



Effects of Forest Management on Understory Plant Traits and Biodiversity

A chronological analysis of fire burned and
managed forests

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Effects of Forest Management on Understory Plant Traits and Biodiversity - A chronological analysis of fire burned and managed forests

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Abstract

Boreal forests are one of the largest terrestrial carbon sinks and provide a variety of ecosystem services. With the threat of climate change and biodiversity loss in these forests, industries that utilize the natural products within the forests share a responsibility to maintain the forest and the ecosystem services they provide. With the majority of vegetation studies focusing on trees, understory vegetation and the services they provide are often overlooked. The Swedish model of forestry is being questioned on its ability to replicate natural disturbances as it is unclear on the differences between clear-cuts and fire disturbances. This study investigates how clear-cuts and fire disturbed forest stands differ over time through nitrogen, plant traits, and biodiversity values. I observed a chronosequence of managed and fire burned stands and measured the total cover, species composition, and available nutrient pools to investigate the differences. The results of this study emphasises the responses forests and their understory have to different disturbances over a long period and show that managed stands had higher available nitrogen pools in the soil, a novel species composition compared to the fire burned stands, and lowered biodiversity values over time. Stands with a known fire history had lower available nitrogen pools, an expected species composition, and higher alpha diversity and lower beta diversity over time. This study highlights the different complex responses understory plants have to management over the long term and shows that management on forests lead to faster degradation of soil and biodiversity over time.

Keywords: biodiversity, nitrogen, plant traits, clear-cut, plant community composition, Bray-Curtis Dissimilarity Index, Simpson's Diversity Index

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Abbreviations

| | |
|------|---|
| SLA | Specific Leaf Area |
| LDMC | Leaf Dry Matter Content |
| SLU | Swedish University of Agricultural Sciences |
| SGH | Stress Gradient Hypothesis |

1. Introduction

The boreal forest, covering 11% of Earth's terrestrial surface, is the dominating biome within Scandinavia, northern Russia, and parts of Canada and the US (Bonan and Shugart 1989; Esseen et al. 1997; Bradshaw and Warkentin 2015). Boreal forests have an important global role as they are the second largest terrestrial carbon sinks, containing around 272 Pg of CO₂, or 32% of the world's forest carbon stock (Pan et al. 2011). The majority of biomass in these forests are found in the trees, but the understory is where most of the biodiversity is found (Gilliam 2007). Swedish boreal forest overstory is dominated by *Pinus sylvestris* L. and *Picea abies* (L.) H.Karst., while the understory vegetation is dominated by three main dwarf shrubs: *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L., and *Empetrum nigrum* L. (Nilsson & Wardle 2005; Figure 1). Feathermoss, lichen, and fungi also inhabit the forest floor. Boreal forests are one of the few biomes that still have large-scale natural disturbances occurring at natural levels (Ruckstuhl et al. 2007). One of the main industries of the boreal forests in general, and in Sweden specifically, is the abundance of wood for wood-based products (Chen et al. 2017). Swedish forestry has a long history, with clear-cut forestry starting in the 1950s (Lundmark et al. 2013). Currently, it is estimated that forestry earns Sweden 10 million Euro in exports (Sandberg et al. 2014). Being an industry based on the harvest of natural materials, a system that can continuously provide wood is ideal. With global threats such as climate change pressuring boreal forest systems, one of the main goals of forestry is maintaining forests and the ecological services they provide, also known as sustainable forestry (Ruckstuhl et al. 2007; Oliver 2003).



Figure 1. Pictured from right to left: *Vaccinium myrtillus*, *Empetrum nigrum*, *Vaccinium vitis-idaea*

The current model of Swedish forestry has become a controversial talking point as there are conflicting viewpoints on the current rotational forestry model in use (Lindahl et al. 2017; Sahlin 2011). With increased stress of forests coming from climate change, it is critical that we understand the implications forestry has on the environment. The consensus on this type of forestry is that it has both benefits and drawbacks concerning their sustainability. It is often claimed that rotational forestry mimics the natural disturbance of fire within boreal forests through clear-cutting stands, but it fails to reintroduce a heterogenous mixture of trees and maintain a multistoried canopy (Kermavnar et al. 2019; Patry et al. 2017; Fedrowitz et al. 2014). Such drastic anthropogenic changes can negatively impact the health of a forest as more alterations are made on an ecosystem (Hobbs et al. 2006; Hooper et al. 2005). In Sweden, clear-cuts are largely planted with native *P. sylvestris* and *Picea abies* following mechanical soil scarification, but non-native trees can also be used (Dynesius 2015). Fires play an important role within the boreal ecosystem as they affect multiple abiotic aspects, such soil nutrient contents, pH, and hydrophobicity (Murphy et al. 2006; Knicker 2007; Neary et al. 1999). Fires also clear ground vegetation and contribute to the structure of the forest (Wade et al. 1980). This in turn can temporarily increase biodiversity by catering to fire dependent species, early colonizers, and fast-growing plants, but it is also seen that clear-cuts can also increase understory biodiversity (Abella & Springer 2015). While these are both large disturbances, they can vary in what plants and in what abundance of said plants can colonize the area. The lack of fires in these areas can cause species that thrive in burnt substrates or fire disturbed areas to vanish (Wikars 1997). Some of the differences that can arise from lack of fires in a forest are the amount of available nitrogen pools, which affect the individual plant traits, competition, and biodiversity (Zhang et al. 2018). Another concern for lack of

forest fires relates to the process of succession, mainly relating to *E. nigrum*. The concern with *E. nigrum* is that it can impede the growth of new seedlings due to allelopathic compounds (Nilsson & Wardle 2005). *E. nigrum* is sensitive to fires and mechanical damage, but fire disturbances can help burn the build-up of allelopathic compounds by burning the leaves (Tybirk et al. 2000). Understanding the differences between the succession of rotational forestry and natural disturbances is critical to advance our knowledge so we can achieve sustainable forestry.

An aspect of forestry that is often overlooked is how the understory is affected and the implications on the ecosystem and its services. While trees hold most of the forest biomass, understory vegetation is where most of the vegetative biodiversity in forests occur where it can mediate a significant amount of nutrient cycling in the soil (Gilliam 2007). The health of the understory can be affected with different types of disturbances (Griffis et al. 2001). Different levels of nutrient, sunlight transmission, water availability, and other factors can greatly affect the understory composition (Hart & Chen 2006). Rotational forestry does not alter the forest the same way as a fire which can lead to an altered composition (Hart & Chen 2008). One difference between clear-cuts and fire disturbances is the overstory canopy cover. Forest fires do not necessarily replace stands, as seen in low intensity fires, but clear-cuts take almost every tree when harvesting, which can temporarily allow a greater amount of light on the stand (Dodson et al. 2007; Windenfalk & Weslien 2009). Another difference is the microclimate variation that can decrease when canopy cover is lost (Zellweger et al. 2009). While this may seem trivial when forestry mainly focuses on trees, the understory can determine the success of tree saplings, which is of great importance to forestry (Légaré et al. 2002). Learning how forestry affects the understory and the nutrients that heavily influence the understory, such as nitrogen, is essential for creating sustainable forestry practices.

