# The moss *Hylocomium splendens* as a bioindicator

## Growth respons in young forests, retention patches, and areas with conservation values

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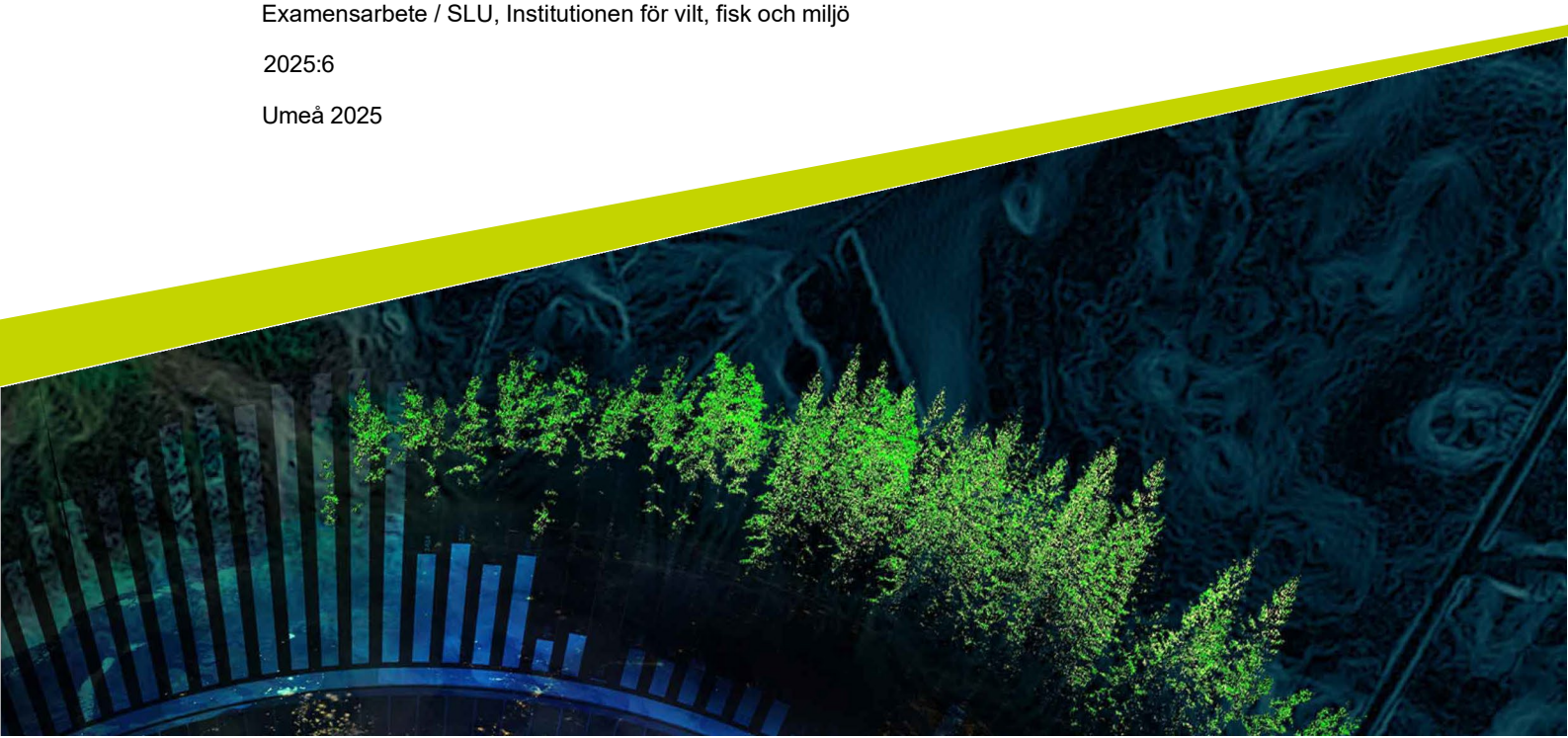

# The moss Hylocomium splendens as a bioindicator: Growth response in young forests, retention patches, and areas with conservation values

*Mossan Hylocomium splendens som bioindikator: Tillväxtrespons i ungskogar, hänsynsytor samt i områden med naturvärden*

Manne Frih

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# Abstract

The industrial forestry has had a negative impact on the biodiversity within boreal forests. To reduce the negative effects of forestry, retention patches aim to maintain the composition of forest species. In this study, the moss *Hylocomium splendens* is applied as a bioindicator to assess how forestry impacts understory growth decades after clear-cutting, and if retention patches function as a life bridge in the longer term. Furthermore, the study will examine *H. splendens* as an indicator of conservation values, which has not been examined before. Samples of *H. splendens*, together with plot-based inventories of bryophytes species, and conservations value assessments, were conducted in young forests (20-35 years), retention patches and old growth forests in southern boreal Sweden. Thereafter, maximum segment width and length were measured, along with a ratio of the compactness of the moss. The results showed that the segment width of *H. splendens* were the same between the forest types, the segment length was longest in young forests while the ratio was highest (i.e. more compact) in retention patches and old growth forests. Moreover, no relationship between the growth metrics of *H. splendens* and the conservation values were demonstrated. While earlier studies have shown the profound negative effects of clear-cuts on understory growth, this study indicates that young forests, as well as retention patches within the young forests, function well in preserving understory growth. However, differences in the morphological growth indicates that retention patches and old growth forests may provide the most suitable environment for understory.

*Keywords:* forestry*, Hylocomium splendens*, conservation values, retention patches, understory growth

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# 1. Introduction

## 1.1 Background

The intensive forestry management has been the dominant impact factor of Scandinavian boreal forests since the 1940s (Östlund et al. 1997). With the introduction of the modern forestry, old growth forests have been clear-cut and replaced by monocultural tree plantations (Östlund et al. 1997; Ahlström et al. 2022). As a consequence, the composition of tree species and age distribution have been altered, the fragmentation of old growth forests has increased and the number of dead snags, logs and large trees has declined (Linder and Östlund 1998; Siitonen 2001; Boucher et al. 2021). Furthermore, the modern forestry with clear-cuts has to a large extent replaced the natural disturbances in the pre-industrial boreal landscape as wind fellings and insect outbreaks in *Picea*-dominated forests and fires in *Pinus*-dominated forests (Kuuluvainen 2009).

