How Swedish Forest Management Impacts Beetle Diversity

Comparing forest beetle diversity across full rotation cycles of managed and unmanaged post-fire chronosequences

Sydney Nute

Degree Project 15 credits
Swedish University of Agricultural Sciences, SLU
Faculty of Forest Science / Department of Forest Ecology and Management
Forest & Landscape / Biology
Examensarbete / SLU, Institutionen för vilt, fisk och miljö
2025:7
Umeå

How Swedish forest management impacts beetle diversity. Comparing forest beetle diversity across full rotation cycles of managed and unmanaged post-fire chronosequences.

Hur det svenska skogsbruket påverkar mångfald av skalbaggar. Jämförelse av skogsskalbaggsmångfald över hela omloppstid genom analys av kronosekvenser av brukade och brand-förnyade skogar.

Sydney Nute

Supervisor:	**Vincent Buness, SLU, Department of Forest Ecology and Management**
Assistant supervisor:	Anne-Maarit Hekkala, SLU, Department of Wildlife, Fish, and Environmental Studies
Examiner:	Therese Löfroth, SLU, Department of Wildlife, Fish, and Environmental Studies

Credits:	15
Level:	First cycle, G2E
Course title:	Independent project in Biology, G2E
Course code:	EX0997
Programme/education:	Forest & Landscape
Course coordinating dept:	Department of Wildlife, Fish, and Environmental Studies
Place of publication:	Umeå
Year of publication:	2025
Title of series:	Examensarbete / SLU, Institutionen för vilt, fisk och miljö
Part number:	2025:7

Keywords:	Beetle diversity, Swedish forest management, Conservation, Red-listed species, Chronosequence, Nature reserves

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Forest Ecology and Management

Abstract

Forestry is an important industry in Sweden, but threatens ecological values within forest ecosystems. Due to the variety of species and their respective sensitivities to environmental factors, beetles can be used to illustrate differences between managed and natural forests. Beetles were collected from rotationally managed and unmanaged fire-regenerated forests on a scale of time since disturbance, and subsequently identified. Beetle abundance, species richness, and red-listed species richness were all higher on the unmanaged fire chronosequence. Basal area and deadwood diversity were drivers of species richness. Based on these results, smaller scale considerations to nature could improve conditions within the stands throughout the rotation, namely an increase in deadwood abundance and diversity. In addition, Swedish forest management needs to shift from the current methods of clearcutting and even-aged management to continuous cover methods of harvest that better mimic natural disturbance regimes. In general, more forest needs to be protected, across age classes, and the managed landscape should be planned with respect to biodiversity.

Keywords: Beetle diversity, Swedish forest management, Conservation, Red-listed species, Chronosequence, Nature reserves

Table of contents

List of Tables

List of Figures

Abbreviations

Abbreviation	**Description**
GAM	Generalized Additive Model
LAI	Leaf Area Index
NMDS	Non-Metric Dimensional Scaling
PCT	Pre-Commercial Thinning
SLU	Swedish University of Agricultural Sciences

1. Introduction

1.1 Importance of forestry in Sweden

The Swedish landscape is dominated by forest, comprising approximately two thirds of the nation's land area (Roberge *et al*., 2020). Of these 28 million hectares, 23.6 million hectares are 'productive forest,' meaning forest that is able to produce more than one cubic meter of wood per hectare per year and is therefore legally allowed to be managed for the production of timber products (Roberge *et al*., 2020). Forestry accounts for 9 – 12 % of the Swedish economy (Roberge *et al*., 2020), and provides valuable, renewable resources. In light of climate change, forest products provide eco-friendly alternatives to fossil fuels for many uses, for example in the manufacturing of consumer goods and fuel for bioenergy. In addition, forest growth sequesters carbon.

1.2 Swedish rotational forestry

Sweden has one of the world's most intensive forest management systems (Kyaschenko *et al.,* 2022). The dominant method of Swedish forest management is rotational forestry, where the majority of stands are even-aged monocultures (Roberge *et al*., 2020). Historically, forests were renewed by natural disturbances such as fire, windthrow, or insect outbreaks. However, these natural factors, specifically fire, have been repressed and replaced by clearcutting (Östlund *et al.*, 1997; Hekkala *et al*., 2014). The soil is mechanically scarified before seedlings are planted, the method through which 84% of new stands are regenerated (Roberge *et al*., 2020). Planted stands often consist of a high density of a single tree species, although naturally regenerated vegetation can contribute additional species diversity. Approx. 10 to 15 years after establishment, the dense stand is thinned (called pre-commercial thinning or PCT) to improve growth of the crop trees. This may be done twice (Skogskunskap, 2024).

Commercial thinning (furthermore called thinning), where removed trees can earn revenue, is done when the stand has reached certain heights, at approx. 30 years, to ensure that the remaining crop trees grow to have the highest possible value (StoraEnso, n.d.). This is done one to three times before final harvest. The dominant harvest method is clearcutting, when almost all of the trees are removed from the stand. The rotation length, the amount of time between each felling, ranges from 65 years as the legal minimum in northern Sweden to 140 years, when forests are considered old-growth (Skogskunskap, 2024), although there is no upper limit on how old of a forest can be harvested.

1.3 Environmental considerations in Swedish forestry

Nature considerations in forests vary at the discretion of the forest owner, and have increased in the last 30 years (Kyaschenko *et al.,* 2022). The 1993 Swedish Forest Act puts environmental considerations and timber production as equal in importance (Nylund, 2010), but gives forest owners ‘freedom under responsibility’ (Roberge *et al*., 2020). This means that certain actions are required by law, but the majority of decisions are at the discretion of the land owner (Roberge *et al*., 2020). These laws extend the length of the rotation, for example reforestation requirements and minimum harvest ages (Skogsstyrelsen, 2023). Forest owners can also choose to become certified, whether through PEFC or FSC (Roberge *et al*., 2020). Certifications have strong market incentives and provide guidelines that actors must follow in order to stay certified, for example at final harvest the retention of high stumps, buffer zones, and at least 10 trees per hectare (PEFC, 2024). Additional stronger considerations to nature, including continuous cover forestry, are less common despite the scientific knowledge of the ecological benefits (Sténs *et al*., 2019; Hertog *et al*., 2022).

1.4 Importance of protecting Swedish forests

Swedish forests provide more than just timber products to society. These are known as ecosystem services and support human life, whether provisioning like clean water, wild game, and berries, or regulating such as air purification. Other ecosystem services are supporting, as in pollination and photosynthesis, or cultural, such as recreation and aesthetics. However, there are often tradeoffs between these and the production of timber products, as forests dominated by rotational management often do not have the same range of ecosystem services as a natural forest, especially when compared with old growth (Jonsson *et al*., 2020). The importance of protecting biodiversity lies in these ecosystem services, that biodiversity is necessary for these systems to function as they should (Cardinale *et al*., 2012). Of the ‘productive’ Swedish forests, 11% are protected from management (Roberge *et al*., 2020).

1.5 Swedish beetle diversity

Swedish forests are home to a vast diversity of species, of plant, lichens, fungi, bryophytes, and animals, including almost 5,000 species of beetles (SLU Artdatabanken, 2025d). Beetles, order Coleoptera, vary greatly between species to form many different guilds based on life strategies and feeding behavior. They feed on a variety of substrates, examples being wood, leaves, seeds, scat, and fungi, even other beetles (Crowson, 1981). There is as much variety in the substrates in which female beetles will lay their eggs (Crowson, 1981). These eggs later hatch and become larvae, which can have different food needs than adult beetles of the same species (Crowson, 1981). Beetle habitat also varies, even within forests, examples being in deadwood or on the ground (Crowson, 1981).

In summary, depending on the species and life stage, beetles can be dependent on fire and deadwood, and are impacted by light levels, tree species richness, forest structure, and time since disturbance, among other factors (Crowson, 1981; Hekkala *et al*., 2014; Hägglund *et al.,* 2020; Heikkala *et al*., 2016; Djupström *et al*., 2008). Because of these sensitivities, beetles can be used as an indicator of biodiversity (Hekkala *et al*., 2014). They have adapted to fill many roles in forest ecosystems, and community analysis can be used to illustrate changes in forest conditions (Martikainen *et al*., 2000). Forestry is the main reason that species in general end up on the red list in Scandinavia, and of all groups, beetles are the most numerous on the list (Hekkala *et al*., 2014).

1.6 Habitat requirements

Forest management impacts the forest in more ways than just harvest. The habitat qualities of rotationally managed and natural forests differ for the entire rotation length. In contrast to managed stands, natural forests typically have multiple layers of vegetation, a variety of tree species of varying ages, an abundance of deadwood of different species, sizes, and decay classes, higher light levels, and more gaps (Hägglund *et al.,* 2020). These are the types of differences that are reflected through changes in community composition (Martikainen *et al*., 2000).