Nitrogen is one of the most important nutrients for plants as it is necessary for growth and amino acid production (Kirkby 1981; Novoa & Loomis 1981). Nitrogen is often seen as the main limiting nutrient in boreal forests (Hyvönen et al. 2008; Sponseller et al. 2016). It is well known that fires release nitrogen into the soil through the mineralization of organic matter (Raison 1979). While rotation forestry tries to imitate natural disturbances, it fails to recreate the effects of fire damage on the soil and understory (Pirainen 2002). Differences in the available nitrogen and the remaining vegetation after disturbances can affect successional trajectory. In the case of clear-cut forestry, removal of ground cover is mainly from mechanical damage when harvesting, so instead of plant materials being mineralized from fires, they decomposed. This can lead to different mineralization rates, which in turn can lead to different nitrogen levels (White 1986). This can cause problems as nitrogen

fixation in depends on the current nitrogen reserves and stand history (Reiners 1981). Nitrogen leaching is also a concern for managed stands. Soil scarification can disrupt underground networks of mycorrhiza, which can prevent nitrogen from leaching (Asghari & Cavagnaro 2012; Fang et al. 2020). Nitrogen stocks can affect the biodiversity of the stands, interspecies competition, and a variety of traits within plants (Suonan et al. 2023).

One of the ways that plants can differ between stands is how they present themselves from a phenotypical perspective. These characteristics can be referred to as individual plant traits. Individual plant traits are affected by a multitude of different aspects within an ecosystem, such as nutrient availability and water availability. (Reich 2014). The plant's primary strategy can also affect how it presents itself in a variety of different stressors (Grimes 1977). According to the Stress Gradient Hypothesis (SGH), when stressors increase, the competition between plants decreases due to less available nutrients (Malkinson & Tielbörger 2010). We can track the amount of stress individual plants are receiving by looking at their plant traits. Plants often have a trade-off between faster development when resources are abundant and easily accessible versus slower, more resource efficient growth when resources are scarce or difficult to process (Reich 2014). Some of the more commonly seen plant traits are Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), and Nitrogen and Carbon contents of the leaves. While fire and clear-cuts are both large disturbances that can drastically alter the forest, the way plants regenerate afterwards can differ due to the differences in sunlight and open patches of soil (Pykälä 2004). Pairing this with the effect of nitrogen, plant composition, biodiversity, and richness can be affected.

One of the main concerns of rotation forestry is its effect on biodiversity. Conservation of species have been a rising concern in the world due to the fragmentation of forests and deforestation, leading to a loss of global biodiversity (Betts et al. 2017; Cardillo 2006; Kouki 2001). The importance of biodiversity cannot be understated, as loss of biodiversity can lead to alterations in forest structure, its functions, and its resilience (Tilman & Downing 1994; Naeem et al. 1994; Cardinale et al. 2012). Not only does biodiversity lead to higher resilience within its respective ecosystem, but it can also affect the functionality of ecosystem services. Currently, the focus of most vegetative studies in boreal forests has focused on trees, but there is a growing interest concerning understory vegetation such as dwarf shrubs, lichens, and mosses. The comparison between fire burned stands and managed stands is where knowledge is lacking. Although trees are the main concern of the majority of vegetation studies in forestry, most of the biodiversity of boreal forests comes from the understory (Roberts 2004).

Sustainable forestry models should be going towards methods that preserve biodiversity and genetic variation of all organisms within the forest ecosystem.

1.1 Research Questions and Hypotheses

This paper aims to resolve the gap of knowledge on the effects clear cut forestry has on available nitrogen stocks, understory plant traits, and biodiversity over time. In order to better understand how forest management affects the boreal forests, I studied how *P. sylvestris* dominated stands responded to clear-cuts and forest fires over a chronological scale. The main questions this thesis seeks to answer are:

1. What are the differences in available inorganic nitrogen pools on the stand level and how do they fluctuate in the soil between managed and burnt stands over time?
2. How are individual plant traits affected by management and fire, and what do they trend towards over time?
3. How is biodiversity, specifically stand level species richness and beta diversity, affected by management and fire?

The hypotheses are as follows:

1. Available inorganic nitrogen pools will be higher in managed and fire burned stands at the start of the chronology, but over time the rate at which the concentrations decrease will be faster in managed stands.
2. Plants within all stands will tend to have phenotypic traits that lean towards slower development at the beginning of the chronosequence, but over time the traits will point towards faster growing, less conservative phenotypic traits. Managed stands will show plants starting at a lower growth rate than fire stands but will move to less conservative growth at a faster rate.
3. Both alpha and beta biodiversity values will be higher immediately after both types of disturbance. Alpha diversity will decrease for the managed stands over time, while fire burned stands will either stay consistent or increase over time due to fires creating more heterogenic environments. For managed stands, this will be due to a combination of more pioneer vegetation and colonizers that respond better to the total loss of canopy. Beta diversity will decrease for both stands but will decrease faster in managed stands because of a lack of variation in microclimates.

2. Materials and Methods

2.1 Area of study

The study areas are located around Arvidsjaur and Jokkmokk in Västerbotten and Norrbotten counties in northern Sweden. The study areas are split into two chronosequences; one chronosequence consists of managed stands that were clear cut (n=18), while the other chronosequence consists of unmanaged with a known fire history (n=18). Thus, the study consisted of 36 stands. Individual stands were found through Sveaskog GIS. The criteria for stand selection was each stand was a mesic site type and dominated by Scots pine (*P. sylvestris*) and dwarf shrubs, and feathermoss understory vegetation. Stands were selected in clusters, when possible, to evenly distribute variation in climate, geology, latitude, and other factors. GPS was used to mark out the ordinal corners of the plot and the center. Managed stands had an age span from 1-109 years, while the fire burned stands had an age span from 4-375. In both cases, this is representative of the range of variation in stand age for managed and unmanaged forests on the landscape (Tahvonen 2013).

2.2 Vegetation plots

In June 2023, we marked 20 vegetation subplots in each stand using a 4x5 pattern with ~10m spacing subplots. Each subplot was measured to be a 0.7x0.7m quadrat. The center of the 4x5 grid aligned with the center of the whole 1 ha plot. (Figure 2). Vegetation subplots were premarked on the GPS prior to field work. Resin pods were installed inside of the subplot to track the nutrient fluxes throughout the field season, mainly focusing on nitrogen. Resin capsules were installed inside the subplot between the organic horizon and the eluviated horizon to track the nutrient fluxes throughout the field season, mainly focusing on inorganic nitrogen.



Figure 2. Example of a plot and the orientation of the vegetation subplots. The plot pictured is M36 and is oriented with north at the top. This image originates from Google maps.