The continued logging of old growth forests, the abscence of natural disturbances, and the transformation to homogenous forests, have had severe effects on the ecosystems (Kuuluvainen 2009; Stein et al. 2014; Ahlström et al. 2022). These ecological changes of the boreal forests pose a threat to biodiversity, resilience of the ecosystems and the long-term ability for climate adaptation (Kuuluvainen and Gauthier 2018). Old growth forests can preserve and regulate a stable microclimate which is of importance for many species (Greiser et al. 2020; Zhang et al. 2024; Lunde et al. 2025), while clear-cuts will highly alter the microclimate with high temperature- and humidity fluctuations (Zhang et al. 2024). The removal of these stable microclimates, together with edge effects, fragmentation of old growth forests and the absence of biological legacies, have led to a decline in the abundance of many late successional species (Lunde et al. 2025; Nirhamo et al. 2025). However, the profound changes of the boreal forests affect not only specialist species dependent of old growth forests, but also abundant keystone species such as billberry (*Vaccinium myrtillus*), the grass *Avenella flexuosa* and the lichens of the genus *Cladonia spp*., which all have declined in abundance during the last decades (Hedwall et al. 2013; Tonteri et al. 2016).

To enhance the biodiversity and structural heterogenity within managed boreal forests across Europe, the EU Forest Strategy for 2030 aims to increase the use of Closer-to-Nature Forest Managements (Larsen et al. 2022). An approach within the Closer-to-Nature forestry that has been practiced for the last 35 years is retention forestry. In retention forestry, biological legacies such as living and dead trees are preserved in small and isolated patches. These retention patches are

usually smaller than 0.5 hectares (ha) and located within the clear-cutted forest (Gustafsson et al. 2012; Gustafsson et al. 2016). Retention patches have been revealed to have a higher buffer capacity of air temperatures and humidity compared to the surrounding clear-cuts (Zhang et al. 2024), which could be of importance for many species (Greiser et al. 2020). While retention patches supports a higher abundance of forest understory species compared to clear-cuts (Fedrowitz et al. 2014), but lower than old growth forests (Perhans et al. 2007), there is uncertainty if the retention forestry can preserve indicator- and red-listed species in the long-term (Perhans et al. 2009; Jönsson et al. 2022). Moreover, the minimum size of the retention patch to maintain the composition of species as pre-harvest is not well understood (Gustafsson et al. 2020), but due to edge effects and wind fellings (Moen and Jonsson 2003; Hylander 2005; Jönsson et al. 2007; Koelemeijer et al. 2023), the retention patches should preferably be as large as possible (Gustafsson et al. 2020).

In this study, the moss *Hylocomium splendens* will be applied as a bioindicator to assess how forestry impacts understory growth. Bioindicators are used to assess the health of our natural ecosystems and detect changes in the environment, (Parmar et al. 2016). *H. splendens* has been used as a bioindicator of understory growth in earlier studies, partly due to its segmented growth pattern (Koelemeijer et al. 2023). Each year, a distinct segment is created above the segments of the previous years, making it possible to evaluate the growth 3-4 years back (Busby et al. 1978; Okland et al. 1995). In earlier studies, multiple measurement methods of *H. splendens* have been utilized to assess growth differences in various environments. Okland (1995) combined the segment width, length and branch numbers to estimate the dry weight, Hylander (2005) and Koelemeijer et al. (2023) measured segment length while Zhang et al. (2025) measured segment width.

Moreover, the moss *H. splendens* will be applied as a bioindicator of understory growth in this study due to its abundance and needs of a stable microclimate. *H. splendens* is one of the most common moss species within boreal forests (Benscoter and Vitt 2007), and the reduction of the moss usually corresponds to the reduction of other understory species (Hylander 2005; Hylander 2009). The growth of *H. splendens* is dependent on several environmental factors, such as temperature, light, nutrient supply and water availability (Tamm 1953). In particular, high water supply and summer temperatures of around 18-19°C, seems important for the growth of *H. splendens* (Potter et al. 1995; He et al. 2016). At very low light intensity, many clonal plants, which involve bryophytes, have been shown to elongate to access light. In contrast, under favorable conditions, plants may receives a more compact growth form (de Kroons and Hutchings 1995; Bergamini and Peintinger 2002).

As microclimate conditions are important for the growth of *H. splendens* (Tamm 1953; Potter et al. 1995; He et al. 2016), changes in the environment including forestry have a negative effect on the abundance of the moss (Tonteri et al. 2016; Zhang et al. 2025). Tonteri et al. (2016) found that *H. splendens* had a slow recovery rate after clear-cutting, but was positively influenced by thinning in managed forests. In a recently published study, Zhang et al. (2025) revealed that retention patches had the ability to reduce some of the negative effect of forestry on the growth of *H. splendens*. While old boreal forests showed the highest growth of the *H. splendens*, retention patches had a higher growth of the moss compared to the surrounding clear-cuts (Zhang et al. 2025). Moreover, biological legacies such as large trees and standing dead wood, were shown to indirectly contribute to *H. splendens* growth through creating a preferable microclimate (Zhang et al. 2025).

In line with the study from Zhang et al. (2025), who examined the growth of *H. splendens* in clear-cuts and surrounding retention patches, it would be of interest to expand our knowledge within the forestry impact on understory species. Firstly, as there is limited knowledge about the long-term ability for retention patches and former clear-cuts to preserve understory species (Jönsson et al. 2022; Zhang et al. 2025), it would be of interest to assess the growth of *H. splendens* in young forests and old retention patches. Secondly, while earlier studies have used *H. splendens* as a bioindicator to show the effects on understory growth as a result of forestry, biological legacies and edge effects (Hylander 2005; Koelemeijer et al. 2023; Zhang et al. 2025), no studies have examined direct links between the forest's conservation values and *H. splendens* growth. By comparing plot based conservation value assessments and the presence of redlisted bryophytes with the growth of *H. splendens*, it would be possible to evaluate if the growth of the moss can function as an indicator species of nature conservation values. Therefore, this study will contribute to a deeper understanding of the managed boreal forest's ability to maintain understory growth, and if the growth of *H. splendens* is useful as an indicator species of boreal forests with high conservation values.