Disturbance, especially fire, can have large impacts on beetle communities. Many beetle species have adapted to fire being present in the landscape, and are attracted to the smell of smoke, as it indicates sunny environments and a large, unclaimed amount of habitat in the fresh deadwood (Heikkala *et al*., 2016; Hägglund *et al.,* 2020). In addition, fire creates many structures, including snags and charred wood, that many of these species are reliant on (Hekkala *et al*., 2014). The lack of fire in the landscape as well as the decreased amount of deadwood and broadleaf tree species in Swedish forests have all been cited as reasons for why beetle species are threatened (Martikainen *et al*., 2000).

Deadwood is proven important when it comes to beetle abundance and species richness, as both habitat and a food source (Seibold *et al*., 2016). Natural disturbances, whether fire, wind throw, or pest attack, leave massive and diverse amounts of deadwood in the forest (Similä *et al*., 2002). In addition to the immediate deaths, these natural disturbances wound trees, allowing for a continuous, diverse supply of deadwood as the wounded trees die over time (Heikkala *et al*., 2016). Obviously, the vast majority of the potential substrate is removed from clear cuts, and regeneration measures (i.e. soil scarification) destroy existing deadwood (Siitonen, 2001). Old growth forests typically have 60-90 m^3 deadwood per ha (Siitonen, 2001), but managed Swedish forests often have only a tenth of this (Joelsson *et al*., 2018), as well as lower diversity of deadwood substrates (Djupström *et al.,* 2008). At minimum, a century must pass before these dynamics are able to recover (Siitonen, 2001), just in time for the forest to be harvested again.

Having monocultural conifer stands further impairs beetle diversity by reducing the amount and diversity of broadleaf species present (Martikainen *et al*., 2000). Certain beetle species are reliant on broadleaf tree species, either as food or habitat, or on the deadwood that the trees create (Seibold *et al*., 2016).

Light levels within the forest can also impact beetle diversity. Lower leaf area index (LAI), meaning higher light levels, has been shown to benefit beetle diversity (Seibold *et al*., 2016). Managed forest stands are typically darker as they are denser for higher volume production (Kyaschenko *et al.,* 2022), and beetles are more active on sunny, warm sites (Seibold *et al.,* 2016).

While fire is often on a large scale, smaller-scale natural disturbances are also important. Insects, wind, and snow can create gaps that are valuable beetle habitat (Hägglund *et al*., 2020), and are common to older, unmanaged forests. These gaps have higher light levels, are continuous sources of deadwood with high diversity, and can increase forest structural variation as new regeneration, including broadleaves, fills in (Hägglund *et al*., 2020).

Rotation forestry limits trees to only a small segment of their potential lifespan. For context, Scots pine (*Pinus sylvestris*) can live for over 700 years, often surviving multiple fire events (Hjort *et al*., 2013). Forests are generally harvested before the trees have the chance to attain large diameters (Siitonen, 2001), an important factor in deadwood diversity for red-listed species (Seibold *et al.*, 2016). These early harvest ages are before the forest has developed a stable natural deadwood supply (Joelsson *et al.,* 2018), and before certain niche deadwood structures can form. For example, old pines have the potential to remain in the forest for an additional 300 years as deadwood (Naturhistoriska Riksmuseet, 2024). Many natural processes do not fit into the limited amount of years allotted to a forestry rotation (Heikkala *et al*., 2016). In addition, red-listed species favor microhabitats that are present in natural old growth (Niemelä, 1997; Joelsson *et al*., 2018).

1.7 Purpose of this thesis

Numerous studies have examined how individual stages of boreal forest management impact beetle diversity (i.e. Heikkala *et al.,* 2016; Hekkala *et al.*, 2014; Similä, 2001; Martikainen *et al*., 2000; Djupström *et al*., 2008) and have highlighted the importance of natural disturbance regimes (Hägglund *et al*., 2020). However, no study has compared beetle diversity of all of the stages of managed forests with the full age range of fire-renewed stands. This is important to know to be able to fully understand how rotational forestry differs from nature, and what consequences these management actions can have on biodiversity.

This thesis examines the impact of rotational forestry on beetle diversity. As forests change through time in many ways, these changes, called environmental factors, will be evaluated to determine which most strongly influence the observed patterns in beetle communities and diversity. We compare two contrasting chronosequences in northern Sweden - one of typical management (1-109 years since disturbance) and one of unmanaged post-fire regeneration (4-375 years since disturbance).

The predictions are as follows:

1. The unmanaged chronosequence will generally have higher beetle abundance as well as higher total species and red-listed species richness (Similä *et al.*, 2002).
2. On the unmanaged chronosequence, species richness will be lowest in middle-aged stands. Disturbance will benefit diversity, especially red-listed species (Hägglund *et al.,* 2020; Martikainen *et al*., 2000). Old growth will also have higher diversity and more red-listed species (Niemelä, 1997; Joelsson *et al.*, 2018). The managed chronosequence will have highest species richness in the oldest stands (Hekkala *et al.*, 2014).
3. The most influential driver of beetle diversity will be deadwood, with either higher abundance or diversity of the substrate corresponding with higher beetle diversity (Djupström *et al*., 2008; Martikainen *et al.*, 2000). Higher broadleaf presence is also predicted to be a driver (Martikainen *et al*., 2000). Leaf area index will also have an influence, with higher light levels corresponding with high richness (Seibold *et al*., 2016). In middle-aged and older stands, the presence of gap dynamics will be a driver (Hägglund *et al*., 2020).

2. Methods

2.1 Study area

The data was collected in boreal forests in northern Sweden (Figure 1). The sites were chosen to fit two chronosequences, meaning a collection of stands that are as similar as possible on a scale of time since disturbance, one representing typical rotational management and the other unmanaged post-fire naturally regenerated forests. Each chronosequence was comprised of 18 one-hectare stands. Time since disturbance varied from 1 - 109 years on the rotational management chronosequence, and from 4 - 375 years on the unmanaged fire chronosequence, disturbance intervals that are representative of these types of forests (Roberge *et al*., 2020; Carcaillet *et al*., 2007). All but two of the fire stands were results of wildfire; the exceptions were prescribed burns. To have as comparable stands as possible, except for the difference in disturbance and time since disturbance, only mesic sites were chosen, as site conditions have a strong influence on vegetation and species present.

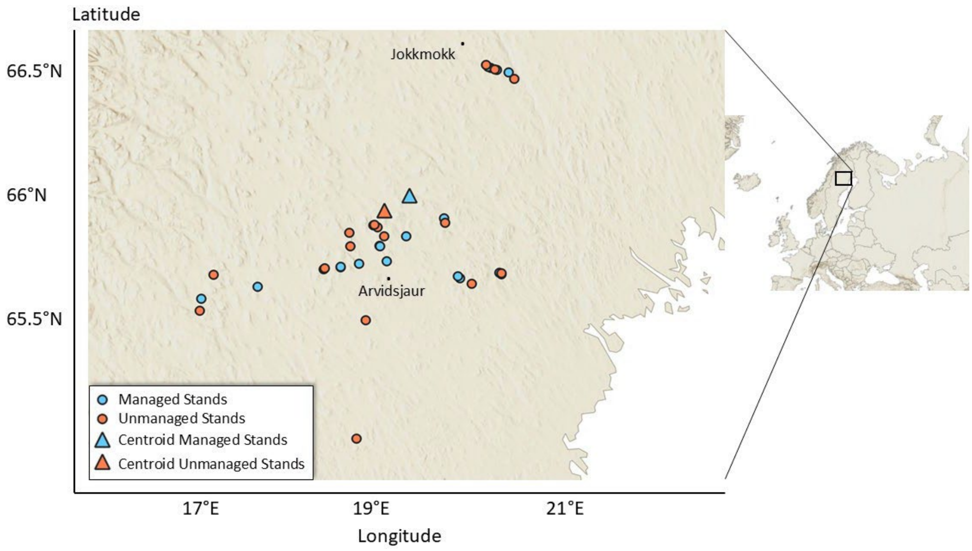


Figure 1: Map of the stands. Credit: Vincent Buness (2024), used with permission.

2.2 Beetle sampling

Beetles were collected using window traps (Figure 1), specifically IBL-2 screen traps from Codimex. Two traps were placed in each stand, one 20 meters north of the plot center and one 20 meters south. The northernmost trap was set in north – south orientation and the other in east – west orientation, in order to account for different wind directions. Exact placement was between two trees, or two stakes in the case of clearcut, aligning with a corridor through the vegetation in order to increase the success of the traps. The top of the trap was approximately two meters from the ground. Propylene glycol was used in the traps to preserve the collected specimens.