Vegetation cover data, plant trait samples, and resin pods were collected in July and August 2023. The vegetation cover data includes all vascular plants, mosses, and lichens. Vegetation cover and species composition was measured using the pin-pointing method as described in Goodall 1952. Within each 0.7mx0.7m sub-plot, a point quadrat ten points long was used to identify the present vascular plant species and the type of ground hit (e.g. rock, bare soil, moss). The point quadrat uses ten straight, downward projected points that are used to count the amount of times vegetation touches each point (Sundqvist et al. 2011; Goodall 1952). The point quadrat was used five times within the quadrat to obtain 50 data points with 50 ground hits. Plants that were within the quadrat and not hit by any of the 50 points were recorded as present within the subplot, but not hit. Percent cover, total percent cover, Bray-Curtis dissimilarity, and Simpson's Index of diversity were calculated using the vegetation cover data. Plant trait data utilized the total cover data for *V. myrtillus*, *V. vitis-idaea*, and *E. nigrum*. For Bray-Curtis dissimilarity and Simpson's Index of diversity, total cover for all vascular plants, mosses, and lichens were used. Percent cover measure the three-dimensional cover species have in the subplot, which can result in percentages higher than 100%. Simpson's Index of Diversity is used to measure species diversity. In this case, we are using it to find the alpha diversity of the plots (DeJong 1975). As the number moves towards 1, the less biodiverse the stand becomes. Simpson's Index for biodiversity was calculated on the stand level. Bray-Curtis Dissimilarity Index calculates the dissimilarity across geographic units, which in our case is the forest stands. As the number trends towards 1, dissimilarity increases, which can be an indication of higher biodiversity (Bloom 1981). In our case, we are using the Bray-Curtis dissimilarity to calculate

the beta diversity between stands. The data used for the Bray-Curtis dissimilarity was a matrix over the entire data set. Resin capsules were removed, bagged, and sent to the lab to test the available inorganic nitrogen pools in the soil.

Leaf matter for plant traits data was collected at nine main points in the plot. The leading stems of *V. myrtillus*, *V. vitis-idaea*, and *E. nigrum* were collected from the cardinal midpoints of the plot, the ordinal corners, and plot center. More leaves would be collected generally throughout the 4x5 vegetation subplot grid. Criteria for the collected samples included minimal pest damage, minimal mechanical damage, and minimal visible stress (e.g. discoloration and galls). The total mass of the collected samples varied, but the minimum amount was around 2g of leaves in total for each stand. This ensured enough leaf mass for chemical analysis. The leaves were placed in paper bags to prevent mold growth. On the day of collection, leaves were picked from randomly selected stems and placed on graph paper and photographed to facilitate calculation of Specific Leaf Area (SLA). Leaves from *V. myrtillus* and *V. vitis-idaea* were counted as they were picked so that I could calculate the average mass per leaf later in data analysis. Criteria for picked leaves included having a petiole and minimal mechanical damage. After taking a picture of the leaves, the leaves were weighed on a scale and the mass was recorded. The leaves were placed into a paper bag, labelled with the corresponding plot, and stored in a cool dry area before transportation to the lab. The leaf area used for SLA was calculated using Procreate© and ImageJ (Schnieder et al. 2012). SLA is described as the ratio of leaf area to leaf dry mass, while LDMC (Leaf Dry Matter Content) is described as the ratio of dry leaf mass to fresh leaf mass (Garnier et al. 2001). Procreate was used to count the leaves of *E. nigrum* by hand due to inaccuracies in counting of ~30% using ImageJ. Leaves were marked, counted, and recorded. Using ImageJ, all the leaves of *V. myrtillus* and *V. vitis-idaea* were measured for leaf area. Due to the mass amount of *E. nigrum* (some totalling over 1,000 leaves), the number of leaves counted was reduced to either 40-60 or 10% of the total leaves, depending on the complexity of the picture.

2.3 Lab work

The leaf matter collected from the plots were placed in a drying oven at 60 degrees Celsius for two days to ensure the leaf matter was dry. Once the leaves were dry, the leaf matter was reweighed on a scale to obtain the dry leaf mass. The dry leaf mass and the wet leaf mass from prior weighing would be used to calculate the Leaf Dry Mass Content (LDMC). The leaves were then ground using a stainless-steel ball mill (Figure 3). The frequency of the ball mill grinder was set to 21

vibrations per second for 3 minutes for *V. myrtillus* and *E. nigrum*, and 5 minutes for *V. vitis-idaea*. The variation in time was due to the thicker, more fibrous *V. vitis-idaea* leaves needing more time to break down than the thinner, less fibrous *V. myrtillus* leaves or the much smaller *E. nigrum* leaves. After grinding, the plant material was checked for any large, fibrous material. If the material appeared too coarse, the material was again placed in the ball mill for further grinding. After the plant material reached a powdery consistency, the powder was removed from the hollow shells and placed into plastic vials. The vials were weighed with the plant material so that the LDMC could be calculated by dividing the dry mass by the wet mass of the leaves. SLA and LDMC can be used to describe whether a plant is prioritizing rapid growth or conservation of nutrients (Garnier et al. 2001; Majeková et al. 2014). This can be a predictor of the state of the soil and its available nutrients. The total percent cover is the 3D cover of understory in the 1m² quadrats. The total percentage of plant cover can exceed 100% due to multiple layers of plant matter being accounted in the point quadrat method. After weighing, the vials were stored in a cool, dry place. The hollow shells were cleaned with a 20% RBV solution to prevent cross contamination between samples. Samples were then sent to the Analytical Lab at the Department of Forest Ecology and Management at SLU, Umea for chemical analysis of carbon and nitrogen content. Carbon and nitrogen are important macronutrients that facilitate multiple functions within plants, such as the synthesis of glucose using carbon or the synthesis of specific amino acids like asparagine and aspartate using nitrogen (Zheng 2009).



Figure 3. Pictured on the left is the 10ml hollow shells with the stainless steel ball. The ball mill grinder that was used is pictured on the right.

2.4 Data Analysis

All data analyses were carried out using R (R Core Team 2023). Linear regressions were calculated using the lme4 package (Douglas et al. 2015) and graphs were plotted using the ggplot2 package (Wickham 2016). All desired residuals were averaged over the 20 subplots to obtain a single mean value for each plot. A total of 36 plot means were used to create the data set. I used simple t-tests in order to find the significance between the managed stands and the fire burned stands.

2.4.1 Nitrogen Trends

Using data from the resin pods, nitrogen trends were calculated using a linear model with a gamma- distribution. The following model was used:

$$lm(\text{Desired Nitrogen value} \sim \text{Age} * \text{Management})$$

Where the desired nitrogen value can be the total nitrogen, NH₄, or NO₃.