## 1.2 Aim, research questions and hypothesis

The aim of this study is to use *H. splendens* as a bioindicator to understand the response of understory growth after forestry managements, as well as to find if the growth of *H. splendens* can indicate forests of conservation value.

The following research questions are addressed: (1) How does the maximum segment width, maximum segment length, and width to length ratio of *H. splendens* differ in young forests, retention patches and old growth forests? (2) Is the growth metrics of *H. splendens* related to the conservation value assessment of

the forest? (3) Is the growth metrics of *H. splendens* related to the presence of red-listed bryophytes?

Following the aim and the research questions, four hypotheses were established: (1) The maximum segment width of *H. splendens* should be widest in old growth forests, followed by retention patches, while being narrowest in young forests. However, the difference between the forest habitats should be lower than the results from Zhang et al. (2025), as there should be some recovery of the microclimate buffering capacity in retention patches and young forests. (2) The maximum segment length should be longest in old growth forests, followed by retention patches, while being shortest in young forests. This hypothesis is based on Koelemeijer et al. (2023), who demonstrated that the moss receives a larger length growth further into the forest, which based on earlier studies of *H. splendens* probably is due to a more stable microclimate. (3) The width to length ratio should be highest in old growth forests, followed by retention patches, and with the lowest ratio in young forests, as some plants receive a more compact growth form in suitable habitats (de Kroons and Hutchings 1995). (4) The growth of *H. splendens* in sampling locations with high conservation values should be higher. *H. splendens* prefers a stable microclimate (He et al. 2016) and biological legacies as dead wood indirectly contributes to a more stable microclimate (Zhang et al. 2024). Therefore, forests with high conservation values, which have larger amounts of these biological legacies (Siitonen 2001), should support a higher growth of *H. splendens*.

# 2. Method

The selection of study area and sites, as well as the collection of data, was carried out as part of the Key Performance Indicators (KPI) project, while the measurement of *H. splendens* and the data analysis were conducted by the author of this study. The KPI project is co-developed by SLU and Stora Enso AB, with the aim of fulfilling the knowledge gap about the long-term biodiversity effects of retention forestry compared to clear-cuts and set asides (old growth forests).

## 2.1 Study area and design

This study was conducted in Hälsingland county, in the southern boreal zone of Sweden (Figure 1). The landscape within the study area consists of managed forests of mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Through field visits and screening of stand data from the forest company Stora Enso AB, 20 sites from each of three distinct forest management types were selected: 1) Young forests that were clear-cut 20-35 years ago and thereafter regenerated with Norway spruce or Scots pine on scarified ground. 2) Retention patches within the young forests 3) Set asides in the form of woodland key habitats, consisting of old growth forest.

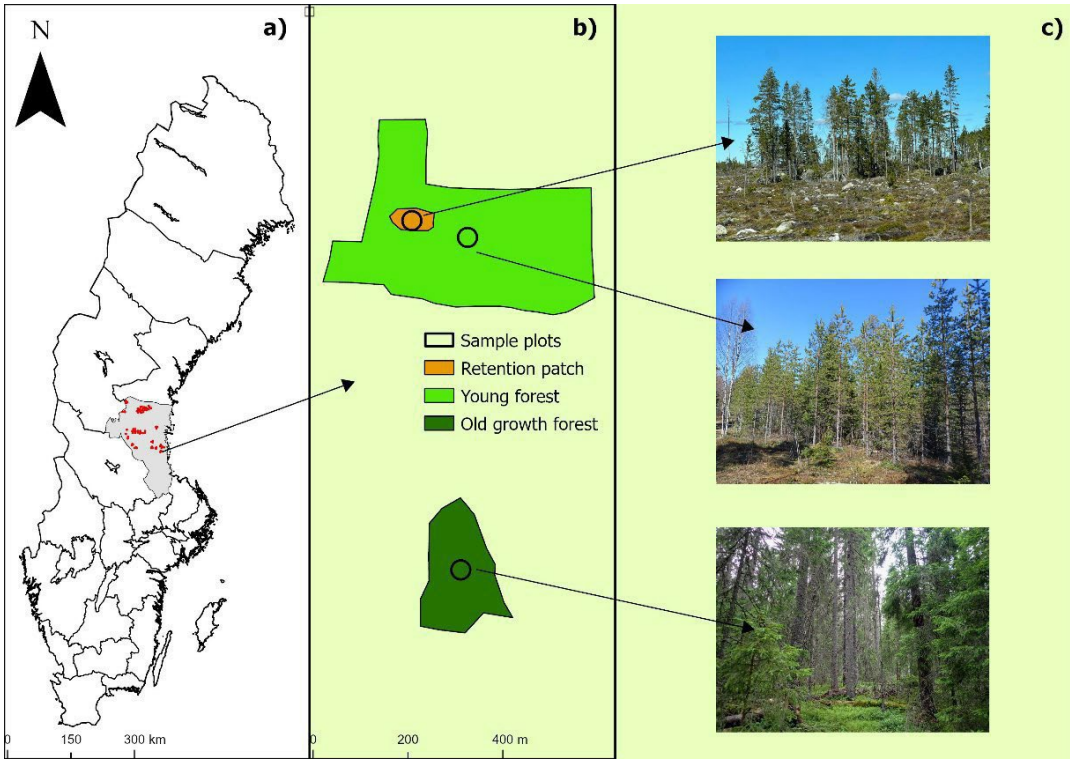


*Figure 1. A map over the study area, the design of the study and reference pictures of the three forest types. a) The study was performed in Hälsingland County (grey area), in the*

*southern boreal zone of Sweden. The red dots on the map shows the study sites. b) The general design of the study. Within each examined young forest, a retention patch and a nearby set aside (old growth forest), were chosen correspondingly. Within the middle of each study site, a sample plot with a radius of 20 meters was set up for the data collection (see 2.2). c) Reference pictures of a young forest, a retention patch and an old growth forest. Note that the retention patches in the study is surrounded by young forest (20-35 years), and not clear cuts as in the reference picture. The pictures, taken by the author to this study, is not from the study area.*

Some rules regarding the location of the sites were applied: 1) Whereas half of the sites for each stand type was dominated by Norway spruce, the other half was dominated by Scots pine. 2) The presence of other tree species within the sites were relatively equal. 3) The stand types were located on mesic to moist soil types. 4) For each stand site of young forest, one retention patch within the young forest with a minimum radius of 20 meters, and one set aside as close as possible to the young forest (usually 500-2000 meter but sometimes further away), were chosen correspondingly (Figure 1). 5) The dominant tree species within the set aside should be the same as in the adjacent young forest.

