20113207>

- Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvold, R., ... & Gustafsson, L. (2014). Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*, 51(6), 1669–1679.
- Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A. M., ... & Ranius, T. (2020). Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. *Ambio*, 49, 1050–1064.
- Fritz, Ö., Gustafsson, L., & Larsson, K. (2008). Does forest continuity matter in conservation? – A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation*, 141(2), 655–668.
<https://doi.org/10.1016/j.biocon.2007.12.006>
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, 349(6250), 819–822.
<https://doi.org/10.1126/science.aaa9092>
- Geiser, L. H., Nelson, P. R., Jovan, S. E., Root, H. T., & Clark, C. M. (2019). Assessing ecological risks from atmospheric deposition of nitrogen and sulfur to US forests using epiphytic macrolichens. *Diversity*, 11(6), 87.
- Granström, A. (2001). Fire management for biodiversity in the European boreal forest. *Scandinavian Journal of Forest Research*, 16(S3), 62–69.
<https://doi.org/10.1080/028275801300090627>
- Gustafsson, L., Andersson, J., Jonsson, F., Jönsson, M., Jonsson, M., Nordin, U., Strengbom, J., & Johansson, V. (2025). Remnant continuity forests are essential for sustaining epiphytic biodiversity in boreal production forest landscapes. *Journal of Applied Ecology*, 62, 1929–1938. <https://doi.org/10.1111/1365-2664.70090>
- Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., Lindenmayer, D. B., Löhmus, A., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W. J. A., Wayne, A., & Franklin, J. F. (2012). Retention forestry to maintain multifunctional forests: a world perspective. *BioScience*, 62(7), 633–645. <https://doi.org/10.1525/bio.2012.62.7.6>
- Hanski, I. (2000). Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici*, 37, 271–280.
- Hedwall et al. (2019) Hedwall, P.-O., Gustafsson, L., Brunet, J., Lindblad, M., Axelsson, A.-L., & Strengbom, J. (2019). Half a century of multiple anthropogenic stressors has altered northern forest understory plant communities. *Ecological Applications*, 29(4), e01874. <https://doi.org/10.1002/eap.1874>
- Hylander, K., 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *J. Appl. Ecol.* 42 (3), 518–525. <https://doi.org/10.1111/j.1365-2664.2005.01033.x>
- IPBES (2019). Global Assessment Report.
- Johansson, V., Jansson, M., & Bergman, K. O. (2026). A 30-year population decline of a threatened forest orchid associated with old growth forests. *Biological Conservation*, 316, 111765.

- Johansson, V., Erbs, C., & Bergman, K. O. (2025). The indicator value of a debated orchid: can *Goodyera repens* predict forests of high conservation potential? *Scandinavian Journal of Forest Research*, 40(5–6), 273–281. <https://doi.org/10.1080/02827581.2025.2530419>
- Johnson, S. (2014). Retention forestry as a conservation measure for boreal forest ground vegetation (Acta Universitatis Agriculturae Sueciae No. 2014:80) [Doctoral dissertation, Swedish University of Agricultural Sciences]. Epsilon Archive.
- Koelemeijer et al. (2022) Koelemeijer, I. A., Ehrlén, J., Jönsson, M., De Frenne, P., Berg, P., Andersson, J., Weibull, H., & Hylander, K. (2022). Interactive effects of drought and edge exposure on old-growth forest understory species. *Landscape Ecology*, 37(7), 1839–1853. <https://doi.org/10.1007/s10980-022-01441-9>
- Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica*, 36, 97–125
- Kuuluvainen, T., Angelstam, P., Frelich, L., Jöngiste, K., Koivula, M., Kubota, Y., Lafleur, B., & Macdonald, E. (2021). Natural disturbance-based forest management: Moving beyond retention and continuous-cover forestry. *Frontiers in Forests and Global Change*, 4, 629020. <https://doi.org/10.3389/ffgc.2021.629020>
- Kuuluvainen, T., Tahvonen, O., & Aakala, T. (2015). Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. *Ambio*, 44(5), 519–533. <https://doi.org/10.1007/s13280-012-0289-y>
- Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology and Evolution*, 24, 564–571. <https://doi.org/10.1016/j.tree.2009.04.011>
- Kyaschenko et al. (2022) Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H., & Ranius, T. (2022). Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: The effect of three decades of biodiversity-oriented forest policy in Swedish forests. *Journal of Environmental Management*, 313, 114993. <https://doi.org/10.1016/j.jenvman.2022.114993>
- Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biol. Conserv.* 131 (3), 433–445. <https://doi.org/10.1016/j.biocon.2006.02.019>.
- Lundmark, H., Josefsson, T., & Östlund, L. (2013). The history of clear-cutting in northern Sweden—Driving forces and myths in boreal silviculture. *Forest Ecology and Management*, 307, 112–122. <https://doi.org/10.1016/j.foreco.2013.07.003>
- Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *J. Appl. Ecol.* 54 (1), 12–27. <https://doi.org/10.1111/1365-2664.12669>.
- Nordén B, Dahlberg A, Brandrud TE, Fritz Ö, Ejrnaes R, Ovaskainen O. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: A review. *Écoscience*. 21(1):34–45. doi:10.2980/21-1-3667.