2.4.2 Plant Traits and their Calculations

I decided to use six plant traits to track the overall growth strategies and individual plant health of the three dominant dwarf shrubs: Specific Leaf Area (SLA), Leaf Dry Mass (LDMC), Carbon content in leaves, Nitrogen content in leaves, the Carbon/Nitrogen ratio, and the total percent cover. In order to simplify the graphs, I decided to use community weighted means. Community weighted values use the percentages of cover each shrub had in relation to each other to weigh the value of each plant (Griffin-Nolan et al. 2018). The community values were calculated using this equation:

$$\text{Community weight of } x \text{ species} = \frac{\% \text{ cover of } x \text{ species}}{(\% \text{ cover of } V. \text{myrtillus} + \% \text{ cover of } V. \text{vitis} - \text{idaea} + \% \text{ cover of } E. \text{nigrum})}$$

X represents one of the three dwarf shrubs. Community weights were multiplied with their corresponding species, then the species were added together to attain the community weighted trait. The equation for finding community weighted traits is depicted below:

$$\begin{aligned} \text{Community weighted trait} &= (\text{Community weight } V. \text{myrtillus} \\ & * x \text{ plant trait } V. \text{myrtillus}) \\ &+ (\text{Community weight } V. \text{vitis} - \text{idaea} * x \text{ plant trait } V. \text{vitis} \\ &- \text{idaea}) + (\text{Community weight } E. \text{nigrum} \\ & * x \text{ plant trait } E. \text{nigrum}) \end{aligned}$$

X represents one of the six previously mentioned plant traits. After calculating the community weighted traits for each plant trait, I used linear regressions utilizing the formula below:

$$lm(\text{Community Weighted } x \text{ Plant trait} \sim \text{Age} * \text{Management})$$

The following two equations were used to calculate SLA and LDMC:

$$SLA = \frac{\text{Leaf Area}}{\text{Leaf Dry Mass}}$$

$$LDMC = \frac{\text{Dry Leaf Mass}}{\text{Fresh Leaf Mass}}$$

Total percent of plant cover can be calculated by:

$$\text{Percent cover of species} = \frac{\text{Total number of hits of species}}{50}$$

This value is multiplied by the community weighted values to create a single residual per plot, but graphing the individual shrubs and their change over time can aid in our understanding of the trends of plant traits. The cover can give us insight on the nutrient values within the soil and how the understory reacts to those values (Légaré et al. 2002).

2.4.3 Calculation of Diversity

The vegan package (Oksanen et al. 2022) was used to carry out both Simpson's Index of Diversity and the Bray-Curtis Dissimilarity Index. Both indices are the most commonly used formulas for finding alpha and beta diversity respectively (Lande 1996).

In He & Hu 2005, Simpson's Index is defined as:

$$\text{Simpson's Index of Diversity} = 1 - \sum_{i=1}^S x_i^2$$

Where x_i is the relative abundance of the i species. As Simpson's Index of Diversity goes towards 1, there is less alpha biodiversity in the area (DeJong 1975).

The Bray-Curtis Dissimilarity index can be used as an index for beta diversity.

Bray-Curtis Dissimilarity Index is defined as:

$$BC_{UV} = \frac{\sum_{j=1}^S |x_{Uj} - x_{Vj}|}{\sum_{j=1}^S |x_{Uj} + x_{Vj}|}$$

Where x_{Uj} and x_{Vj} stands for the abundance of species in plot U and V (Ricotta & Podani 2017). As the Bray-Curtis Dissimilarity index goes towards 1, the more dissimilar the plots become. Diversities were made into a linear regression with the following equation:

$$lm(\text{Diversity} \sim \text{Age} * \text{Management})$$

Where Diversity can be substituted for either alpha or beta diversity.

3. Results

I analyzed nitrogen trends, plant traits, and diversity using a chronosequence comprising of 36 forest stands. 18 stands had a fire chronology, and the other 18 stands had a managed chronology. The results show that nitrogen totals decrease at a faster rate in managed stands yet start at a higher nitrogen concentration. Plant traits were trending towards faster growth rates in both stands. Alpha biodiversity decreased in managed stands and slightly increased in fire burned stands. Beta diversity decreased in both.

I used linear regressions to test the hypotheses and a t-test to test for significance between the regressions. Adjusted R^2 values were used as they are a more accurate way of reporting than R^2 when using linear regressions (Fox 1997).

3.1 Nitrogen Trends

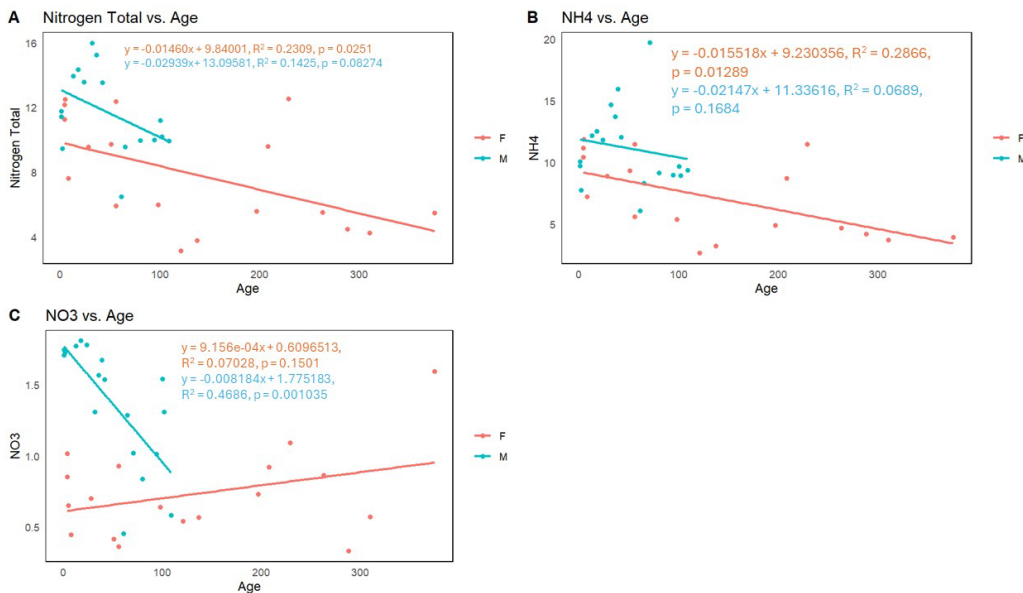


Figure 4. Available nitrogen pools over time (A = Nitrogen totals, B = NH4, C = NO3). Fire burned stands are shown in red and managed stands are shown in blue. The equations are color coded to the management style and display slope, R^2 value, and the p-value.

Table 1. Slope, correlation, and significance of the management on the nitrogen values over time. * indicates a significant p value (p-value < 0.05).

| Nitrogen Value and Management Type | Slope Equation | R ² adjusted | p-value |
|------------------------------------|------------------------------|-------------------------|-----------|
| Total nitrogen Fire | $y = -0.01460x + 9.84001$ | 0.2309 | 0.0251* |
| Total nitrogen Managed | $y = -0.02939x + 13.09581$ | 0.1425 | 0.08274 |
| NH ₄ Fire | $y = -0.015518x + 9.230356$ | 0.2866 | 0.01289* |
| NH ₄ Managed | $y = -0.02147x + 11.33616$ | 0.0689 | 0.1684 |
| NO ₃ Fire | $y = 0.0009156x + 0.6096513$ | 0.07028 | 0.1501 |
| NO ₃ Managed | $y = -0.008184x + 1.775183$ | 0.4686 | 0.001035* |

According to the available data, we can see that in all stands the nitrogen decreases with age (Figure 4). Differences arise between managed and fire burned stands with the rate at which the nitrogen decreases and the starting amount of nitrogen. All nitrogen forms are seen to have positive correlations, with managed stands starting at high concentrations. Fire burned stands had a positive correlation and trended downwards, while managed stands also had a positive correlation, but trended downwards at a faster rate (Figure 4; Table 1). There is a significant difference between the two trends (Table 2).

