The effect of forestry and cervid densities on annual growth of ericaceous shrub species

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Abstract

Ericaceous shrubs, such as bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*), and heather (*Calluna vulgaris*), dominate the understory in Swedish forests. Their important role of providing forage for wild deer is well established. Human-wildlife conflicts arise when there is a shortage in forage forcing deer to switch to feeding on young production trees. Due to current forestry practices involving dense planting of coniferous trees under short-rotation regimes, there has been a steady decline in the appearance of these shrubs. Here, I identified the role of various forestry-related factors, such as basal area and forest age, as well as soil characteristics and cervid browsing pressure, on the annual production of biomass of the ericaceous shrubs by collecting data on the biomass proportion produced over the last growing season under different forest conditions. While the annual growth of the shrubs was highly affected by the forest's basal area and time since clear-cutting, the effect of cervid browsing pressure did not show any significant influence. Furthermore, there was a significant difference in the impact on the annual growth between Scots pine- (*Pinus sylvestris*) and Norway spruce- (*Picea abies*) dominated forest stands. Shrubs found in spruce forest stands were significantly more negatively affected by basal area and time since clear-cutting than in pine stands. Soil characteristics also differed significantly between both forest types. My findings suggest that in order to secure long-term forage availability for wild deer, which leads to reduced conflicts with forest owners, forestry practices including the planting of coniferous trees, especially spruce, in dense monocultures, have to be avoided.

Keywords: production forest, conifer, silviculture, plant-animal interaction, forest management, ungulate

Preface

This master thesis project is part of a larger research project, called "The puzzle of forestry and ungulate interactions – a missing piece is in the understory". The project is funded by FORMAS, the Swedish research council for sustainable development, and led by Assoc. Prof. Annika Felton together with Assoc. Prof. Per-Ola Hedwall. The principal researcher is PhD student Laura Juvany Canovas, who in 2020 collected field data used in this thesis. I have myself collected additional data in the laboratory and analyzed the data.

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Abbreviations

ANOVA	Analysis of variance
BB	Bilberry
C/N ratio	Carbon/Nitrogen ratio
CB	Cowberry
DBH	Diameter at breast height
DNA	Deoxyribonucleic acid
FORMAS	The Swedish Research Council for Sustainable Development
GLMM	Generalized linear mixed model
H	Heather
NFI	National forest inventory
SFA	Swedish Forest Agency
SFIF	Swedish Forest Industries Federation
SLU	Swedish University of Agricultural Sciences
SMHI	Swedish Meteorological and Hydrological Institute

1. Introduction

Forests are known to be a vital aspect of all of life on earth (Daily, 1997). Not only do forests provide habitat for wild animals and plants and goods such as food and timber for humans, but they also provide key ecosystem services like nutrient cycling and purification of water and soil, and thereby secure livelihood for all humans (Brockerhoff et al., 2017). Especially now in an ever-changing world, forests are a crucial aspect of climate change mitigation due to their function as a carbon sink (Harris et al., 2021).

Sweden plays a large role in the forestry industry, being the third-largest exporter of sawn timber, pulp, and paper in the world despite only having 1% of the worldwide forest cover (SFIF, 2018). This means that many Swedish production forests are intensively managed to maximize the yield. However, decision-makers in forest management still depend on research to shed light on the sustainability of forests under such intensive management strategies. With an improved understanding of the complex interactions in forest systems, policymakers and forest owners are better equipped to sustainably manage the forests, securing resilience, mitigating climate change, and putting biodiversity loss on hold.

An important part of forest biodiversity is understory vegetation. In Sweden, the understory is dominated by ericaceous shrubs, such as bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*) (Hedwall et al., 2013). These shrubs provide an important food and habitat resource for several other species, such as deer (A. M. Felton et al., 2020), insects (Szujecki, 1986), capercaillie (Selås, 2001), and brown bear (Hertel et al., 2018). Despite this, national forest inventory (NFI) data shows that ericaceous shrubs have declined by 50% since the 1950s in the hemiboreal part of Sweden (Hedwall et al., 2019a). These species are put at risk due to current intensive forestry strategies involving clearcutting and planting of coniferous trees, primarily Norway Spruce (*Picea abies*) and Scots Pine (*Pinus sylvestris*), in monocultures with short rotation periods (Hedwall et al., 2019b). This leads to dense, evenly aged, and uniform forests with low light availability in the understory (Hedwall et al., 2019b). Forests become less inhabitable for ericaceous shrubs because the overstory species composition and canopy structure heavily impact temperature, water availability, soil nutrients, and light availability for the understory (Hedwall et al., 2019b). This problem is even more accelerated in southern Sweden, where it is becoming common practice to replace pine-dominated stands with spruce-dominated stands, which are even denser and thus allow less light to reach the forest floor, and have shown to be detrimental for the understory vegetation (Petersson et al., 2019)