Figure 2: Photo of a beetle trap and placement on the sampling plot. Credit: Vincent Buness (2024), used with permission.

The traps were emptied twice, once in early July and once in early August, corresponding with the duration of peak beetle activity in northern Sweden, from the beginning of June until early August. Unfortunately, stand F121 was vandalized so only 35 of the stands will be used in this analysis.

Samples were taken back to the lab and were processed, sorting out beetles from debris and other insects for ease of identification. The samples were then sent to an expert for species identification, which followed the Artdatabanken nomenclature (SLU Artdatabanken, 2025d).

2.3 Environmental data

As this project is part of a larger investigation of biodiversity and the impact of management using the two chronosequences (Buness *et al.*, 2025), data was available for many environmental factors. Table 1 shows which of these were selected for use in this analysis, and Figure 2 shows the relationship between these variables and time for each chronosequence. Deadwood diversity was a Shannon index calculated using which tree species the deadwood originated from, size class (diameter), and decay stage.

Table 1: Chosen environmental variables.

Type of data	Metric
Deadwood	Total volume
	Diversity
Basal area	BA total

	Percent broadleaves
Leaf area index	LAI
Forest structure	Structure
Gap	Deep Gap Fraction

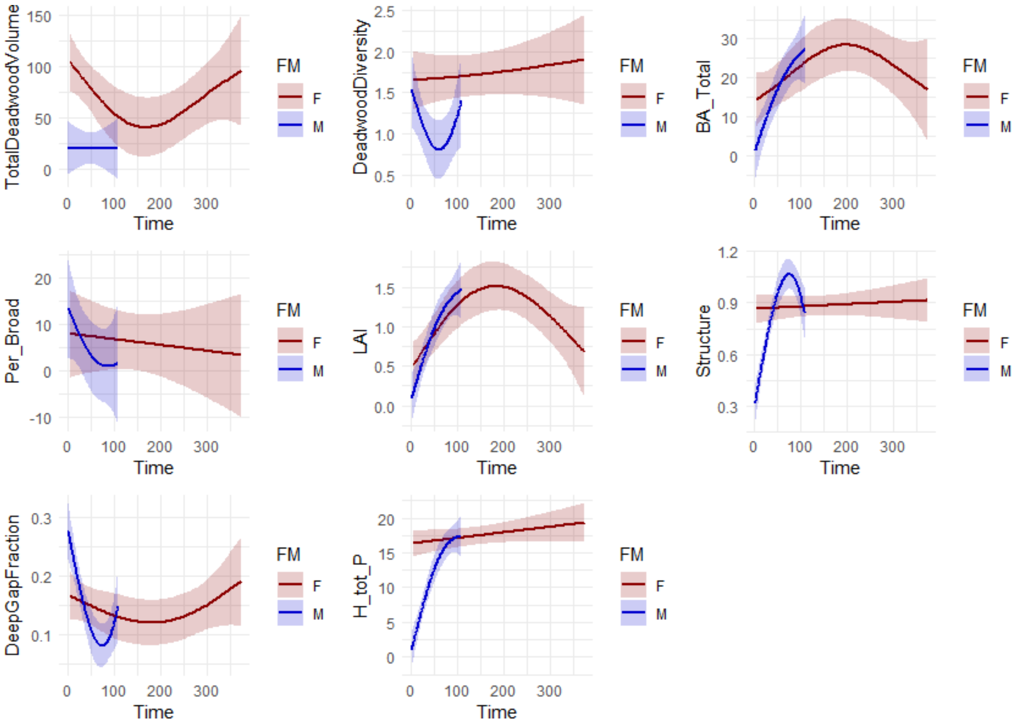


Figure 3: Relationship between environmental variables and time since disturbance for each chronosequence. Each graph shows a calculated GAM with the respective environmental variables as the explained variable and time since disturbance as the predictor, and treatment as the categorical variable (Wood, 2011). Every x axis shows time since disturbance. The y axis differs in each plot to explain the environmental factor illustrated. Color indicates treatment, with red representing the unmanaged fire chronosequence and blue the managed. Graphed using ggplot2 *in R-Studio (Wickham, 2016). Statistics in appendix Table 1.*

2.4 Data analysis

Data analysis was done in R-Studio version 4.4.2 (R Core Team, 2024). Some aid in fixing code was sourced from ChatGPT OpenAI. Species data was aggregated to stand level for the entire sampling period.

Species richness for each chronosequence was calculated by summing the number of different species found in each stand. The relationship between species richness and time since disturbance was evaluated by fitting a generalized additive model (GAM) to the data. This was done using the mgcv package (Wood, 2011). Time since disturbance was the predictor and total species richness the explained variable, using treatment as a categorical variable to have a separate smoothed (k = 5) curve for each chronosequence. Summary statistics were calculated.

The data set was filtered for red-listed species, to get the red-listed species richness for each stand. This was the number of different red-listed species found in each stand. The Swedish Red List is created by SLU based on the IUCN Red List Criteria to evaluate the extinction risk of species (SLU Artdatabanken, 2020). All species not denoted least concern were considered red-listed. The method of model creation was the same as for total species richness.

In order to visualize which stands had similar beetle assemblages, non-metric dimensional scaling (NMDS) was run using the function metaMDS from the vegan package (Oksanen *et al.*, 2025). The matrix used was the initial beetle data of identified individuals present in each stand. The result was plotted using ggplot2 (Wickham, 2016). Using the function envfit, the significant environmental drivers were added to the NMDS plot as vectors to show the relationships of these factors with the stands. The significance of the vectors, of whether these correlated with the distribution of the stands, was calculated. Management classes were added to the stand, categorizing the stands by the typical actions done in forests of comparable ages (Roberge *et al.*, 2020; Skogskunskap, 2024; StoraEnso, n.d.). The red-listed species were also plotted, based on their coordinates calculated in the NMDS, to show their relationship with the stands.

A linear model combined the calculated species richness metric as the explained variable with the environmental data in Table 1 as predictors to find which of the environmental factors could be drivers of species richness. Initially the model was run with all of the environmental variables (Table 1) and subsequently reduced based on the summary statistics to identify variables that are significant ($p < 0.05$) in the model to find the best fit and avoid overfitting. The vif function from the car package (Fox & Weisberg, 2019) was also used to test for collinearity between predictors. The plot function was used to identify influential outliers, and as one stand, M2, was outside Cook’s distance lines, it was removed to improve model quality. Two predictors remained significant in the resulting model.

A separate linear model identified drivers of red-listed species richness, using the same procedure as for drivers of total species richness.

3. Results

3.1 Beetle abundance and species richness

In total, 6,465 individuals from 372 species were identified. The unmanaged fire chronosequence had 3,888 individuals from 300 species, and the rotational management chronosequence had 2,577 individuals from 266 species.

While time since disturbance did not have a significant influence on species richness for either chronosequence, nor was the difference between the two chronosequences significant (Table 2) immediately after disturbance (t = 0), general trends can nonetheless be observed (Figure 3). Both chronosequences saw the highest species richness at the middle of the respective rotation length, and the unmanaged fire chronosequence had higher species richness overall.

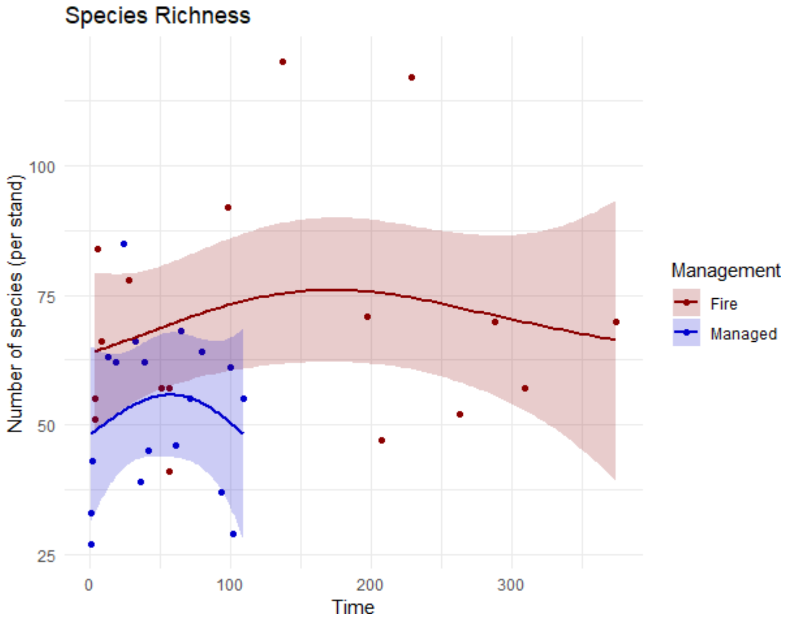


Figure 4: Relationship between species richness and time for each chronosequence. Based on the calculated GAM, time since disturbance is on the x axis and the number of species per stand on the y. Color indicates treatment, with red being the unmanaged fire chronosequence and blue the managed.