For NH₄, it decreases slightly slower with time in fire burned stands than in managed stands. There is significance in the fire chronology, along with a positive correlation with age. There is a significant difference between managed stands and fire burned stands (Table 2).

NO₃⁻ showed a sharp, significant decrease with time in managed stands, but increased with time in fire burned stands (Table 2). Both managed and fire burned chronologies have positive correlations with age. We can see that NO₃ has a higher starting value in managed stands than fire burned stands (Table 2).

Table 2. Results of t-test of Nitrogen values (Total Nitrogen, NH₄, and NO₃). * indicates a significant p value (p-value < 0.05).

| Compared Value | Analysis Method | Degrees of Freedom | Test Statistic Value | p-value |
|-----------------|-------------------|--------------------|----------------------|------------|
| Nitrogen total | Two sample t-test | 33.965 | -4.0921 | 2.488e-04* |
| NH ₄ | Two sample t-test | 33.988 | -3.647 | 8.794e-04* |
| NO ₃ | Two sample t-test | 31.084 | -5.1083 | 1.564e-05* |

3.2 Plant Traits

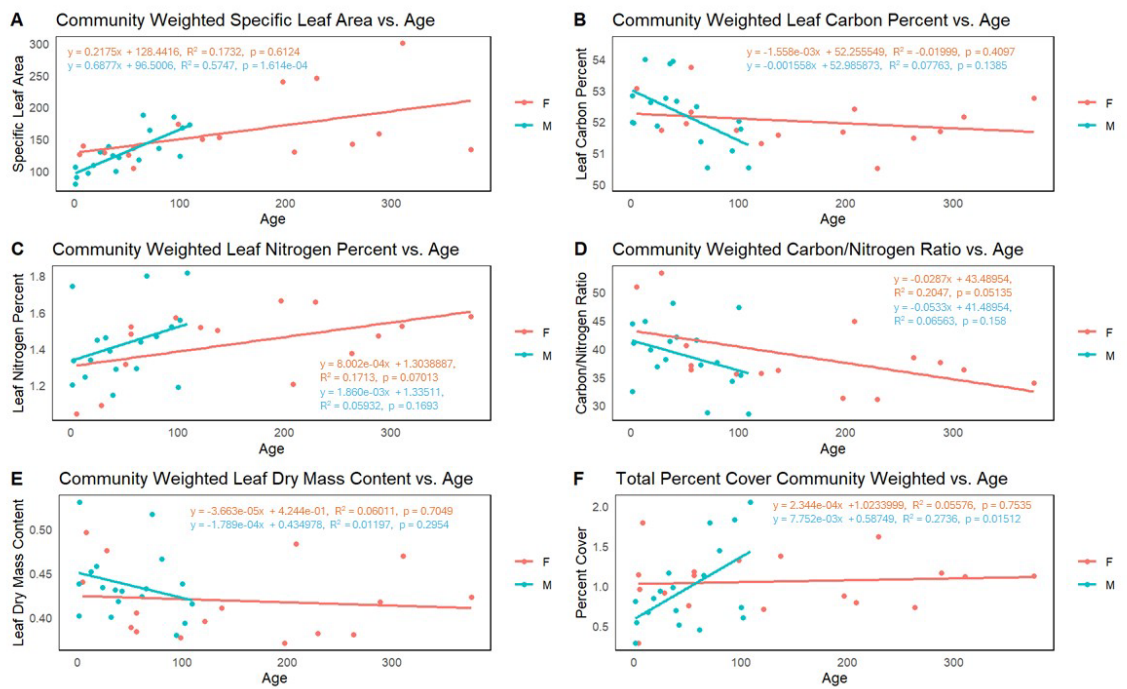


Figure 5. Community weighted plant traits over time. Plant traits include Specific Leaf Area (SLA), leaf percentage of carbon, leaf percentage of nitrogen, carbon/nitrogen ratio, Leaf Dry Mass Content (LDMC), and the total percent cover.

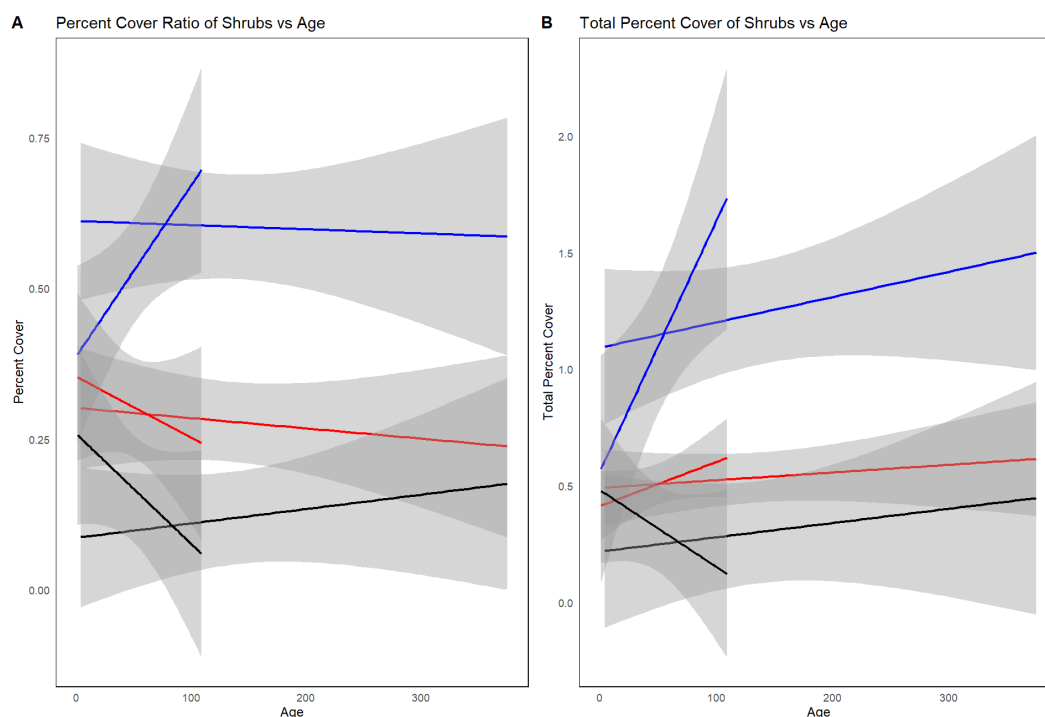


Figure 6. Percent cover of *V. myrtillus* (blue), *V. vitis-idaea* (red), and *E. nigrum* (black) over time. The shorter chronology is the managed stands while the longer chronology is the fire burned stands. A is the ratio of the three shrubs. B is the total % cover.