- Nordén, J., R. Penttilä, J. Siitonen, E. Tomppo & O. Ovaskainen, 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology*, 101: 701–712.
- Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, 4(4), 355–364.
- Peck, J. E., & McCune, B. (1997). Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. *Ecological Applications*, 7(4), 1181–1187.
- Rolstad, J., Gjerde, I., Gundersen, V. S., & Sætersdal, M. (2002). Use of indicator species to assess forest continuity: A critique. *Conservation Biology*, 16(1), 253–257. <https://doi.org/10.1046/j.1523-1739.2002.00245.x>
- SLU Artdatabanken (2025). *Artportalen (Swedish Species Observation System)*. [Database]. Available at: <https://www.artportalen.se> [Accessed: 2025-09-16].
- SLU Swedish Species Information Centre. (2026). Species Facts: *Alectoria sarmentosa*. [Online]. Available at: <https://artfakta.se/taxa/6425/rodlistning> [Accessed: 2026-05-09].
- SLU Swedish Species Information Centre. (2026). Species Facts: *Goodyera repens*. [Online]. Available at: <https://artfakta.se/taxa/220787/rodlistning> [Accessed: 2026-05-09].
- Smith SE, Read DJ. 1997. *Mycorrhizal symbiosis*. London, UK: Academic Press.
- Svenning (2002) Svenning, J.-C. (2002). A review of natural vegetation openness in north-western Europe. *Biological Conservation*, 104, 133–148.
- Těšitelová, T., Klimešová, L., Vogt-Schilb, H., Kotlínek, M., & Jersáková, J. (2022). Addition of fungal inoculum increases germination of orchid seeds in restored grasslands. *Basic and Applied Ecology*, 63, 71–82. <https://doi.org/10.1016/j.baae.2022.04.001>
- Tsiftsis, S., Tsiripidis, I., & Papaioannou, A. (2012). Ecology of the orchid *Goodyera repens* in its southern distribution limits. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, 146(4), 857–866. <https://doi.org/10.1080/11263504.2011.642416>
- Widenfalk, O., Weslien, J., 2009. Plant species richness in managed boreal forests—effects of stand succession and thinning. *For. Ecol. Manag.* 257 (5), 1386–1393. <https://doi.org/10.1016/j.foreco.2008.12.010>.
- Winter, S., & Möller, G. C. (2008). Microhabitats in lowland beech forests as monitoring tool for nature conservation. *Forest Ecology and Management*, 255, 1251–1261.
- Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., ... & Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, 368(6492), 772–775.
- Zhang, S., Sjögren, J., Hylander, K., Koelemeijer, I. A., & Jönsson, M. (2025). Retention forestry enhances the resilience of the moss *Hylocomium splendens* to extreme

- drought in boreal forests. *Journal of Applied Ecology*, 62, 899–910.
<https://doi.org/10.1111/1365-2664.70016>
- Zhang, S., Sjögren, J., & Jönsson, M. (2024). Retention forestry amplifies microclimate buffering in boreal forests. *Agricultural and Forest Meteorology*, 350, 109973.
- Åström, M., Dynesius, M., Hylander, K., & Nilsson, C. (2007). Slope aspect modifies community responses to clear-cutting in boreal forests. *Ecology*, 88(3), 749–758
- Östlund, L., Zackrisson, O., & Axelsson, A. L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian journal of forest research*, 27(8), 1198-1206.