Deer communities are both contributing factors and victims of this decline in ericaceous shrubs. Besides providing ecosystem services for people and increasing biodiversity in the forests, these dwarf shrubs also make up one of the most important food sources for deer species such as red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), and moose (*Alces alces*) (A. M. Felton et al., 2020). Furthermore, research has found that herbivore browsing can induce a variety of responses on plants, both negative and positive (Hobbs, 1996).

One problem that many forest owners are facing is the deer damage caused by browsing on young production trees (Gill, 1992). Recent research has shown that this damage may be driven by poorer availability of ericaceous shrubs which increases the feeding competition between moose and deer (hereon referred to as cervids) and in return leads to more feeding on young pine trees (Spitzer et al., 2021). Considering the economic loss for forest owners (Bergquist et al., 2019), there is a big interest in discovering how current forest management influences the availability, distribution, and quality of cervid forage.

Therefore, to secure forest ecosystem services and biodiversity, and to maintain economic values, a management strategy should be developed which ensures the persistence of ericaceous shrubs. So far, research has focussed on factors influencing dwarf shrub cover, such as in Hedwall et al. (2013) and Mathisen et al. (2010). This project aims to assist this process, by studying relationships between the annual production of ericaceous shrub forage, and factors such as light, site productivity, disturbance, as well as cervid density. This will improve our understanding of how the annual production of edible biomass is determined and help developing models that assess forage availability under different forestry scenarios. Once these models are established, forest owners can be informed about the carrying capacity of forest areas to make well-founded decisions regarding game and forest management.

To do so, a study design consisting of two parts was developed by a research team at SLU. In the exclosure study, the effect of herbivory on the productivity, measured as the annual growth portion, of ericaceous shrubs was analyzed in two locations in northern and central Sweden. The two study sites in each region have known and differing deer densities, enabling the comparison of plant traits along a deer density gradient, whilst providing similar forest conditions (such as stand age, tree composition, site index, and time after clear-cutting). Additionally, both study sites were equipped with deer exclosures and camera traps, allowing the direct comparison of shrub productivity between browsed and unbrowsed plots. Subsequently, the landscape survey investigates the impact of other forestry-related variables, such as tree species composition, age of the forest, and tree basal area on a larger latitudinal and environmental scale. Together, both parts of the study shed light on the complex interactions between plant productivity and biotic and abiotic factors relevant to management.

I hypothesize that:

1) The annual growth fraction, defined as the new growth of the last growing season divided by total plant biomass, of bilberry, cowberry, and heather in Swedish production forests is influenced by:

- Cervid browsing pressure, in a negative way, if such browsing pressure is high;
- Forest-context-related factors, in either positive or negative ways, depending on the variable involved:
    - time since clear-cutting (negatively with increasing time, assuming that shrub age is positively correlated to forest age which lowers the proportion of total biomass in form of annual shoots),
    - tree species composition (negatively in spruce-dominated forests compared to pine-dominated forests, primarily due to light availability), and
    - tree basal area (negatively with higher basal area, assuming that high basal area mirrors low light availability);

2) High levels of cervid browsing affects the morphological traits of the ramets, namely by reducing the ramet height and by increasing the number of branches.

2. Materials and methods

2.1. Study areas and experimental design

This study is divided into two parts. The exclosure study comprises an exclosure experiment to capture the impact of cervid browsing on annual biomass production. For this, exclosures were built in Nordmaling in Västerbotten county (Northern Sweden) and Öster Malma in Sörmland county (Central Sweden). These study sites have records of cervid densities going back to 2013 as part of the SLU project “Beyond Moose”, enabling the choice of a subset of stands that capture a variation in cervid density. The landscape survey aimed to capture environmental and latitudinal variance across Swedish production forests in Vindeln in Västerbotten county (Northern Sweden), Siljansfors in Dalarna county (Central Sweden), and Asa in Kronoberg county (Southern Sweden) (Figure 1).