## 2.2 Data collection

The data consist of 60 distinct sites. In the middle of each study site, a circle with a radius of 20 meters (0.125 ha) was set up (Figure 1). Within these circular plots, sampling of *H. splendens*, inventory of bryophyte species and the conservation value assessments were conducted. Data collection took place during the field seasons from 2021 to 2023.

### *2.2.1* Sampling of *H. splendens*

Samples of *H. splendens* were collected randomly within the 20 meters radius sample plot. If *H. splendens* was abundant within the sample plot, small stalks of the moss were gathered from several parts rather than from one single patch within the sample plot.

### 2.2.2 Inventory of bryophytes

Within each 20-meter radius sample plot, a thorough inventory of all bryophyte species was conducted by experts. As a result, plot-based data of the presence/absence of all bryophyte species were collected.

### 2.2.3 Conservation value assessments

A conservation value assessment method developed by Skogsbiologerna AB was used during the field work to assess the conservation values within each sample

plot. The field workers searched for the occurrence of 50 different structures/stand characteristics in the 20-meter radius plots. These searched features included structures as dead wood or habitat trees and stand characteristics as steep inclines or signs of natural disturbances as fires. After the notation of the occurrence of these features, a Habitat Heterogeneity Score reaching between 0-30 was received.

## *2.3* Measurements of *H. splendens*

In this study, the growth of *H. splendens* was examined by measuring both maximum segment width and maximum segment length, as well as a ratio of the maximum segment width divided by the maximum segment length. Prior to measurement, all shoots were rehydrated in the paper bag where they were stored. After the rehydration process, shoots from *H. splendens* that were dead were removed from the paper bag along with any other species that had been accidentally collected and stored.

Thereafter, five randomly chosen shoots of *H. splendens* were selected. For all of these five shoots, the length and the width from the last three segments were measured. In total, this resulted in 879 measurements each for the segment length and width. The length of the segments was measured between the base of the segment and the apical tip. As the segments of the moss usually were curved, each segment was flattened out as much as possible and positioned in a straight line in order to measure its actual length. During the measuring of the width of the segment, the segment was placed with the concave side downwards to flatten it out as much as possible. Subsequently, the segment width was measured perpendicular to its length, across the widest point of the branching. The measurements of the segment length and width were conducted with a digital calliper with a precision of 0.01 mm.

During the measurement of *H. splendens*, observed anomalies of the moss were tested through $X^2$-tests to see if they appeared more frequent in any of the forest types. Most common among these anomalies, were that segments of *H. splendens* were broken on the tip or at the base of the segment. The maximum width of the segment should not be affected of broken segments on the tip or the base, as the widest point of the segment most often occurred nearby the middle of each segment. Obviously, the length of the segment will be degraded if the segment itself is broken. However, as no significant differences in the abundance of broken segments were found in the $X^2$-test ($p = 0.296$) (Appendix 1), these anomalies should not affect the results. Moreover, sometimes more than one segment was produced for a year. In that case, one of the segments were randomly selected. Nevertheless, as the production of multiple segments does not influence the

overall growth (Zhang et al. 2025), and as the $X^2$-test in this study had a p-value of 0.961 (Appendix 1), this should not influence the results of the study. Furthermore, some shoots of *H. splendens* had only produced two segments, but there were no significant differences in the frequency of these shoots between the forest types (p = 0.156) (Appendix 1). Additionally, as most new growthpoints arises sympodially, which means that the new segment grows from one of the lateral branches (Zhang et al. 2025), a minority of the new growing points can arise monopodial in which the main axis grows continuously (Okland et al. 1995). However, this should not affect the robustness of the length-based measurements (Okland et al. 1995), and had a non-significant p-value of 0.695 in frequency between the forest types in this study (Appendix 1). Lastly, in a few shoots of *H. splendens* the latest produced segment was too small to measure, which was the case if it had not produced any leaf and only consisted of a small bud. In this case, the measurement was done on the following three segments. This observation had a significance of p = 0.00865 (Appendix 1) as it was only observed in old growth forests and retention patches. Nonetheless, as a segment reaches its full branching width after approximately 1.5 year (Okland et al. 1995), the maximum length and width of segment four (which was measured when starting one segment down), should not differ in any significant way compared to segment two and three.

## 2.4 Data analysis

Before conducting any tests, a mean of the maximum segment length, maximum segment width and a ratio of the maximum segment width divided on the maximum segment length were produced. As mentioned in 2.3, five moss specimens from each sample plot were measured and for each moss, the three latest segments were measured. The widest as well as the longest segment out of the three segments from each moss was selected. These selected values were then used to create a ratio of the segment width divided on segment length for each moss, in which a higher ratio would indicate a higher compactness of the moss. Thereafter, a mean value of the five maximum segment lengths and widths, as well as the ratio from each moss, was produced. Through this method, whereas one mean value for each metric was generated per sample plot, the number of replicates for the forest types become n = 20.

The statistical tests, performed in Excel, included both parametric and non-parametric tests as some of the data was normally distributed and some were not. Whereas the data was normally distributed for the first two research questions, the data set was not normally distributed when dividing the growth metrics between sample sites with or without red-listed bryophytes. Therefore, one-way ANOVA's and regression analysis were conducted for research questions one and two while Mann-Whitney U tests were performed for research question three. To conduct if

there were any differences in *H. splendens* growth metrics (maximum width, length and ratio) between the different forest types, a one-way ANOVA for each measure were made which resulted in three one-way ANOVA's. If the differences were significant ($p < 0.05$), a post hoc test through Tukey's HSD-test was conducted to determine between which forest types the differences were significant. Furthermore, regression analyses were conducted in which the conservation value assessments (independent variable) were analysed to assess if they affected the metrics from the maximum width, length and ratio (dependent variables). All forest types were analysed together but also separately, resulting in a total of 12 regression analyses. Additionally, Mann-Whitney U tests were conducted to assess whether the presence or absence of red-listed bryophytes within each sample plot affected the growth metrics of *H. splendens* (maximum width, length and ratio). In total, three Mann-Whitney U tests were performed, one for each growth measure of *H. splendens*.