Table 2: Generalized additive model results for total species richness by chronosequence type (M: rotational management chronosequence, F: unmanaged fire chronosequence). Significant p values < 0.05.

Term type	Term	Estimate / edf	SE / Ref.df	t- / F-value	p-value
Parametric	Intercept	69.103	5.031	13.735	1.9e-14
	F vs M	-25.891	25.115	-1.031	0.311
Smooth	s(Time):F	1.679	2.076	0.668	0.553

	s(Time):M	1.441	1.693	0.137	0.892
Model summary	Adjusted r²	0.158	-	-	-
	Deviance explained (%)	26	-	-	-
	n	35	-	-	-

3.2 Red-listed species

Red-listed species were found in 28 of the stands, a total of 107 individuals from 27 species. The unmanaged fire chronosequence had 20 species, and the rotational management chronosequence had 15.

Time since disturbance was not significant with relation to the number of red-listed species, nor did the chronosequences differ significantly (Table 3). However, for the unmanaged chronosequence, a general trend was observed of more red-listed species with an increase in time since disturbance (Figure 4). The managed chronosequence had a decrease in red-listed species richness with time. The unmanaged chronosequence had higher red-listed species richness overall.

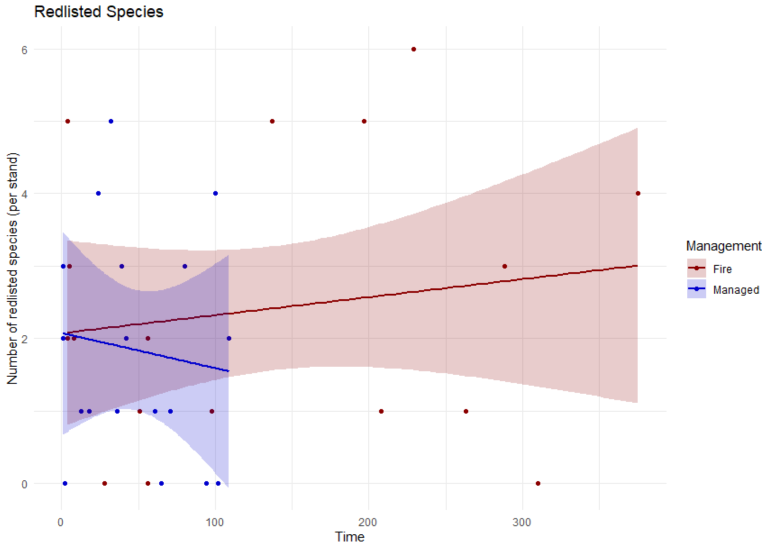


Figure 5: Relationship between red-listed species richness and time for each chronosequence. Based on the calculated GAM, time since disturbance is on the x axis and the number of red-listed species per stand on the y. Color indicates treatment, with red being the unmanaged fire chronosequence and blue the managed.

Table 3: Generalized additive model results for red-listed species richness by chronosequence type (M: rotational management chronosequence, F: unmanaged fire chronosequence). Significant p values < 0.05.

Term type	Term	Estimate / edf	SE / Ref.df	t- / F-value	p-value
Parametric	Intercept	2.3007	0.4660	4.937	2.57e-5
	F vs M	-0.6724	0.8040	-0.836	0.409

Smooth	s(Time):F	1	1	0.468	0.499
	s(Time):M	1	1	0.169	0.684
Model summary	Adjusted r^2	-0.0449	-	-	-
	Deviance explained (%)	4.73	-	-	-
	n	35	-	-	-

3.3 NMDS

The relationship of the stands with each other based on beetle assemblages was plotted via NMDS (Figure 5). The stress value was 0.224. The fact that the stands had two different treatments was not clearly reflected in the clustering of the data. Instead, time since disturbance was a significant influence on the distribution of the stands (Table 4). All vectors of beetle metrics were statistically significant and correlated, meaning that the stands with high species richness, red-listed species richness, and total abundance had similar beetle assemblages. This can be observed with the size of the points as well, that stands with high total species richness seem to cluster, namely F98, F137, and F229.

Of the environmental factors, total basal area, LAI, structure, and the deep gap fraction were significant (Table 4). Deadwood vectors correspond with the vectors of beetle metrics, although not significantly (Figure 5). Vectors for total basal area, total height, and LAI were associated with time. Higher gap fractions and broadleaf percentages corresponded with species assemblages of younger managed stands. Stands with multiple layers had similar species assemblages to old fire stands.

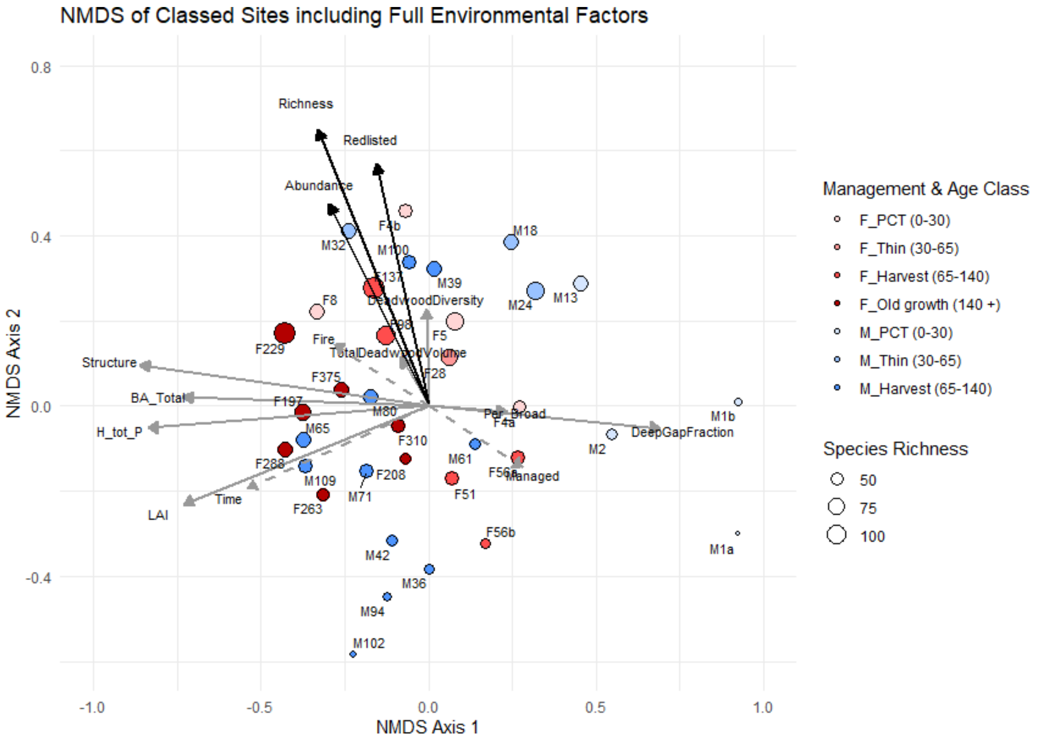


Figure 6: NMDS of beetle assemblages in each stand with environmental vectors. NMDS was run to illustrate which stands were similar based on which beetles (both amount and species) were present. Stands from the unmanaged fire chronosequence are in red and the managed chronosequence in blue, and labelled with stand names. The opacity of the points indicates time since disturbance, classifying the stands based on typical management actions possible at each stage. The size of the points shows total species richness in the stand. The arrows provide insight into which ways the different factors correlate with the position of the stands. Black arrows represent beetle metrics. Gray solid arrows represent environmental factors. Gray dashed arrows are chronosequence types. The length of the arrows correspond to the rr^2 values (Table 4), and therefore how correlated that vector is with the distribution of the stands. The statistical significance of the arrows is shown in Table 4 with p values.

Table 4: Vector statistics (envfit). Significant p values (< 0.05) mean that the variable is correlated with the distribution of the stands based on species assemblages.