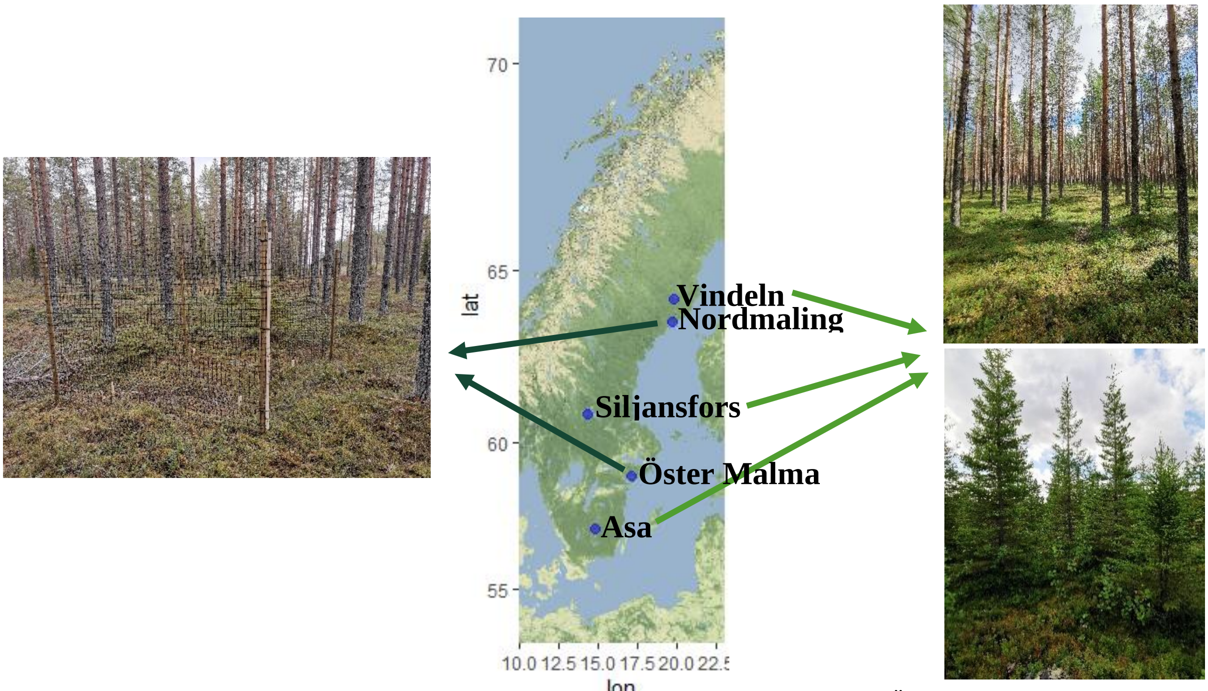

Figure 1. Map showing the five study sites Vindeln, Normaling, Siljansfors, Öster Malma and Asa in Sweden. Left photo: cervid exclosure as used in the exclosure study, right photo (top): pine-dominated stand, (bottom): spruce-dominated stand as used in the landscape survey. Photos: Laura Juvany Canovas.

The study area covers large parts of Sweden, including both boreal (Vindeln, Nordmaling, and Siljansfors), and boreo-nemoral (Asa and Öster Malma) vegetation zones.

They hence differ in annual mean temperature (SMHI, 2021a), annual mean precipitation (SMHI, 2021b), and the mean number of days with a snow cover of >10cm measured at the nearest SMHI measuring stations to the stands (SMHI, 2021c) (table 1).

Table 1. Annual mean temperature, annual mean precipitation, and mean number of days with snow cover >10cm measured between 2018 and 2020 for five study sites stretching from southern to northern Sweden.