# 3. Results

## 3.1 Growth of *H. splendens in the forest types*

### 3.1.1 Width growth of *H. splendens*

Differences in the maximum segment width of *H. splendens* were non-significant (p-value of 0.121). The width growth of *H. splendens* was 30.4 ± 0.951 mm (mean ± SE) in young forest, 28.6 ± 0.917 mm in retention forest and 31.6 ± 1.08 mm in old growth forest (Figure 2).

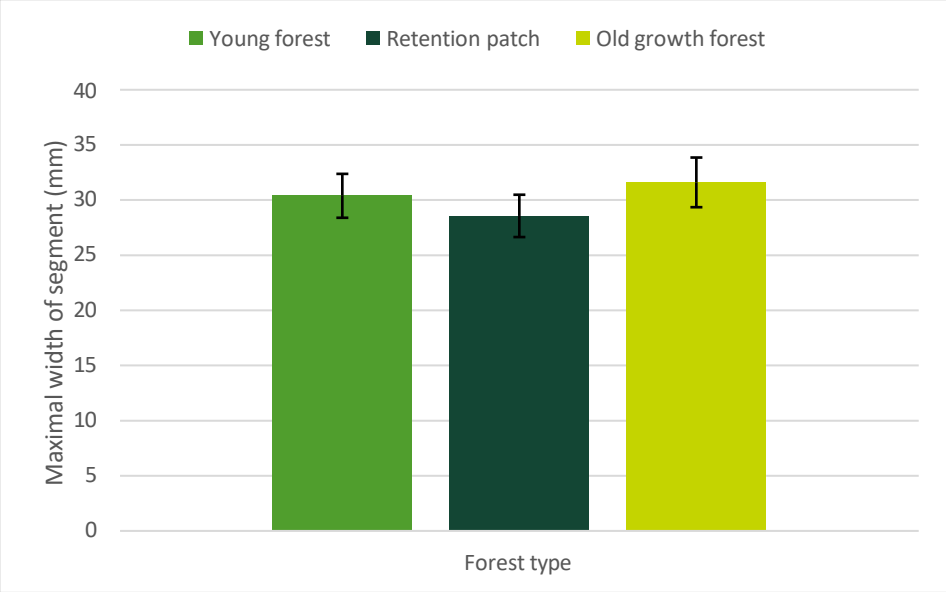


*Figure 2. The width growth of H. splendens. The bars represent the mean values of the maximum segment width of H. splendens in the different forest types while the error bars represent 95% confidence intervals (mean ± 2.093 * SE).*

### 3.1.2 Length growth of *H. splendens*

The performed one-way ANOVA revealed that there was a significant difference in the maximum segment length of *H. splendens* ($p < 0.001$). A Tukey HSD-test gave HSD-values of 5.03 (Appendix 2), indicating that shoots in young forest had a significantly longer maximum segment length (37.6 ± 1.17 mm) than retention forest (30.2 ± 1.40 mm) (Figure 3). Old growth forest, with a mean maximum segment length of 32.9 ± 1.54 mm, revealed no significant differences compared to the other forest types.

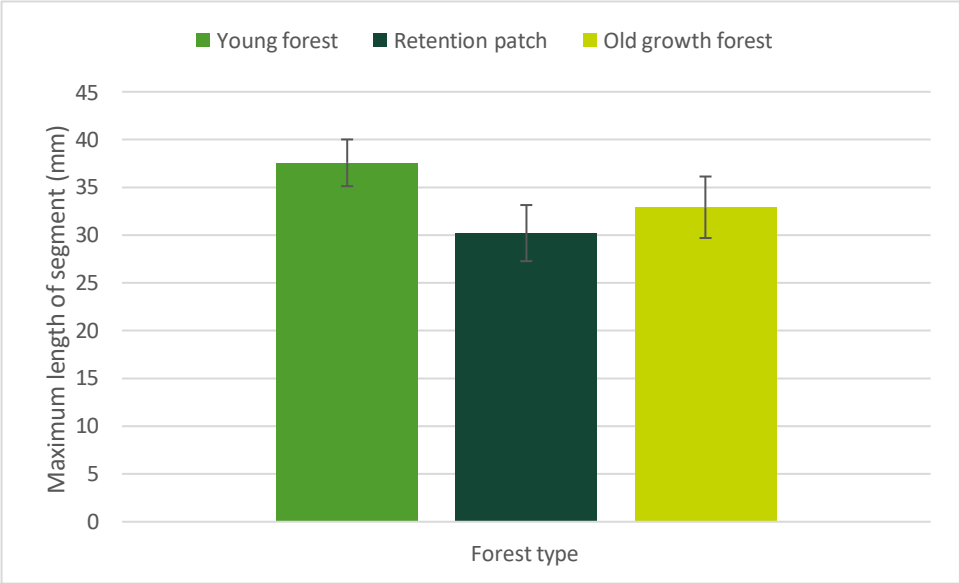


*Figure 3. The length growth of H. splendens. The bars represent the mean values of the maximum segment length of H. splendens in the different forest types while the error bars represent 95% confidence intervals (mean ± 2.093 * SE).*

### 3.1.3 Width/length ratio of *H. splendens*

The ratio of the width/length of *H. splendens*, which can be seen as an indicator of the growth form of the moss where a higher value indicates a more compact growth, had significant differences between the young forest compared to the retention forest and old growth forest ($p < 0.001$). In the old growth- and retention forests, the width/length ratio were 1.00 ± 0.0337 and 1.00 ± 0.0316 respectively, while the young forest had a width/length ratio of 0.848 ± 0.0279 (Figure 4). As the Tukey HSD-test gave a HSD-value of 0.114, the significant differences of the segment width/length ratio were observed between the young forest and both the other forest types (Appendix 2).