Variable	rr^2	p-value
Richness	0.5319	0.001
Redlisted	0.3490	0.001
Abundance	0.3135	0.004
Time	0.3326	0.004
Fire	0.1012	0.197
Managed	0.1012	0.197
DeadwoodDiversity	0.0521	0.456
BA_Total	0.5409	0.001
TotalDeadwoodVolume	0.0202	0.721
Per_Broad	0.0563	0.416

LAI	0.5906	0.001
Structure	0.7552	0.001
DeepGapFraction	0.4831	0.001

3.4 Environmental drivers

3.4.1 Possible drivers of total species richness

The environmental factors that were identified as most influential were deadwood diversity and total basal area (Figure 6, Table 5). Higher basal area (p = 0.0013) and more diverse deadwood (p = 0.0311) both correlated with higher species richness. The model explained 30 % of variance.

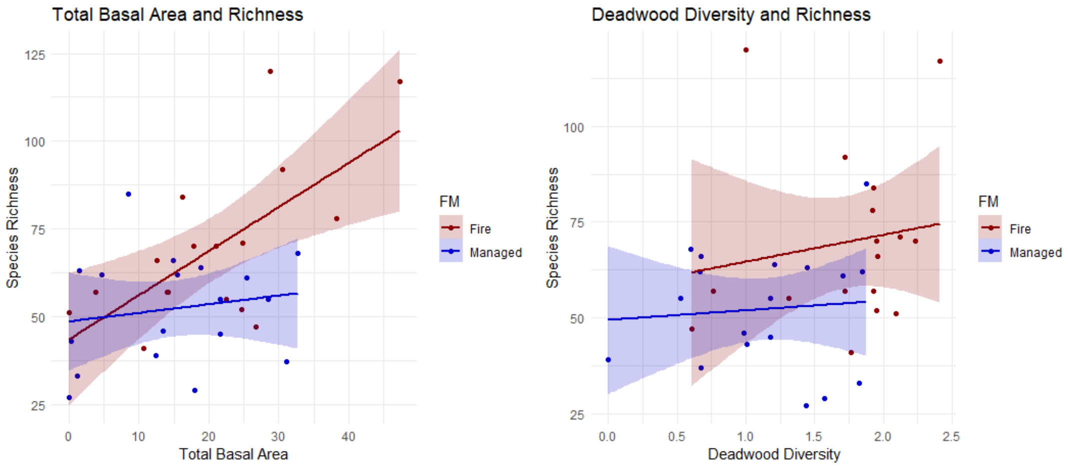


Figure 7: Environmental drivers of species richness. Based on the linear model, these are total basal area and deadwood diversity. The x axis in each graph shows the driver, and the y axis shows total species richness. Color indicates chronosequence type, with red being the unmanaged fire chronosequence and blue the managed.

Table 5: Linear model results for the environmental drivers of total species richness. Significant p values < 0.05.

Predictor	Estimate	SE	t-value	p-value	Adjusted r^2
(Intercept)	26.9740	9.6018	2.809	0.0085	-
Deadwood diversity	11.5247	5.1035	2.258	0.0311	-
Total basal area	0.9665	0.2732	3.538	0.0013	-
(Model summary)	-	-	-	0.0013	0.3084

3.4.2 Possible drivers of red-listed species richness

There were no statistically significant linear model results that showed a correlation between any environmental factors and red-listed species richness (Table 6).

Table 6: Linear model results for the environmental drivers of red-listed species richness. Significant p values < 0.05.

Predictor	Estimate	SE	t-value	p-value	Adjusted r^2
(Intercept)	1.1254	0.8072	1.394	0.173	-
Deadwood diversity	0.7315	0.5682	1.287	0.208	-
Percent broadleaves	0.0056	0.0534	0.105	0.917	
(Model summary)	-	-	-	0.3634	0.0029

4. Discussion

4.1 Management negatively impacts beetle diversity

The results show that rotational management has an impact on beetle communities in Northern Swedish boreal pine forests. Abundance, total, and red-listed species richness were all found to be higher on the unmanaged fire chronosequence, which confirms the first prediction. These findings are in accordance with Similä *et al.* (2002), who also found higher abundance and species richness in seminatural forests of varying ages when compared to managed forests. This can be attributed to the differences between the two forest types, as observed in Figure 2. The trends in species richness are mirrored in both treatments, but match the length of the respective chronosequence. The higher natural values in the unmanaged chronosequence, as illustrated by the environmental factors in Figure 2, are enabling those stands to accumulate higher species richness and to maintain it longer. The negative impact of management on diversity is especially clear with the trends in red-listed species richness over time (Figure 4). While unmanaged stands increased in red-listed species richness over time, managed stands decreased, highlighting that older managed stands have decreased habitat quality when compared with natural forests.

The trend of highest total species richness observed in middle-aged stands for both chronosequences (Figure 3) is however contrary to expectations. Rather, as in the second prediction, Hägglund *et al.* (2020) saw high species richness the first 10 years after fire or even clearcut due to fresh substrates that subsequently declined to pre-disturbance levels. It was also expected that the older forests would have higher diversity. This differing result, of highest species richness in middle-aged stands, is likely showing that there is some other driver of beetle diversity that is more significant than time since disturbance.

NMDS results did not show a clear difference between the two chronosequences (Figure 5). This means that while the unmanaged fire chronosequence had higher beetle abundance and species richness, the overall community assemblages were relatively similar between the two treatments. Time since disturbance had a bigger impact on which species were present in the stands. Using the assemblages to identify potential drivers, stands with high beetle diversity have similar assemblages to stands with high deadwood abundance and diversity.

4.2 Drivers of beetle diversity

Deadwood is important for beetle diversity

As predicted, deadwood had a significant impact on total species richness (Figure 6). While diversity was modelled as most significant, it is likely that deadwood diversity and abundance covaried. The importance of deadwood diversity for beetle diversity is likely due to the variety of niches that comes with higher deadwood diversity allowing for a larger variety of species in a stand (Djupström *et al.*, 2008; Seibold *et al.,* 2016). The result of higher species richness following more diverse deadwood in the unmanaged forests (Figures 2 & 3) was also observed in Djupström *et al.* (2008). Broadleaf presence was not a driver as predicted, but could have covaried with deadwood diversity, possibly showing that the main impact that broadleaves have on forest beetle diversity is their contribution to deadwood diversity.

The linear model result of higher species richness following higher deadwood diversity matches the result of Martikainen *et al.* (2000), where having more diverse deadwood increased species richness. In addition, the trends in deadwood diversity (Figure 3) are typical of a managed forest, with middle-aged stands having the smallest amount of deadwood diversity (Heikkala *et al.*, 2016). It is proven that diverse deadwood is important for beetle diversity and the low amounts seen in middle-aged stands are therefore not likely supportive of high species richness (Seibold *et al.,* 2016). Therefore, it is possible that another factor not included in the model, could have caused the peak in total richness at the middle-aged stands. This unmeasured factor could be productivity, as Hämäläinen *et al.* (2024) found that more productive stands had higher biodiversity.

If existing scientific knowledge about the relationship between deadwood and beetle diversity was to be applied to management recommendations, calling for more deadwood in the forest can facilitate higher deadwood diversity and thereby beetle diversity. Having more diverse habitat creates more niches for a variety of species, and more habitat facilitates larger population sizes (Seibold *et al.,* 2016; Siitonen, 2001).

Basal area impacts beetle diversity

Basal area was also a significant environmental driver of total species richness (Figure 7), which was not predicted. Mirroring the trend of species richness (Figure 4), basal area was highest in the middle of the time range for the unmanaged stands, and highest just before harvest in the managed stands (Figure 3). Basal area, a metric representing the volume of wood present in a stand, is not generally considered to be connected to beetle diversity. If it was, the expectation would be that a low basal area, and therefore lower LAI, which was predicted, causing a brighter forest would in turn have higher diversity (Seibold *et al.,* 2016).

Joelsson *et al.* (2018) also identified basal area as a significant factor, and found that the result was driven by the differences between older forests and clear cuts, due to the lack of tree cover. They found that the beetle assemblages were significantly different on clear cuts when compared to older forests. Basal area also corresponded with the directional clustering of the oldest stands in Figure 6, meaning that the species that correspond with high basal area stands are present in these old stands, rather than clearcut sites, so this likely coincides with the results of Joelsson *et al.* (2018). This shows that while many qualities of the forest have the potential to influence beetle diversity, these factors are negligible if forest is not actually present.