Site	Annual mean temperature [°C]	Annual mean precipitation [mm]	Mean number of days with snow cover >10cm [days]
Asa	7.5	750	14
Öster Malma	8	600	29
Siljansfors	4.5	650	79
Nordmaling	5	600	144
Vindeln	3.5	700	158

Cervid communities in Sweden comprise of moose (*Alces alces*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and roe deer (*Capreolus capreolus*), but their presence and densities differ between the five sites (Viltdata, 2021). Moose and roe deer are present in all sites. Red deer are found everywhere except Vindeln. Fallow deer are absent in Vindeln and Siljansfors. Generally, the highest cervid densities are reached in Öster Malma.

All sites are predominantly coniferous, with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) being the most common tree species. The most common broadleaf tree found in all sites is birch (*Betula spp.*). Additionally, the tree surveys found oak (*Quercus robur*) in Asa, aspen (*Populus spp.*) in Vindeln, and aspen and larch (*Larix spp.)* in Siljansfors.

2.2. Exclosure study

For the exclosure study, one exclosure of 3x3 m and with a fence of 2.5 m height, was placed in each of 10 stands in Nordmaling and Öster Malma in 2020 before the growing season. The ten stands were selected from the Beyond Moose project sampling grids that have 1x1 km square transects that are at least 3 km apart over an area of 76 km² in Nordmaling and 50 km² in Öster Malma. All stands were Scots pine-dominated and between 45 and 70 years old but with differing cervid densities.

Exclosures and control plots of 10 m radius were selected to be as similar as possible in their understory and overstory composition. These were located at least 20 m from each other.

At the end of the growing season in 2020, ramets from the three species of ericaceous shrubs (bilberry, cowberry, and heather) were collected both in the exclosure and in the control plot. For dates refer to table A1 in the appendix. A ramet was defined as an individual of a clonal colony of shrubs. Within each plot, the sampling area consisted of a 2x2 m grid of 16 subplots, from which 3 subplots were randomly selected. Per subplot, up to 3 ramets (depending on occurrence) per plant species were selected randomly to measure top height and harvested for further measurements. After ramet collection, the number of branches per ramet was counted within three days of collecting the ramets in the field for bilberry and cowberry.

Next, from each ramet sample, the annual growth, the last growing season's new biomass, was visually assessed and separated from the previous growth and stored separately. The annual growth was defined as the portion emerging from the proximal bud, the bud that was formed after the previous year's growing season. For the deciduous bilberry, this meant all leaves in a ramet were considered new growth. For both plant species, annual growth determination followed the methods described by Tolvanen (1995). Differences in the color of the stems helped to identify the new growth. For heather, the annual growth fraction was determined as the portion from the leading long shoots until a bare zone where the previous year's flowers have been shed, excluding short shoots that may have developed in the previous years. This was done according to Mohamed and Gimingham (1970). A more detailed explanation with drawings can be found in the respective papers.

In early 2021, we dried all samples for 24 h at 60 °C using a heating cabinet, and all fractions (old growth, new growth, leaves and stems, only leaves) were weighed separately. Additionally, for bilberry and cowberry, leaves were removed from stems to weigh the leaf fractions without woody stem parts. Later, subsets from all sites and plant species were dried at 103 °C for 12 h and weighed again. We calculated a regression line between subsamples dried at 60 °C and 103 °C to extrapolate weights at 103 °C for all samples. This method allows samples dried at 60 °C to remain intact for future nutritional analyses.

Additionally, control plots were equipped with camera traps (Model: Reconyx hyperfire HC 500) to determine the on-plot cervid density. Cameras were running from April until September in Öster Malma, and from May until August in Nordmaling, covering the entire growing season of the ericaceous shrubs. Cameras were fixed to trees at 50 cm above the ground, facing north to avoid sun reflection. In all stands, the cameras had between 10 and 15 m of clear vision, without vegetation disturbing the line of sight in close proximity to avoid empty triggers. Three consecutive pictures were taken upon triggering of the cameras due to movement and heat detection beyond a set threshold. Additionally, cameras had infrared sensors for night vision. They were set up to take a daily picture at noon to determine camera operability. Ramet sampling coincided with the collection of camera traps at the end of the growing season. In autumn 2020, as part of a previous, shorter project, I analyzed all camera trap pictures using the software TRAPPER (Bubnicki et al., 2016) with the help of a mammal identification guide (T. Hofmeester, 2017). I focused on the species red deer, fallow deer, roe deer (from here on referred to as small deer), and moose (figure 2). I calculated an estimation of small deer and moose passage rate per stand as follows:

$$passage\ rate = \frac{number\ of\ passages\ recorded\ on\ camera}{number\ of\ days\ camera\ operated}\ .$$

For more information on exact dates and camera operability per stand and location, see table A2 in the appendix. In the analysis, I used both the pooled passage rate of moose and smaller deer, referred to as “cervid passage rate”, as well as both units separately.