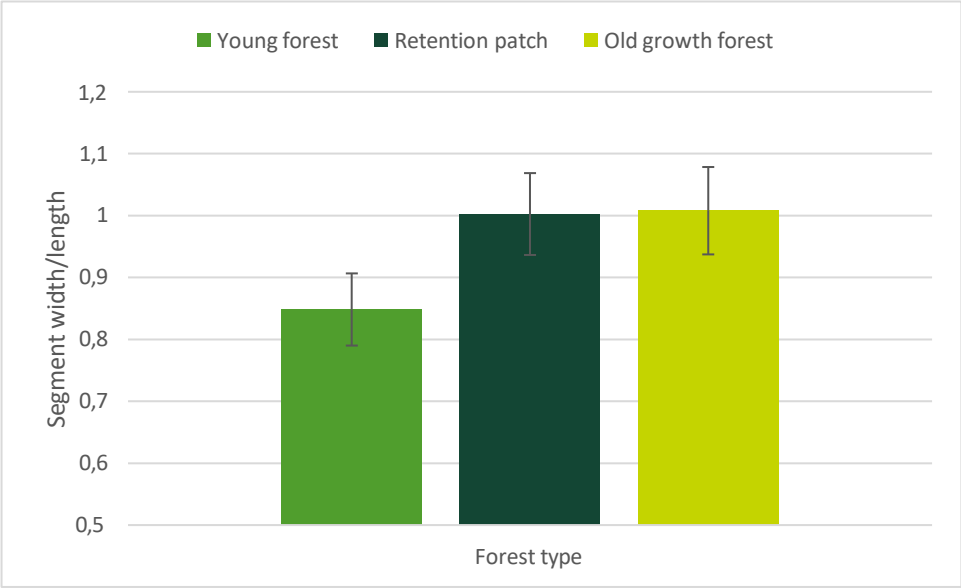


*Figure 4. Ratio of the segment width divided on the length of H. splendens. The bars represent the mean values of the maximum segment width divided on the maximum segment length of H. splendens in the different forest types while the error bars represent 95% confidence intervals (mean ± 2.093 * SE).*

## 3.2 *H. splendens* as indicator of conservation values

### 3.2.1 *H. splendens* growth and conservation value assessment

The growth of *H. splendens* does not relate to the conservation value assessment of the forest (Figure 5). Regression analysis was both performed with all forest types combined and with all forest types separate. When combining the forest types, the conducted p-values were 0.610; 0.0899 and 0.122 respectively for the segment width; segment length and segment width/length ratio (Appendix 3). Moreover, the regression analyses for the forest types separately did not either resulted in any significant results (Appendix 3).

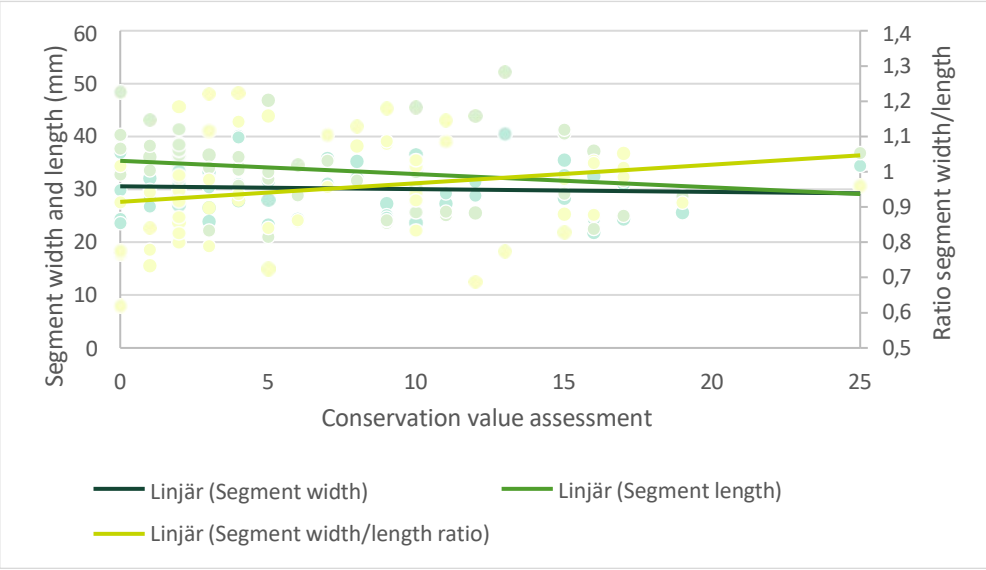


*Figure 5. Scatter plot of the conservation value assessment on the x-axis and the growth measurements on the y-axis (segment width and length on the left y-axis and ratio on the right y-axis). The dots in the figure shows all individual values, while the lines illustrate the trend lines for each growth measure. Within this scatter plot, all forest types are combined in the values of the different growth metrics of H. splendens.*

### 3.2.2 *H. splendens* growth and red-listed species

The performed Mann-Whitney U tests indicates that the growth of *H. splendens* does not differ between samples plots with or without the presence of red-listed bryophytes species (Table 1). The growth metrics of *H. splendens* in sample plots with and without the presence of red-listed bryophytes were 29.3 ± 1.05 mm and 30.4 ± 0.722 mm respectively for the segment width, 32.5 ± 1.68 mm and 33.9 ± 1.02 mm respectively for the segment length, 0.946 ± 0.0243 and 0.955 ± 0.0249 respectively for the segment width/length ratio (Appendix 4).

*Table 1. Compared mean values of H. splendens growth measurement between sample plots with the presence of redlisted bryophyte species (row "Red-listed species") and with the absence of redlisted bryophyte species (row "No red-listed species"). p-values were received through Mann-Whitney U tests.*

| | **Segment width (mm)** | **Segment length (mm)** | **Ratio segment width/length** |
|---|---|---|---|
| **Red-listed species** | 29.3 | 32.5 | 0.946 |
| **No red-listed species** | 30.4 | 33.9 | 0.955 |
| **p-value** | 0.609 | 0.622 | 0.979 |

# 4. Discussion

The main result from this study suggest that young forests have regained their potential for understory growth, as segment width did not differ between forest types (Figure 2). In contrast, the segment length was significantly longer in young forests than in retention patches, while the segment width/length ratio (i.e compactness of the moss) was highest in old growth forests and retention patches (Figure 3 and 4). Furthermore, the results of this study suggest that the growth of *H. splendens* is not a reliable indicator of forest conservation value, as none of the growth metrics showed a relationship with the conservation value assessment nor the presence of red-listed bryophyte species (Figure 5; Table 1). These results will be further discussed within the following sections (4.1, 4.2, 4.3) in relation to previous studies and with possible management implementations.