4.3 Rotational forestry's divergence from natural forests

Rotational forestry does not replicate natural disturbances

While rotational forest management has been argued to replicate natural disturbances, often citing the increase in light levels and the subsequent opportunities for regeneration (Hägglund *et al.*, 2020), the differences between the chronosequences from time = 0 shows that this is not the case. This was also seen in boreal Canada, where species assemblages differed significantly following harvest compared with post-fire, differences that persisted for 30 years post-disturbance (Hammond *et al.,* 2017). One clear explanation of this difference is the lack of deadwood following harvest. In order to keep this valuable substrate when harvesting, managers should work to leave more deadwood on clearcuts, whether as slash (Ranius *et al.*, 2014) or existing deadwood to preserve decay classes (Siitonen, 2001).

Stand replacing fire also allows the forest succession path to naturally start over, favoring broadleaf species in a way not done by managed forestry (Hägglund *et al.*, 2020). These young post-fire stands are missing on the landscape level, with most forests in these age classes being managed and many reserves focusing on old growth. However, there are different beetle species assemblages in these young post-fire forests that also need protecting, as they are not supported by young managed stands or old-growth (Gran & Götmark, 2021; Similä *et al.*, 2002). By taking existing young forests, restoring them with fire, and creating new nature reserves, these younger post-fire stands will once again be present in the landscape, while being more cost-effective for land owners interested in set asides as young stands have a lower net present value than old forests (Lundström *et al.*, 2011).

There is the added impact of fire itself being absent from the ecosystem, as it provides specific structures that some beetle species are reliant on (Hekkala *et al.*, 2014), although fire is already beginning to be restored to the landscape in the form of controlled burns. While this analysis did not show a significant relationship between gaps or structure as predicted, these smaller scale disturbances seen in unmanaged forests are important. Management actions to mimic this are already in place, namely PCT and thinning, although those are done with different motivations and are homogenous on the stand scale. In order to continue to execute these actions but also with respect to biodiversity, broadleaves should be left (Roberge *et al*., 2020) and light levels within the forest should be considered to create true gaps, even if this has not been proven by these results. Instead of clearcutting, harvesting can better replicate natural disturbances with continuous cover methods (Kyaschenko *et al.,* 2022), as completely stand-replacing disturbances are naturally not as dominant as formerly believed (Kuuluvainen, 2009). Part of the ability of certain species to recover after a disturbance is the continuity of host trees (Siitonen, 2001), and Joelsson *et al.* (2018) found that species assemblages in uneven-aged managed stands were similar to those of mature or old forests.

Rotational forestry prevents old growth

Rotational forestry harvests the forest before it has the opportunity to develop old growth characteristics. While richness peaked before the end of the managed chronosequence, the unmanaged fire chronosequence did not hit peak species richness until after it became classified as old growth, after 140 years (Figure 4). These later years are crucial for species, often red-listed, that are reliant on old growth structures and continuous, undisturbed habitat. This is shown in Figure 5 as the amount of red-listed species continues to increase well after the management stands would have been harvested, proving the second prediction that older stands would have more red-listed species. Many red-listed species, such as *Pytho abieticola, Epuraea oblonga,* and *Atomaria abietina* (Appendix Figure 1; SLU Artdatabanken, 2025a/b/c), are reliant on undisturbed habitat, hence the importance of having continuous unmanaged forests. In order to better benefit red-listed species in managed forests, broadleaves can be prioritized, deadwood can be left, and fire can be reintroduced (Hekkala *et al.,* 2014; Similä *et al.,* 2002). In addition, longer rotation lengths can be used and specific old-growth structures can be preserved throughout the rotation (Bauhus *et al*., 2009). However, the reality is that some species are simply incompatible with rotational forest management (Niemelä, 1997; Joelsson *et al*., 2018).

4.4 Uncertainty and further research opportunities

Some uncertainty arises when considering that the traps could have caught visitors to the stands, meaning that the beetles trapped are not necessarily actively reproducing in these forests (Niemelä, 1997). Similar reports have larger data sets (ie., Djupström *et al*., 2008; Heikkala *et al*., 2016), so the smaller data set used in this analysis could be the cause of issues in convergence and model reliability. One of the reasons for the small data set was errors by lab personnel missing the smallest beetle species when cleaning the samples. A larger data set would likely have a larger amount of red-listed species, which could be used to create a more accurate linear model of drivers of red-listed species richness, as this data set was too small to get a result. Some environmental variables may have been missed as the ordination (Figure 6) was not able to be fully explained by the included variables. Further opportunities for research lie in the species assemblages, in conclusions that can be drawn from the data and trends based on which species or guilds were present in which stands. In addition, a landscape-scale consideration of management intensity should be attempted, as beetles are mobile and are not limited to these specific stands. This larger perspective could provide insight into the impacts of landscape degradation by management in comparison to the contributions that the patches of remaining natural forest make to biodiversity.

4.5 Implications for the future of Swedish forests

As shown, intensive forestry is a threat to biodiversity (Djupström *et al.*, 2008). The rotational forests that replace the natural counterparts differ greatly, degrading and reducing habitat (Figure 3, Djupström *et al.*, 2008). Clearcutting and the building of forest roads fragment habitat, isolating species. The forest that remains does not have the same structures and processes of a natural forest (Figure 3, Hägglund *et al.*, 2020).

In general, more forest should be preserved and formally protected with the remaining natural forest (Swedish *urskog*) as the priority. While setting aside forest is important, this is likely insufficient to reverse the decline in biodiversity (Hägglund *et al.*, 2020). Abandoned forests that have previously been intensively managed do not have the same habitat qualities as natural forests. Allowing for natural disturbance or even working to ecologically restore the forest can improve the habitat quality (Heikkala *et al.*, 2016). While this thesis has focused on beetles, these factors illustrated impact the whole of the forest taxa, as the ecosystem is interconnected.

Forestry is still necessary; therefore, the current methods need to be updated to further accommodate ecological values. Stands must be able to be used for timber production while also providing habitat (Felton *et al.*, 2020). Ideally, the even-aged protocol would be mostly left behind in favor of uneven-aged, multi-story silvicultural practices (Joelsson *et al.,* 2018), namely continuous cover forestry (Kyaschenko *et al.,* 2022). If a clearcut is to be done, care should be taken to mimic a stand replacing fire as much as possible – leaving large amounts of deadwood, damaged trees, and unique structures (Niemelä, 1997; Heikkala *et al.*, 2015). However, a balance needs to be found between benefiting biodiversity while still respecting the economy of the forest owner (Seibold *et al.*, 2016).

These actions should be planned in order to create a matrix of old growth, managed stands, and fire-regenerated forests within dispersal range of species and with decent connectivity on a landscape scale (Heikkala *et al*., 2016). By ensuring that all types of forests and disturbances are represented on the landscape level, both spatially and temporally, the different species will be able to maintain both source and sink populations (Niemelä, 1997; Gibb *et al.,* 2013). Only by having a landscape perspective is it possible to balance profiting from the forest with preserving ecological values, which are necessary to sustain our way of life.

5. Conclusion

Forestry is an important and necessary industry in Sweden. However, as shown through results and literature, rotational forest management negatively impacts beetle diversity, as it alters habitat quality in the forest. Natural forests need to be protected and the conditions within managed forests need to be improved in order to ensure species richness and biodiversity for the future. These actions should be done on a landscape scale and with variety in order to successfully facilitate beetle diversity while staying considerate of economic practicalities. The modern forest landscape is dominated by humans, but the biodiversity that society is so reliant on is threatened by these actions. In order to sustain forest use for the future, some control has to be given back to nature and its disturbance regimes.

References

Barbone, J.M. & Garbuszus, J.M. (2025). openxlsx2: Read, Write and Edit 'xlsx' Files. R package version 1.15. URL: https://github.com/JanMarvin/openxlsx2.

Barrett. T., Dowle, M., Srinivasan, A., Gorecki, J., Chirico, M., Hocking, T., Schwendinger, B. & Krylov, I. (2025). data.Table: Extension of `data.frame`. R package version 1.17.0, https://CRAN.R-project.org/package=data.Table.

Bauhus, J., Puettmann, K. & Messier, C. (2009). Silviculture for old-growth attributes. Forest ecology and management, 258 (4), 525–537. https://doi.org/10.1016/j.foreco.2009.01.053.

Buness, V., Sundqvist, M.K., Tuhin Ali, S., Annighöfer, P., Miguel Aragon, C., Lanzrein, I., Metcalfe, D.B., Nilsson, M. & Gundale, M.J. (2025). Resource quantity and heterogeneity drive successional plant diversity in managed and unmanaged boreal forests. *Ecography (Copenhagen)*,. https://doi.org/10.1111/ecog.07676.