Table 3. Slope, correlation, and significance of plant trait values. * indicates a significant p value (p -value < 0.05).

| Plant Trait and Management Style | Value | Slope Equation | R ² adjusted | p-value |
|----------------------------------|-------|------------------------------|-------------------------|------------|
| Specific Leaf Area Fire | | $y = 0.2175x + 128.4416$ | 0.1732 | 0.06124 |
| Specific Leaf Area Managed | | $y = 0.6877x + 96.5006$ | 0.5747 | 0.0001614* |
| Leaf Carbon Percentage Fire | | $y = -0.001558x + 52.255549$ | -0.01999 | 0.4097 |
| Leaf Carbon Percentage Managed | | $y = -0.011901x + 52.985873$ | 0.07763 | 0.1385 |
| Leaf Nitrogen Percentage Fire | | $y = 0.0008002x + 1.3038887$ | 0.1713 | 0.07013* |
| Leaf Nitrogen Percentage Managed | | $y = 0.001860x + 1.333511$ | 0.05932 | 0.1693 |
| Carbon/Nitrogen Ratio Fire | | $y = -0.0287x + 43.23787$ | 0.2047 | 0.05135 |

| | | |
|-------------------------------|-----------------------------|----------|
| Carbon/Nitrogen Ratio Managed | $y = -0.05330x + 0.06563$ | 0.158 |
| Leaf Dry Mass Content Fire | $y = -3.663e-05x + 0.06011$ | 0.7049 |
| Leaf Dry Mass Content Managed | $y = -0.0001789x + 0.01197$ | 0.2954 |
| Total Percent Cover Fire | $y = 0.0002334x + 0.05576$ | 0.7535 |
| Total Percent Cover Managed | $y = 0.007752x + 0.2736$ | 0.01512* |

Table 4. Results of t-test of community weighted plant traits (Specific Leaf Area, Leaf Carbon, Leaf Nitrogen, Leaf Carbon/ Nitrogen ratio, Leaf Dry Mass Content, Total Percent Cover). * indicates a significant p value (p-value < 0.05).

| Compared value | Analysis Method | Degrees of Freedoms | Test Statistic value | p-value |
|-----------------------------|-------------------|---------------------|----------------------|---------|
| Specific leaf Area | Two sample t-test | 24.304 | 2.0054 | 0.05618 |
| Leaf Carbon | Two sample t-test | 29.311 | -1.1275 | 0.2687 |
| Leaf Nitrogen | Two sample t-test | 30.474 | 0.1105 | 0.9127 |
| Leaf Carbon/ Nitrogen Ratio | Two sample t-test | 28.179 | -0.11959 | 0.9057 |
| Leaf Dry Mass Content | Two sample t-test | 30.799 | -1.2866 | 0.2078 |
| Total percent cover | Two sample t-test | 30.256 | 0.57716 | 0.5681 |

3.2.1 SLA and LMDC

We can see that SLA increased at a much faster rate in managed stands than in fire burned stands (Figure 5; Table 3). This follows the trend of the percent cover of each shrub, as *V. myrtillus* increases sharply over time in managed stands while the shrub composition of fire burned stands are less volatile (Figure 5). SLA started higher in fire burned stands but became lower by the end of the managed chronosequence. Differences in SLA are not significant (Table 4).

LDMC decreased at a faster rate in managed stands than in the fire chronosequence (Table 3). LDMC starts at a higher value in managed stands than in fire burned stands. There is no significant difference between the two (Table 4).

3.2.2 Carbon and Nitrogen

The results show that leaf carbon content decreased at a faster rate in managed stands than in fire burned stands (Table 3). There is no significant difference between carbon rates in the leaves (Table 4).

Leaf nitrogen increases for both managed and fire burned stands, but it increases at a higher rate in managed stands. Both chronologies were positively correlated with each other (Table 3). There is no significant difference between the two (Table 4).

The C:N ratios in both managed and fire burned stands decrease over time (Table 3). Fire burned stands start with a higher C:N ratio and maintain a higher ratio throughout the chronology. There is no significant difference between fire burned stands and managed stands (Table 4).

3.2.3 Percent Cover

The percent cover of both managed stands and fire burned stands increase over time and were positively correlated (Table 3). This follows the trend of the unweighted percent cover as the total cover of *V. myrtillus* drastically increased over time in managed stands (Figure 5). There is no significant difference between the fire and managed chronosequences (Table 4).

3.3 Diversity

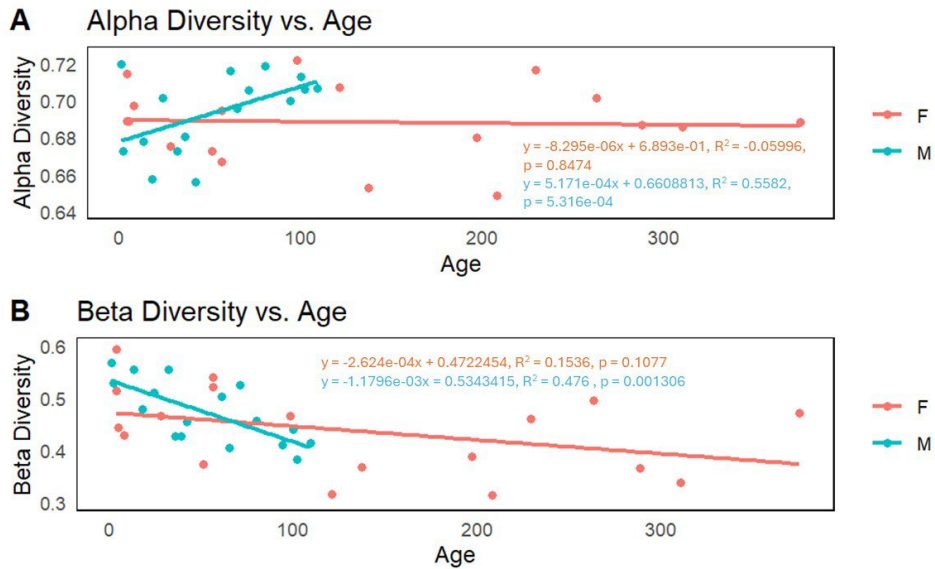


Figure 7. Alpha Diversity (Simpson's Index) and Beta Diversity (Bray-Curtis Dissimilarity) over time. Fire burned stands are shown in red and managed stands are shown in blue. The equations are color coded to their respective management style.

Table 5. Slope, correlation, and significance of diversity. * indicates a significant p value (p-value < 0.05).

| Diversity Value and Management Style | Slope Equation | R ² adjusted | p-value |
|--------------------------------------|-------------------------------|-------------------------|------------|
| Alpha Diversity Fire | $y = -8.295e-06x + 6.893e-01$ | -0.05996 | 0.8474 |
| Alpha Diversity Managed | $y = 0.0005171x + 0.6608813$ | 0.5582 | 0.0005316* |
| Beta Diversity Fire | $y = -0.0002624x + 0.4722454$ | 0.1536 | 0.1077 |
| Beta Diversity Managed | $y = -0.0011796x + 0.5343415$ | 0.476 | 0.001306* |

In total, we found 58 plant species over the 36 plots. The results show that alpha diversity trended towards less biodiversity in managed stands but trended slightly towards an increase in biodiversity in managed stands (Figure 7; Table 5). We can see that within the chronology of the managed stands, beta diversity values become less biodiverse than the fire burned stands. For alpha diversity, the two chronosequences intersected 65 years of age. For beta diversity, the value intersected around 68 years of age. Both diversity indices showed a significant change through time in the managed stands, but not in the fire chronosequence (Table 5). There is not a significant difference between the two (Table 6).