## 4.1 *H. splendens* growth in retention patches and young forests

This study showed no significant differences in the segment width of *H. splendens* in the diverse forest types (Figure 2). The hypothesis was that the segment width would be widest in old growth forests, followed by retention patches, with the narrowest segment width in young forests, as Zhang et al. (2025) demonstrated the profound negative effects of understory growth in clear-cuts. However, as the width growth of *H. splendens* in young forests and retention patches returned to the same level as in old growth forests, these results indicates that retention patches and young forests can preserve the understory growth decades after clear-cutting. As the branching patterns of *H. splendens* depends on the microclimate, which involves high moisture and low temperatures (Okland and Okland 1996; He et al. 2016), there are reasons to assume that the similarities in segment width between the forest types is due to a return of the microclimate buffer capacity within the young forests. While old growth forest may still provide the highest buffering capacity (Frey et al. 2016), Starck et al. (2025) revealed that a strong temperature buffer capacity is reached approximately 30 years following a clear-cut, which could be an explanation of the segment width results from this study.

The segment length of *H. splendens* was significantly longer in young forests than in the retention patches (Figure 3). As the hypothesis was that the differences in segment length would be the opposite compared to this result, it was unexpected that the length of the segments were much longer in young forest than retention patches. The profound differences in segment length may be a result of the different environments in the forest types. Young forests in the managed landscape are usually very dense (Sonesson et al. 2014), retention patches on the

other hand may be relatively open as a result of high portions of tree mortality (Jönsson et al. 2007). Clonal plants, including some mosses, have in experimental studies been shown to elongate in the absence of light, while becoming shorter in the presence of it (de Kroons and Hutchings 1995; Bergamini and Peintinger 2002). Therefore, the results of the segment length of *H. splendens* may be due to an elongation process as the presence of light should be more scarce in young forests.

While earlier studies on *H. splendens* growth in response to environmental changes have measured frequency and ground cover (Hylander 2009; Tonteri et al. 2016), dry weight (Okland 1995), segment length (Hylander 2005; Koelemeijer et al. 2023) and segment width (Zhang et al. 2025), this study has also evaluated the ratio of the segment width/length. This ratio can be seen as a measure of the compactness of the moss, which was hypothesized to be highest in old growth forests (i.e. more compact), followed by retention patches and lastly young forests. The results showed that old growth forests and retention patches had a significantly higher ratio than young forests (Figure 4). It has earlier been demonstrated that *H. splendens* has the ability of morphological plasticity, which allows it to respond to changes in the environment (Rossi et al. 2001). Under favorable microclimate conditions, clonal plants, including mosses, are expected to possess a compact growth form (de Kroons and Hutchings 1995; Bergamini and Peintinger 2002). Therefore, the ratio of the segment width/length from this study indicates that the old growth forests and retention patches provides the most suitable microclimate for understory.

Whereas the results of *H. splendens* growth in the different forest types provides somewhat mixed results (Figure 2,3 and 4), some conclusions can be drawn. Firstly, while the narrow segment width of *H. splendens* in clear-cuts has been demonstrated (Zhang et al. 2025), this study has shown that segment width of *H. splendens* recovers in young forests (Figure 2). Consequently, it can be concluded that young forests (20-35 years) provide understory growth much better than clear-cuts. Secondly, retention patches within the young forests of this study, function well in preserving understory growth, as neither of the growth metrics differ from old growth forests (Figure 2 and 4). Thirdly, a long segment length and sparce growth form in young forests (Figure 3 and 4), indicates that retention patches and old growth forests may provide the most favorable conditions for understory growth. Further studies should analyze if the low ratio of *H. splendens* segment width/length in young forests only is a result of its large segment length in young forests, or if the sparse growth form may be explained by environmental conditions. Furthermore, as this study demonstrated that different growth parameters can give different results, the includation of several paramters can be of importance to give a comprehensive picture of *H. splendens* as a bioindicator

of understory growth. Lastly, it would be of interest to assess if there is a minimum size of the retention patches needed to preserve understory growth.

## 4.2 *H. splendens* as an indicator of forest conservation values

The results of this study indicate that *H. splendens* does not function as an indicator of forest conservation values. In this study, both the presence of structures and stand characteristics through the conservation value assessment, and the presence of red-listed species through the plot-based data of red-listed bryophytes, were tested to analyse if *H. splendens* could function as an indicator species. However, this study shows that neither the conservation value assessment, nor the presence of red-listed bryophytes within the sample plots, related to the growth metrics of *H. splendens* (Figure 5; Table 1). As forests with high conservation values may have a more stable microclimate due to its long continuity and biological legacies (Frey et al. 2016; Zhang et al. 2024), the hypothesis was that *H. splendens* would exhibit higher growth in forests with high conservation values. The lack of difference though, indicates that the conservation values of the forest, neither directly nor indirectly, contributes to the growth of *H. splendens*.

The most possible explanation to the lack of differences in *H. splendens* growth depending on the forest conservation values is that *H. splendens* is too much of a generalist to function as an indicator species. Whereas there are bryophytes that function as indicator species for old growth forests and the presence of red-listed species (Gustafsson et al. 2004), these bryophytes are usually specialist species dependent on substrats as dead wood or environmental conditions such as high humidity. *H. splendens* on the other hand, is a generalist species that thrives in different environmental conditions, which probably makes it less suitable as an indicator species. Furthermore, while Zhang et al. (2025) reveald that *H. splendens* grows better in areas with presence of biological legacies as they may promote a favourable microclimate, this study could not show similar results in forests with conservation values, which usually contains large amount of biological legacies (Siitonen 2001). However, these microclimatic changes may have an impact on micro-habitat lever more than stand level. Therefore, the microclimatic differences between the sample plots may be relatively small, which could explain the lack of differences in the growth metrics of *H. splendens.*

## 4.3 Implications for forest management

As 88% of the productive forest land in Sweden is actively managed (SCB 2024), and as understory vegetation is crucial for the boreal ecosystems (Eldridge et al.

2023), it's of importance to understand and reduce negative consequences of understory growth related to forestry. This study shows that both young forests and retention patches function well in supporting understory growth (Figure 2). However, this study also shows that *H. splendens* in young forests possess morphology traits which may indicate less suitable environmental conditions (Bergamini and Peintinger 2002; Figure 3 and 4). Therefore, the productive forest landscape in Sweden, which consists of 40% young forests aged 40 or less (SLU 2024), may have negative effects on the understory growth.