Carcaillet, C., Bergman, I., Delorme, S., Hornberg, G. & Zackrisson, O. (2007). Long-term fire frequency not linked to prehistoric occupations in northern Swedish boreal forest. *Ecology (Durham)*, 88 (2), 465–477. https://doi.org/10.1890/0012-9658(2007)88[465:LFFNLT]2.0.CO;2.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature (London)*, 486 (7401), 59–67. https://doi.org/10.1038/nature11148.

Crowson, R.A. (1981). *The Biology of the Coleoptera*. Academic Press. https://doi.org/10.1016/C2013-0-07304-5.

Djupström, L.B., Weslien, J. & Schroeder, L.M. (2008). Dead wood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. *Forest ecology and management*, 255 (8), 3340–3350. https://doi.org/10.1016/j.foreco.2008.02.015.

Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindbladh, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämås, T., Brunet, J., Kalén, C., Kriström, B., Gemmel, P. & Ranius, T. (2020). Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. Ambio, 49 (5), 1050–1066. https://doi.org/10.1007/s13280-019-01248-0.

Fox, J. & Weisberg, S. (2019). An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. Package car version 3.1-3. https://www.john-fox.ca/Companion/.

Gibb, H., Johansson, T., Stenbacka, F. & Hjältén, J. (2013). Functional Roles Affect Diversity-Succession Relationships for Boreal Beetles. PloS one, 8 (8), e72764–e72764. https://doi.org/10.1371/journal.pone.0072764.

Gran, O. & Götmark, F. (2021). Saproxylic beetles in pre-commercially thinned Norway spruce stands and woodland key habitats: How do conservation values differ? Forest ecology and management, 479, 118584-. https://doi.org/10.1016/j.foreco.2020.118584.

Heikkala, O., Martikainen, P. & Kouki, J. (2016). Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. *Biological conservation*, 194, 39–47. https://doi.org/10.1016/j.biocon.2015.12.002.

Hekkala, A., Päätalo, M., Tarvainen, O. & Tolvanen, A. (2014). Restoration of Young Forests in Eastern Finland: Benefits for Saproxylic Beetles (Coleoptera). *Restoration ecology*, 22 (2), 151–159. https://doi.org/10.1111/rec.12050.

Hertog, I.M., Brogaard, S. & Krause, T. (2022). Barriers to expanding continuous cover forestry in Sweden for delivering multiple ecosystem services. *Ecosystem services*, 53, 101392-. https://doi.org/10.1016/j.ecoser.2021.101392.

Hjort, R., Pettersson, B., Andersson, R., Mossberg, B. & Sverige. Skogsstyrelsen (2013). *Våra skogsträd*. [Ny utg.]. Print, in Swedish. Skogsstyrelsen.

Hägglund, R., Dynesius, M., Löfroth, T., Olsson, J., Roberge, J.-M. & Hjältén, J. (2020). Restoration measures emulating natural disturbances alter beetle assemblages in boreal forest. *Forest ecology and management*, 462, 117934-. https://doi.org/10.1016/j.foreco.2020.117934.

Hämäläinen, A., Runnel, K., Ranius, T. & Strengbom, J. (2024). Diversity of forest structures important for biodiversity is determined by the combined effects of productivity, stand age, and management. Ambio, 53 (5), 718–729. https://doi.org/10.1007/s13280-023-01971-9.

Joelsson, K., Hjältén, J. & Gibb, H. (2018). Forest management strategy affects saproxylic beetle assemblages: A comparison of even and uneven-aged silviculture using direct and indirect sampling. *PloS one*, 13 (4), e0194905–e0194905. https://doi.org/10.1371/journal.pone.0194905.

Jonsson, M., Bengtsson, J., Moen, J., Gamfeldt, L. & Snäll, T. (2020). Stand age and climate influence forest ecosystem service delivery and multifunctionality. Environmental research letters, 15 (9), 940-. https://doi.org/10.1088/1748-9326/abaf1c.

Kuuluvainen, T. (2009). Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe: The Complexity Challenge. Ambio, 38 (6), 309–315. https://doi.org/10.1579/08-A-490.1.

Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H. & Ranius, T. (2022). Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: The effect of three decades of biodiversity-oriented forest policy in Swedish forests. *Journal of environmental management*, 313, 114993–114993. https://doi.org/10.1016/j.jenvman.2022.114993.

Lundström, J., Öhman, K., Perhans, K., Rönnqvist, M. & Gustafsson, L. (2011). Cost-effective age structure and geographical distribution of boreal forest reserves. *The*

Journal of applied ecology, 48 (1), 133–142. https://doi.org/10.1111/j.1365-2664.2010.01897.x.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological conservation*, 94 (2), 199–209. https://doi.org/10.1016/S0006-3207(99)00175-5.

Naturhistoriska Riksmuseet. (2024). *Tall.* Available in Swedish at: https://www.nrm.se/fakta-om-naturen/vaxter/trad/tall (Accessed: 30-04-2025).

Niemelä, J. (1997). Invertebrates and boreal forest management. *Conservation biology*, 11 (3), 601–610. https://doi.org/10.1046/j.1523-1739.1997.06008.x.

Nylund, J.E. (2010). Swedish forest policy since 1990. *Rapport (SLU, Institutionen för skogens produkter)*, (16).

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J. & Borman, T. (2025). vegan: Community Ecology Package. R package version 2.6-10, https://CRAN.R-project.org/package=vegan.

Pedersen, T. (2024). patchwork: The Composer of Plots. R package version 1.3.0, https://CRAN.R-project.org/package=patchwork.

PEFC. (2024). Skogsbruksstandard, in Swedish. *Dokument med understrukna ändringar 2024-05-22.* PEFC SWE 002:5. Available at www.pefc.se.

R Core Team. (2024). R: A Language and Environment for Statistical Computing. Version 4.4.2. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ranius, T., Caruso, A., Jonsell, M., Juutinen, A., Thor, G. & Rudolphi, J. (2014). Dead wood creation to compensate for habitat loss from intensive forestry. Biological conservation, 169, 277–284. https://doi.org/10.1016/j.biocon.2013.11.029.

Roberge, J.M., Fries, C., Normark, E., Mårald, E., Sténs, A., Sandström, C., Sonesson, J., Appelqvist, C. and Lundmark, T. (2020). Forest management in Sweden current practice and historical background. *Skogsstyrelsen*.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D. & Müller, J. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *The Journal of applied ecology*, 53 (3), 934–943. https://doi.org/10.1111/1365-2664.12607.

Similä, M., Kouki, J., Martikainen, P. & Uotila, A. (2002). Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. *Biological conservation*, 106 (1), 19–27. https://doi.org/10.1016/S0006-3207(01)00225-7.

Siitonen, J. (2001). Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. *Ecological bulletins*, (49), 11–41.

Skogskunskap. (2024). *När ska jag slutavverka?* Available in Swedish at: https://www.skogskunskap.se/skota-barrskog/slutavverka/slutavverkningens-grunder/nar-ska-jag-slutavverka/ (Accessed: 30-04-2025).

Skogsstyrelsen. (2023). The Forestry Act. Available at: https://www.skogsstyrelsen.se/en/laws-and-regulations/skogsvardslagen/ (Accessed: 30-04-2025).

Slowikowski, K. (2024). ggrepel: Automatically Position Non-Overlapping Text Labels with 'ggplot2'. R package version 0.9.6, https://CRAN.R-project.org/package=ggrepel.

SLU Artdatabanken, (2020). Rödlistade arter i Sverige 2020. SLU, Uppsala.

SLU Artdatabanken (2025a). *Artfakta: Atomaria abietina*. Available in Swedish at: https://artfakta.se/taxa/100420 (Accessed: 30-04-2025).

SLU Artdatabanken (2025b). *Artfakta: Epuraea oblonga*. Available in Swedish at: https://artfakta.se/taxa/105389 (Accessed: 30-04-2025).

SLU Artdatabanken (2025c). *Artfakta: mindre barkplattbagge (Pytho abieticola).* Available in Swedish at: https://artfakta.se/taxa/101691 (Accessed: 30-04-2025).

SLU Artdatabanken. (2025d). *Artfakta: skalbaggar (Coleoptera).* Available in Swedish at: https://artfakta.se/taxa/3000181 (Accessed: 19-05-2025).

Sténs, A., Roberge, J.-M., Löfmarck, E., Beland Lindahl, K., Felton, A., Widmark, C., Rist, L., Johansson, J., Nordin, A., Nilsson, U., Laudon, H. & Ranius, T. (2019). From ecological knowledge to conservation policy: a case study on green tree retention and continuous-cover forestry in Sweden. *Biodiversity and conservation*, 28 (13), 3547–3574. https://doi.org/10.1007/s10531-019-01836-2.