Popular science summary

Boreal forests contain ecosystems of high complexity which provide important habitats for specialized species. Two examples of these kinds of species are the epiphytic lichen Witch's hair (*Alectoria sarmentosa*) and the terrestrial orchid Creeping Lady's Tresses (*Goodyera repens*). Both of these species serve as important indicators of the forest's health in the form of its continuity and stability. Modern forest management which is dominated by clear-cutting has however fundamentally changed the structured components of these landscapes. This study examined how the chosen indicator species are able to survive and return to a landscape after clear-cutting. This was done by examining forests of different ages across three different spatial scales as well as comparing different management methods.

One main component of this study was the assessment across several spatial scales, meaning that data was collected at landscape-, within-stand- and local occurrence levels over a time period of 12 years. The results showed different responses for the different species across the different spatial resolutions. Populations could for example seem stable at the landscape level while the higher resolutions showed local decreases in the forest stands. *G. repens* showed a significant decrease in older forests in the higher spatial resolution scales, indicating that the species could be experiencing a potential extinction debt which is a delayed response to a historic fragmentation in the landscape.

The study also examined *A. sarmentosa*'s ability to return to and spread within managed production stands following clear-cutting. The species showed a high ability to recolonize production stands of younger ages, showing a significant increase of occurrence inside of all three spatial scales. These results would suggest that the forest stands reach the required structural stability for supporting certain epiphytes relatively quickly. An important factor for the spread of this species is the surrounding landscape which provides the dispersal fragments necessary for a successful re-establishment.

In order to explore new ways of lessening the negative impact from modern forest management, an experiment in Uppland was conducted where the effects of clear-cutting was compared to shelterwood logging regarding the survival of *G. repens*. Shelterwood logging is a forestry method where approximately 50% of the forest canopy is retained and should potentially offer a more stable microclimate for the orchid. The results showed a significant decline in the populations inside the clear-cut areas compared to the unlogged reference areas while the shelterwood logging areas attained an intermediate position, not significantly differing from either the clear-cut areas or the unlogged reference areas. The amount of canopy cover was also assessed here in order to examine a potential correlation between the survival and the canopy cover. A significant correlation was however not found. This result suggests that the survivability of *G. repens* may be driven by other factors rather than only the amount of solar radiation. These factors could for example be physical damage from the harvesting process, change in the soil

moisture or the disrupting effects on mycorrhizal networks which are important for the nutrient cycling of *G. repens*.

The two different species showed different responses in this study which highlights that a “one size fits all” strategy is the wrong approach when trying to protect a wider range of species. For *G. repens*, the initial disturbance of the forestry seems to cause the most problems for the species. For *A. sarmentosa*, the presence of nearby landscapes allowing for dispersal seems to be the most important factor for its survival. So to ensure the future of a rich boreal forest biodiversity, forest management needs to move towards more diverse methods that take into account the preservation of these species. Examples of such strategies are preserving old-growth forests and preserving the connectivity of the landscape.

Publishing and archiving

Approved students' theses at SLU can be published online. As a student you own the copyright to your work and in such cases, you need to approve the publication. In connection with your approval of publication, SLU will process your personal data (name) to make the work searchable on the internet. You can revoke your consent at any time by contacting the library.

Even if you choose not to publish the work or if you revoke your approval, the thesis will be archived digitally according to archive legislation.

You will find links to SLU's publication agreement and SLU's processing of personal data and your rights on this page:

- <https://libanswers.slu.se/en/faq/228318>

☒ YES, I, Johannes Nord, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this

☐ NO, I/we do not give my/our permission to publish the full text of this work. However, the work will be uploaded for archiving and the metadata and summary will be visible and searchable.