*Table 6. Results of t-test of diversity (Alpha Diversity and Beta Diversity). * indicates a significant p value (p-value < 0.05).*

| Compared Value | Analysis Method | Degrees of Freedom | Test statistic value | p-value |
|-----------------|-------------------|--------------------|----------------------|---------|
| Alpha Diversity | Two sample t-test | 29.496 | 0.27682 | 0.7838 |
| Beta Diversity | Two sample t-test | 33.949 | -1.8276 | 0.07641 |

4. Discussion

I investigated how rotational forestry differed from stands that have a known fire history over 300 years. A large chronosequence in conjunction with nutrient and plant cover data allowed me to examine the difference that can arise when rotational forestry is implemented. Therefore, several insights can be gained from these comparisons of unmanaged stands with a known fire history and managed stands.

4.1 Nitrogen

We found that available nitrogen pools in both types of stands decreased over time. Based on previous research, it was expected that the available nitrogen pools would decrease over time due to ecosystem retrogression and soil degradation (Reich 2014; Dlamini 2014; Wardle et al. 2007). There were significantly higher concentrations of nitrogen in managed stands in the beginning of the chronosequence. Between the two disturbance styles, managed stands tended to have higher available nitrogen pools throughout their chronosequence versus the wildfire chronosequence. The introduction of synthetic fertilizers is a possible factor that leads to the higher nitrogen values in managed stands. Extensive use of fertilizers in forestry persisted in Sweden until the 90's and is still used today (Lindkvist et al. 2011). Fertilizers can have a variety of compounds, but a common synthetic fertilizer is ammonium nitrate (NH_4NO_3) (Sabry 2015). Fertilization effects are not isolated to the current rotation either. It has been seen that nitrogen from fertilization of a rotational stand can carry over to the next generation (From et al. 2015). Increased nitrogen deposition at the start of a stand's history as well as a history of fertilization can contribute to higher overall nitrogen levels. If ammonium nitrate was used to fertilize the stands, this would also explain the discrepancy between the NO_3^- levels between the two chronosequences. The biggest difference between the two systems was the NO_3^- . In managed stands, NO_3^- depleted at a much faster rate versus the fire burned stands that saw an increase in NO_3^- . A loss of Mycorrhizal fungi after clear-cutting could also affect this. It has

been seen that mycorrhizal networks can reduce the amount of both nitrate and ammonium that is leached from soils (Asghari & Cavagnaro 2012). Soil scarification and trenching can disturb the underground mycorrhizal networks, which can lead to less effective mycorrhiza. The increase of NO_3^- depletion could be due to higher rates of soil leaching. With a lack of overstory and decreasing amounts of below ground biomass, water is able to reach the soil more easily. This can facilitate faster leaching versus a forest with an intact overstory and abundant, living below ground biomass (Riley et al. 2001).

Another factor that could have an effect on the nitrogen in the fire stands is the intensity of the fires. While lower, less intense fires can deposit ash and mineralize soil to deposit nitrogen into the soil, more intense fires can reduce the amount of available nitrogen (Knicker 2007). Our stands did not consider the fire severity, which can cause the range of nitrogen deposition at the beginning of its known history to be quite variable.

Nitrogen turnover through litter can also affect nitrogen levels over time. Litter deposition from plants is essential to nitrogen and carbon turnover in forests (Berglund et al. 2013). Due to the lack of trees in the youngest managed stands, litterfall is not a likely contributor to the soil nitrogen levels. However, slash material from a logging event can serve as a source of mineralizable N. In most of our fire burned stands, there was an overstory that could provide consistent litter fall, making nitrogen turnover more stable source than the managed stands.

4.2 Plant Traits

In terms of the direction of trends within the chronosequences, every plant trait trended the same way between managed and fire burned stands. SLA was the only trait that was nearly significantly different. The difference between the two chronosequences lie in the rates that the traits changed. In all cases, stands with a known fire history had less drastic changes in traits throughout the chronosequence than managed stands. The results are what we expected as it shows that for community weighted traits, growth rates looked to increase as age increases (De Toma et al. 2021). A possible explanation of this trend is the increase of the ratio of *V. myrtillus* in our stands compared to the other two dwarf shrubs. We would suspect that *E. nigrum* has a higher ratio of cover the older a stand becomes compared to *V. myrtillus* and *V. vitis-idaea*, which is supported in our fire disturbed stands (Wardle et al. 1997). The managed stands are seen to have the opposite composition as total percentages of *E. nigrum* fall over time. Light limitations could be a possible cause for this as *E. nigrum* is light demanding (Chu et al. 2011). This

would coincide with what looks like a faster growth strategy due to the rising SLA and the lowering LDMC in the managed stands. Instead of a faster growth strategy being implemented by all the shrubs, it seems that the increasing amount of *V. myrtillus*, a plant with much bigger and thinner leaves than both *V. vitis-idaea* and *E. nigrum*, caused the values to look like they were adopting a faster growth strategy (Figure 6). Available nitrogen could also be a cause as to why *V. myrtillus* increased in the managed stands. Fertilization has been seen to increase *V. myrtillus* biomass to a greater extent than *V. vitis-idaea* and *E. nigrum* (Parsons et al. 1994).

The low starting total cover of *V. myrtillus* and the rapid decrease in *E. nigrum* in the managed stands can be due to clear-cutting and the open canopy (Tonteri et al. 2016). *E. nigrum* is a light demanding plant that can outcompete the more shade tolerant *V. myrtillus* (Chu et al. 2011; Bell & Tallis 1973). As tree cover increases, more shade tolerant plants can outcompete light demanding plants. With a more homogenous canopy, managed stands do not have the gaps needed to support *E. nigrum* as well as a fire burned stand with significant canopy gaps. As the evergreens sacrifice better photosynthetic capabilities for a longer growth season, deciduous plants such as *V. myrtillus* have a shorter growth season but have higher photosynthetic capabilities (Karlsson 1989).

SLA and LDMC had unexpected results in the stands as we would expect the decreasing nitrogen levels in the soil to cause plants to go towards a more conservative growth strategy (Garnier et al. 2001). Again, I believe we can attribute this to the increase the ratio of *V. myrtillus* to *E. nigrum* over time. If we look at the equations for SLA and LDMC, we can see that higher values will be given to plants with thinner, larger leaves. The amount of light the understory received could have affected these values as well. As the evergreens sacrifice better photosynthetic capabilities for a longer growth season, deciduous plants such as *V. myrtillus* have a shorter growth season but have higher photosynthetic capabilities (Karlsson 1989). This can be reflected in the bigger leaves of *V. myrtillus* that can capture much more sunlight than *E. nigrum*. This adaptation can allow the *V. myrtillus* to thrive later in the chronosequence as light is more diffuse due to canopy cover.