StoraEnso. (n.d.). *Gallring för tillväxt*. Available in Swedish at: https://forest.storaenso.com/sv-se/for-skogsagare/tjanster/gallra (Accessed: 30-04-2025).

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Version 3.5.1. Springer-Verlag New York. https://ggplot2.tidyverse.org.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. & Yutani, H. (2019). “Welcome to the tidyverse.” Journal of Open Source Software, *4*(43), 1686. doi:10.21105/joss.01686 https://doi.org/10.21105/joss.01686.

Wickham, H. & Bryan, J. (2025). readxl: Read Excel Files. R package version 1.4.5, https://CRAN.R-project.org/package=readxl.

Wickham, H., François, R., Henry, L., Müller, K. & Vaughan, D. (2023). dplyr: A Grammar of Data Manipulation. R package version 1.1.4, https://CRAN.R-project.org/package=dplyr.

Wickham, H., Vaughan, D. & Girlich, M. (2024). tidyr: Tidy Messy Data. R package version 1.3.1, https://CRAN.R-project.org/package=tidyr.

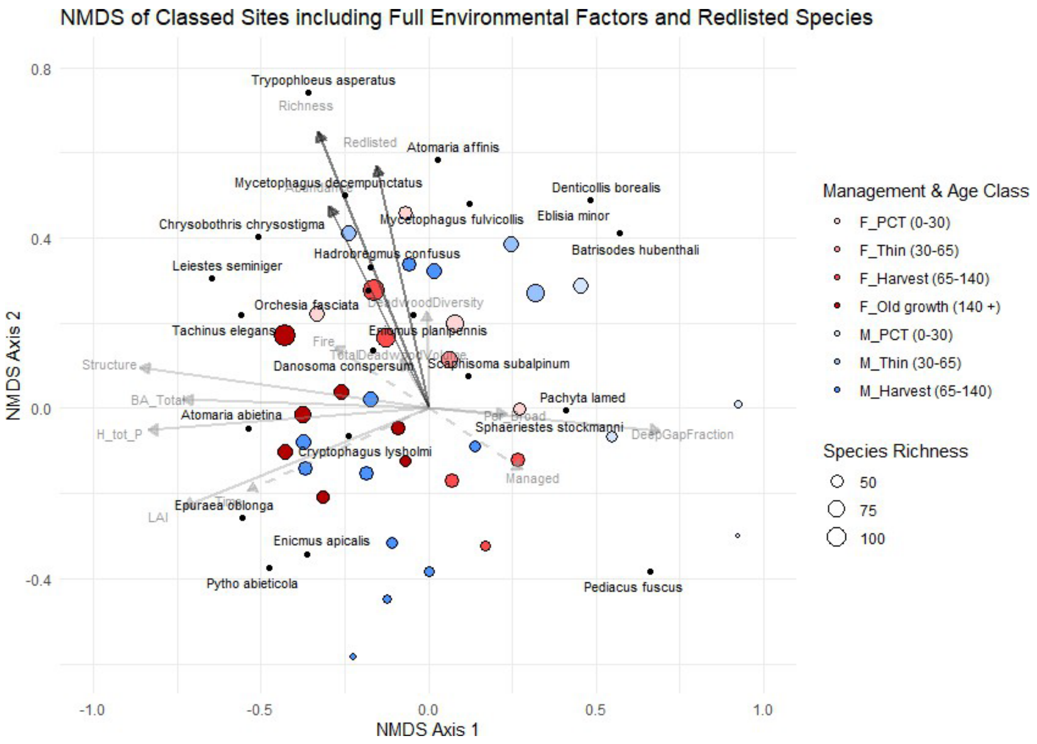
Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Package mgcv version 1.9-3. Journal of the Royal Statistical Society (B) 73(1):3-36.

Östlund, L., Zackrisson, O. & Axelsson, A.L. (1997). History and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian journal of forest research*, 27 (8), 1198–1206. https://doi.org/10.1139/x97-070.

Acknowledgements

A huge thank you to Vincent Buness for being a great supervisor; your careful explanations, advice, and patience were much appreciated. Thank you as well to Anne-Maarit Hekkala for your expert guidance and making time for my questions. Working with you guys made this whole experience more enjoyable, so thank you!

Appendix



Appendix Figure 1: NMDS of beetle assemblages in each stand with environmental vectors and red-listed species plotted. NMDS was run to illustrate which stands were similar based on which beetles (both amount and species) were present. Stands from the unmanaged fire chronosequence are in red and the managed chronosequence in blue, and labelled with stand names. The opacity of the points indicates time since disturbance, classifying the stands based on typical management actions possible at each stage. The size of the points shows total species richness in the stand. The arrows provide insight into which ways the different factors correlate with the position of the stands. Black arrows represent beetle metrics. Gray solid arrows represent environmental factors. Gray dashed arrows are chronosequence types. The length of the arrows correspond to the rr^2 values (Table 4), and therefore how correlated that vector is with the distribution of the stands. The statistical significance of the arrows is shown in Table 4 with p values.

Appendix Table 1: Statistics of GAMs for graphing environmental data.

Type of data	Metric	Term type	Term	Estimate / edf	SE / Ref.df	t- / F-value	p-value
Deadwood	Total volume	Parametric	Intercept	77.810	8.737	8.906	7.17e-10
			F vs M	-57.705	14.925	-3.866	0.0006
		Smooth	s(Time):F	2.425	2.938	3.195	0.0487
			s(Time):M	1.000	1.000	0.001	0.9720
		Model summary	Adjusted R^2	0.467	-	-	-
			Deviance explained (%)	53.6	-	-	-
			n	35	-	-	-
	Diversity	Parametric	Intercept	1.6975	0.1279	13.270	4.24e-14
			F vs M	0.2626	1.3535	0.194	0.847
		Smooth	s(Time):F	1.088	1.170	0.445	0.600
			s(Time):M	1.868	2.053	1.088	0.494
		Model summary	Adjusted R^2	0.315	-	-	-
			Deviance explained (%)	39.4	-	-	-
			n	35	-	-	-
Basal Area	BA total	Parametric	Intercept	19.6003	2.1749	9.012	6.23e-10
			F vs M	0.1726	12.2698	0.014	0.989
		Smooth	s(Time):F	2.276	2.776	2.703	0.0615
			s(Time):M	1.527	1.786	8.937	0.0012
		Model summary	Adjusted R^2	0.479	-	-	-
			Deviance explained (%)	55.2	-	-	-
			n	35	-	-	-
	% Broad	Parametric	Intercept	6.7952	3.3441	2.032	0.0512
			F vs M	-0.3062	16.5621	-0.018	0.9854
		Smooth	s(Time):F	1.000	1.000	0.228	0.637
			s(Time):M	1.445	1.698	0.994	0.377
		Model summary	Adjusted R^2	0.0020	-	-	-
			Deviance explained (%)	10.6	-	-	-
			n	34	-	-	-
Leaf Area Index	LAI	Parametric	Intercept	0.9497	0.0901	10.545	2.27e-11
			F vs M	0.1611	0.6693	0.241	0.812
		Smooth	s(Time):F	2.669	3.192	2.462	0.0015
			s(Time):M	1.702	1.939	17.210	1.46e-5
		Model summary	Adjusted R^2	0.625	-	-	-
			Deviance explained (%)	68.5	-	-	-

			n	35	-	-	-
Structure	Structure	Parametric	Intercept	0.8768	0.0310	28.280	2e-16
			F vs M	-0.6796	0.7931	-0.857	0.398
		Smooth	s(Time):F	1.000	1.000	0.31	0.582
			s(Time):M	1.984	2.025	36.27	2e-16
		Model summary	Adjusted R²	0.725	-	-	-
			Deviance explained (%)	75.7	-	-	-
			n	35	-	-	-
Gap	Deep Gap Fraction	Parametric	Intercept	0.1487	0.0131	11.315	3.57e-12
			F vs M	0.2163	0.2170	0.997	0.327
		Smooth	s(Time):F	1.972	2.368	1.329	0.2541
			s(Time):M	1.932	2.005	12.564	0.0002
		Model summary	Adjusted R²	0.489	-	-	-
			Deviance explained (%)	56.3	-	-	-
			n	35	-	-	-
Height	Total Pine	Parametric	Intercept	17.0408	0.6887	24.743	2e-16
			F vs M	-5.7166	8.3582	-0.684	0.499
		Smooth	s(Time):F	1.000	1.000	2.22	0.147
			s(Time):M	1.924	2.094	44.09	2e-16
		Model summary	Adjusted R²	0.81	-	-	-
			Deviance explained (%)	83.2	-	-	-
			n	35	-	-	-

Publishing and archiving

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

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

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

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

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

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