Through this study, there are two main recommendations to enhance the understory growth in managed boreal forests: 1) Thinning in young forests is of importance to enhance understory growth. The morphological traits of *H. splendens* indicate some light deficiency as the shoots had elongated and was sparce in the young forests (Figure 3 and 4). The importance of thinning is supported by Tonteri et al. (2016), who showed the positive effects of understory after thinning as more light reaches the forest floor. 2) Retention patches function relatively well, both in the short- and longer term (Zhang et al. 2025; Figure 2), to maintain understory growth. If the purpose is to maintain forest living understory species, the retention patch should preferably be as large as possible, located in a northern direction close to an old growth forest (Gustafsson et al. 2016).

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# Appendix 1

*Appendix 1. Performed $X^2$-tests of observed anomalies during the measurement of H. splendens.*

| | **Several segments one year** | **Not several segments one year** |
|---|---|---|
| Retention patches | 9 | 91 |
| Young forests | 8 | 92 |
| Old growth forests | 8 | 92 |
| Total | 25 | 275 |
| p-value | 0.961 | |
| | **Broken segment** | **Not broken segment** |
| Retention patches | 20 | 80 |
| Young forests | 13 | 87 |
| Old growth forests | 22 | 78 |
| Total | 55 | 245 |
| p-value | 0.296 | |
| | **Monopodial growth** | **Sympodially growth** |
| Retention patches | 5 | 95 |
| Young forests | 3 | 97 |
| Old growth forests | 3 | 97 |
| Total | 11 | 289 |
| p-value | 0.695 | |
| | **Only two segments present** | **At least three segments present** |
| Retention patches | 6 | 94 |
| Young forests | 11 | 89 |
| Old growth forests | 4 | 96 |
| Total | 21 | 279 |
| p-value | 0.156 | |
| | **Latest segment too small** | **Latest segment measured** |

| | | |
|---|---|---|
| Retention patches | 6 | 94 |
| Young forests | 0 | 100 |
| Old growth forests | 10 | 90 |
| Total | 16 | 284 |
| p-value | 0.00865 | |

# Appendix 2

*Appendix 2. Table over the performed One-Way Anova's. In total, three One-Way Anova's were conducted, one for each growth measure of H. splendens .*

| **Segment width** | | | | |
|---|---|---|---|---|
| Forest type | Young forest | Retention patches | Old growth forest | Total |
| Replicates | 20 | 20 | 20 | 60 |
| Mean value | 30.4 | 28.6 | 31.6 | |
| Standard error | 0.951 | 0.917 | 1.076 | |
| F-value | | | | 2.19 |
| MKv within groups | | | | 21.4 |
| p-value | | | | 0.121 |
| HSD-value | | | | |
| **Segment length** | | | | |
| Forest type | Young forest | Retention patches | Old growth forest | Total |
| Replicates | 20 | 20 | 20 | 60 |
| Mean value | 37.6 | 30.2 | 32.9 | |
| Standard error | 1.17 | 1.40 | 1.54 | |
| F-value | | | | 7.29 |
| MKv within groups | | | | 38.0 |
| p-value | | | | 0.00152 |
| HSD-value | | | | 5.03 |
| **Ratio segment width/length** | | | | |
| Forest type | Young forest | Retention patches | Old growth forest | Total |
| Replicates | 20 | 20 | 20 | 60 |
| Mean value | 0.848 | 1.00 | 1.01 | |
| Standard error | 0.0279 | 0.0316 | 0.0337 | |
| F-value | | | | 8.46 |
| MKv within groups | | | | 0.0194 |
| p-value | | | | 0.000606 |
| HSD-value | | | | 0.114 |

# Appendix 3

*Appendix 3. Performed regression analysis. In total, 12 regression analyses were performed. Three regression analysis for each forest type, and three for all forests together.*

| **Segment width all forests** | **Value** |
|---|---|
| Replicates | 60 |
| Multiple R | 0.0672 |
| p-value | 0.610 |
| **Segment length all forests** | |
| Replicates | 60 |
| Multiple R | 0.2209 |
| p-value | 0.0899 |
| **Ratio all forests** | |
| Replicates | 60 |
| Multiple R | 0.202 |
| p-value | 0.122 |
| **Segment width young forests** | |
| Replicates | 20 |
| Multiple R | 0.0686 |
| p-value | 0.774 |
| **Segment lenght young forests** | |
| Replicates | 20 |
| Multiple R | 0.134 |
| p-value | 0.573 |
| **Ratio young forests** | |
| Replicates | 20 |
| Multiple R | 0.0409 |
| p-value | 0.864 |
| **Segment width retention patches** | |
| Replicates | 20 |
| Multiple R | 0.171 |
| p-value | 0.472 |
| **Segment length retention patches** | |
| Replicates | 20 |
| Multiple R | 0.144 |
| p-value | 0.544 |
| **Ratio retention patches** | |
| Replicates | 20 |

| | |
|---|---|
| Multiple R | 0.00386 |
| p-value | 0.987 |
| **Segment width old growth forests** | |
| Replicates | 20 |
| Multiple R | 0.211 |
| p-value | 0.372 |
| **Segment length old growth forests** | |
| Replicates | 20 |
| Multiple R | 0.0322 |
| p-value | 0.893 |
| **Ratio old growth forests** | |
| Replicates | 20 |
| Multiple R | 0.242 |
| p-value | 0.304 |

# Appendix 4

*Appendix 4. Performed Mann-Whitney U tests. In total, three Mann-Whitney U tests were conducted.*

| **Segment width** | | | |
|---|---|---|---|
| Red-listed | Yes | No | Total |
| Replicates | 13 | 47 | 60 |
| Mean | 29.3 | 30.4 | |
| Standard error | 1.05 | 0.722 | |
| p-value | | | 0.609 |
| **Segment length** | | | |
| Red-listed | Yes | No | Total |
| Replicates | 13 | 47 | 60 |
| Mean | 32.5 | 33.9 | |
| Standard error | 1.68 | 1.02 | |
| p-value | | | 0.622 |
| **Ratio** | | | |
| Red-listed | Yes | No | Total |
| Replicates | 13 | 47 | 60 |
| Mean | 0.946 | 0.955 | |
| Standard error | 0.0243 | 0.0249 | |
| p-value | | | 0.979 |

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