Carbon and nitrogen ratios were also unexpected as the results show a trend towards higher nitrogen levels over time. This could be due to the higher available inorganic nitrogen in the soil, which means the plants are not limited by nitrogen and therefore do not need to utilize organic nitrogen. This in turn would cause plants to continue up taking nitrogen, driving the C:N ratio down. Again, the unexpected ratio of *V. myrtillus* to *V. vitis-idaea* and *E. nigrum* caused the community weighted traits to look like the plants were adopting a faster growth strategy.

The total percent cover for managed stands is unexpected, but understandable as the community weighted values were heavily influenced by *V. myrtillus*. Both *V. myrtillus* and *V. vitis-idaea* tend to grow upwards, while *E. nigrum* tends to sprawl across the ground (Ritchie 1956; Bell & Tallis 1973). These growth strategies can cause plants to have higher total cover as they are able to utilize more vertical space and still be able to spread horizontally. When using point-intercept, we measure the three-dimensional space. The inclusion of the height dimension allows plants that have better upward growth strategies to be more likely to be hit multiple times in a single point. The size of the leaves and stems of the plant can also contribute to how much total cover a plant can have. Smaller leaves that can be appressed to the stem have less of a chance to be hit than large leaves that lay perpendicular to the stem.

4.3 Diversity

While the stands with a known fire history had lower biodiversity values than the managed stands in the start of the chronosequence, we can see that over time the stands with a known fire history stay relatively stable throughout their chronology, with alpha diversity having more diversity over time. The higher alpha diversity in these stands is critical for maintaining resilience (Kuuluvainen & Gauthier 2018). In terms of beta diversity, we see that stands become more homogenous over time, but managed stands become less diverse at a much faster rate than the fire burned stands. The compounding differences of available inorganic nitrogen, light levels, and other factors between fires and clear-cuts are possible reasons as to the differences. While the fire burned stands had no significance in their slopes, managed stands had high significance in their chronosequence. This trend is consistent with the SGH and the decreasing nutrients as the forest ages.

The low p-value of the fire burned stands can be due to differences in fire severity, while the high significance in the managed stands can be due to more consistent starts to their history. As stated earlier, differences in fire severity can affect the nitrogen levels, hydrophobicity, and other important factors that can affect biodiversity (Murphy et al. 2006, Knicker 2007; Neary et al. 1999). With such a wide spectrum of affected factors related to fire intensity, it is understandable how drastically different biodiversity levels can be within fire burned stands. The higher starting biodiversity within managed stands can be explained with the drastic opening of the canopy and possible fertilization prior to harvest.

A factor that could have prevented alpha and beta biodiversity from increasing in managed stands is the prevalence of *E. nigrum* in managed stands. *E. nigrum* has a phenolic compound within its leaves that can prevent the growth of other plants called batasin-III (Nilsson & Wardle 2005; Lorion & Small 2021). Allelopathic compounds in conjunction with strong sunlight tolerance could allow *E. nigrum* to release more of the allelopathic compounds into the soil of open canopy managed stands. Even though we see that the percent cover of *E. nigrum* decreases over time (Figure 4), this does not take into account the amount of allelopathic compounds left in the soil. Having a higher starting ratio of these compounds could impact the succession and cause certain plants to be excluded from later successive phases.

Our data showed that the dissimilarity of the chronosequences decreases over time. This essentially means that the stands become more homogenous over time. This also coincides with the SGH, as we see the increase nitrogen levels in the managed stands lead to lower biodiversity levels over time. While alpha diversity measures the overall species count in the stand, beta diversity measures the number of species that are not shared between stands. We can see that both managed and fire burned stands become more homogenous, but managed stands lose their beta diversity at a much faster rate than the fire burned stands. One factor that could attribute to how homogenous managed stands become is the differences of microclimatic conditions between managed and fire burned stands. With unmanaged, fire burned stands, there are variable gaps in the canopy, large pieces of deadwood on the ground, depressions and hills, and a variety of other factors that cause a variable landscape. The varied buffering capacity of the overstory throughout the forest's history can also create a variety of microclimates (Zellweger et al. 2020). Within a managed stand, variability in the stand is substantially less as forest plots are treated to create a consistent quality of wood. With a standard of wood quality in place, the plot needs to be consistent throughout to ensure the trees have similar wood quality. This lack of variability within the stands can cause the same niches to appear throughout managed stands, causing beta diversity to be lower. Vice versa, the higher variability of unmanaged stands can allow a higher variety of plants that can live in these niches. It has been seen that differences in microclimates between plots can lead to lower beta diversity (Sebastia et al. 2005).

5. Conclusion

Based on the results of this thesis, clear cut management of stands lead to lower biodiversity values and an altered ratio of the ericaceous shrubs in the understory over time. In this study I highlighted the differences between clear-cut forestry and fire disturbances on understory vegetation and available nutrients over time in the boreal forest. The results suggest that clear-cuts start with higher nutrient and biodiversity values, but regress at a faster rate than the fire disturbed stands. This coincides with the SGH and explains as to why fire burned stands eventually had better biodiversity values over the chronology. The composition of the understory was also affected as *V. myrtillus* began to dominate managed stands as they aged versus the expected rise of *E. nigrum* in the later years as seen in the fire disturbed stands. This altered composition of the understory led to community weighted plant traits to stray from what would be considered normal. Further investigation into the plant traits of more than the three dominant shrubs and more abiotic factors would be needed to better understand as to why the composition of the understory was so heavily affected.

Overall, the results of this study provide much needed research on how understory vegetation is affected by forestry. This study aids in the understanding of clear-cut forestry and its implications on nutrient availability and biodiversity on the understory vegetation. Such knowledge can aid in creating more sustainable forestry options in the face of current climatic challenges and biodiversity loss. More sustainable forestry can help the boreal forest have stronger resilience to the increase stressors climate change and deforestation present.

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Popular science summary

Climate change and loss of biodiversity is affecting the resilience of ecosystems around the world. With increased stress on ecosystems and less resilience, the services these ecosystems provide could be greatly affected and in turn affected humankind. Deforestation is a great concern regarding biodiversity, and the Swedish model of clear-cut forestry is being questioned as to whether it is a sustainable practice in the boreal forest. Clear-cuts aim to mimic the way fires disturb the forest, but there is conflicting evidence whether it does. While the trees are well studied, the nitrogen levels, understory vegetation, and its reaction to clear-cutting is less understood. Since the long-term effects of forestry on the understory is not well studied, this study investigates the effects of management on understory vegetation over time. The study sites were found in northern Sweden, where there is a large presence of clear-cut forestry. It was found that plots that were clear-cut had higher levels of nitrogen and loss biodiversity faster over time. The composition of the understory vegetation was unexpected as *Vaccinium myrtillus* increased at a much faster rate than expected. Stands that were fire burned had less nitrogen and retained their biodiversity better. The results of this study show that clear-cut forestry can lead to high nitrogen, lower biodiversity levels, and a different understory composition over time.

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