Figure 2. (A) Red deer, (B) Roe deer, (C) Moose with calf, (D) Fallow deer. Pictures are footage from camera traps in Öster Malma and Nordmaling from summer 2020.

2.3. The landscape survey

The landscape survey aimed to capture the effect of forest stand characteristics and the environment on the annual growth of ericaceous shrubs on several levels. The three study sites allowed the coverage of a wide range of climate variations by including northern, central, and southern Swedish production forests (Vindeln, Siljansfors, and Asa, respectively). All three sites have SLU field stations nearby, which enabled obtaining detailed data about the areas. In every site, we studied 15 or 16 stands. Stands were selected based on species composition (forests dominated by either Scots pine (8 stands) or Norway spruce (8 stands)), time since clear-cutting (four stand ages) (table 2), and site index (high and low). Time since clear-cutting was estimated by selecting the tree with the biggest diameter in each of two plots per stand, measuring their height, and coring them at 1.3 m height to count the number of rings. Tree species composition is defined as the dominating plant species on a stand level, either Norway spruce, or Scots pine. A tree species was categorized as "dominating" when a minimum of 70 % of stem density was contributed by that species. Tree basal area was determined within sampling plots (8 m radius for most stands; 3 m for stands <15 years) by measuring the diameter at breast height (DBH, 1.3 m height) and using the following formula per measured tree:

$$\text{Tree basal area (m}^2\text{) per plot} = \frac{\left(\frac{DBH\ (m)}{2}\right)^2 * \pi}{Area\ of\ the\ plot} * 0.0001.$$

By adding up individual tree basal areas, the plot basal area was calculated.

Both dominant plant species and site index values were provided by the respective field stations per site and were used to choose different forest stands. Site index is an estimation of the height of spruce or pine at 100 years. Indices differ greatly across Sweden, with forests in the north generally providing lower site indices as compared to the south. This measure can be used as an estimation of site fertility and thus helped to choose forest stands to capture a variety of conditions. Additionally, soil samples were taken at each subplot by coring soils four times to a depth of 10 cm per plot and later pooled together for analysis of carbon (C) and nitrogen (N) contents.

Ramets were collected in plots with a sampling grid of 2x2 m using the same design as described in 2.2. For exact dates of ramet collection, refer to table A1 in the appendix.

Table 2.Variables used in the survey with a short description, range of values (among means of stand/plot), and unit. (B=Bilberry; C=Cowberry; H=Heather); (Study part I=exclosure study; study part II=landscape survey)

Variable	Unit	Description	Range	Level and Sample size	Study part
Annual growth fraction	ratio	Biomass that was produced in the growing season 2020 as a fraction of total plot biomass per plant species	0.13-0.5 (B) 0.05-0.63 (C) 0.03-0.44 (H)	Stand-level: n=20 (B), 20 (C), 9 (H)	I
				Plot level: n=135 (B), 115 (C), 39(H)	II
Ramet height	cm	Top height of ramet from soil to top without stretching plant	14.2-30.4 (B) 9.2-20.5 (C) 17.4-31.2 (H)	Plot-level: n=20 (B), 19 (C), 7 (H)	I
Number of branches	count	Number of branches per ramet	12.2-79.3 (B) 1.7-6 (C)	Plot-level: n=20 (B), 19 (C)	I
Small deer passage rate	Count/day	Number of small deer recorded using camera traps per number of operative days of camera	0-0.48	Stand-level: n=19	I
Moose passage rate	Count/day	Number of moose recorded using camera traps per number of operative days of camera	0-0.04	Stand-level: n=12	I
Cervid passage rate	Count/day	Sum of moose and small deer count/day	0.02-0.5	Stand-level: n=20	I
Tree dominance	Categorical	Dominant species: Norway spruce or Scots pine		Stand-level: n=24 (Spruce), 24 (Pine)	II
Basal area	m^2	Area occupied by tree stems at breast height per plot	0.08 - 67.25	Plot-level: n=141	II
C/N	ratio	Carbon to nitrogen ratio from soil samples	18.6 – 82.5	Plot-level: n=141	II
Age of stand (time since clear-cutting)	categorical	(very young=5-15 years, young=15-45 years, middle-aged=45-70 years, and “old”=70+ years[1])	5-70+	Stand-level: n=12 per age class	II
	years	Mean age coring biggest trees at breast height	6-152	Stand-level: n= 47	II

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[1] ”Old” is here used in terms of production trees, not trees in natural forests

2.4. Data analysis

All data were analyzed using RStudio (R Core Team, 2020). Prior to analysis, the data were checked for completeness and plausibility. Two data points had to be removed from the analysis. One showed inconsistency across different measurements, and the other lacked an annual fraction entirely, resulting in a fraction of 0. As a response variable, I used the annual growth fraction as a proportion of total biomass per plot and plant species. Using a proportion enabled me to account for variations in total biomass between different ramet samples that would affect the biomass of the annual growth. From here on I refer to this ratio as "the annual growth fraction”. The annual growth fraction was tested both as total biomass (including leaves and stems) and as leaf-only biomass (excluding stems). Correlation analysis of both variables is shown in the appendix (Figure A4). Since there was a high correlation of these two measures for both bilberry (R^2=0.7) and cowberry (R^2=0.93), only results including total biomass are shown in the results section. For the exclosure study, the annual growth fraction is used as a mean per stand, since data on cervid densities were available on a stand level. In the landscape study, I used the annual growth fraction on a plot level, as a mean of all ramet samples collected per plot, since stand characteristics were measured on a plot level. Before analysis, I checked for autocorrelation amongst my explanatory variables using the Pearson method. To account for the fact that the dependent variable is restricted to the interval (0,1), I decided to perform beta regressions using Generalized Linear Mixed Models with Template Model Builder (glmmTMB) from the R package *glmm* (Brooks et al., 2017).

In the exclosure study, models were applied with a logit link-function. Then, I tested the response of bilberry, cowberry, and heather annual growth fractions on both smaller deer and moose passage rates separately but also grouped as cervid passage rate. Plot was also added as a variable to test for differences in annual growth fraction between control and exclosure plots, i.e. the effect of browsing.

In the landscape analysis, the response of the annual growth fraction of the same three plant species was tested to the basal area, time since clear-cutting, C/N ratio of the soil, and dominant tree species. Basal area and time since clear-cutting were highly correlated (r=0.74), so they were used in separate models that both included interactions with dominant tree species. The dependent variable was square-root transformed prior to analysis due to skewness. Best fitting models were selected by using the *dredge* function from the R package *MuMIn* (Kamil, 2016). Model fitness was tested using the *DHARMa* package from R (Hartig, 2018). Model fitness did not improve when using site as a variable, so it was excluded from further analyses. The C/N ratio showed significant collinearity with dominant tree species (p=0.012, R^2= 0.33) and was therefore excluded from the models. Instead, after observing differences in initial annual growth between spruce and pine-dominated stands, C/N ratio differences between the forest types were tested via ANOVA and are included as a separate result. See table 2 for sample size per variable. Plant morphology analyses were performed by building a linear model with ramet height and number of branches as dependent variables respectively, and cervid passage rate as the predictor.

3. Results

3.1. Exclosure study: Cervid density as a predictor of annual growth and plant morphological traits of ericaceous shrubs in Sweden

3.1.1. Cervid passage rate and annual growth fraction

In the exclosure study, fieldwork yielded ramet samples of bilberry and cowberry in all 20 stands, whereas heather was only found in 9 stands. Camera traps captured 330 cervid encounters in total, 306 out of which were small deer (48 in Nordmaling, and 258 in Öster Malma), and 24 were moose (8 in Nordmaling, and 16 in Öster Malma).

There was no significant difference in the annual growth fraction between exclosure and control plots for any of the three plant species (Figure 3). Neither was there a significant linear relationship between the annual growth fraction and animal passage rate, no matter if moose and small deer were treated separately (Table 3) or grouped (Figure 3, Table A3).

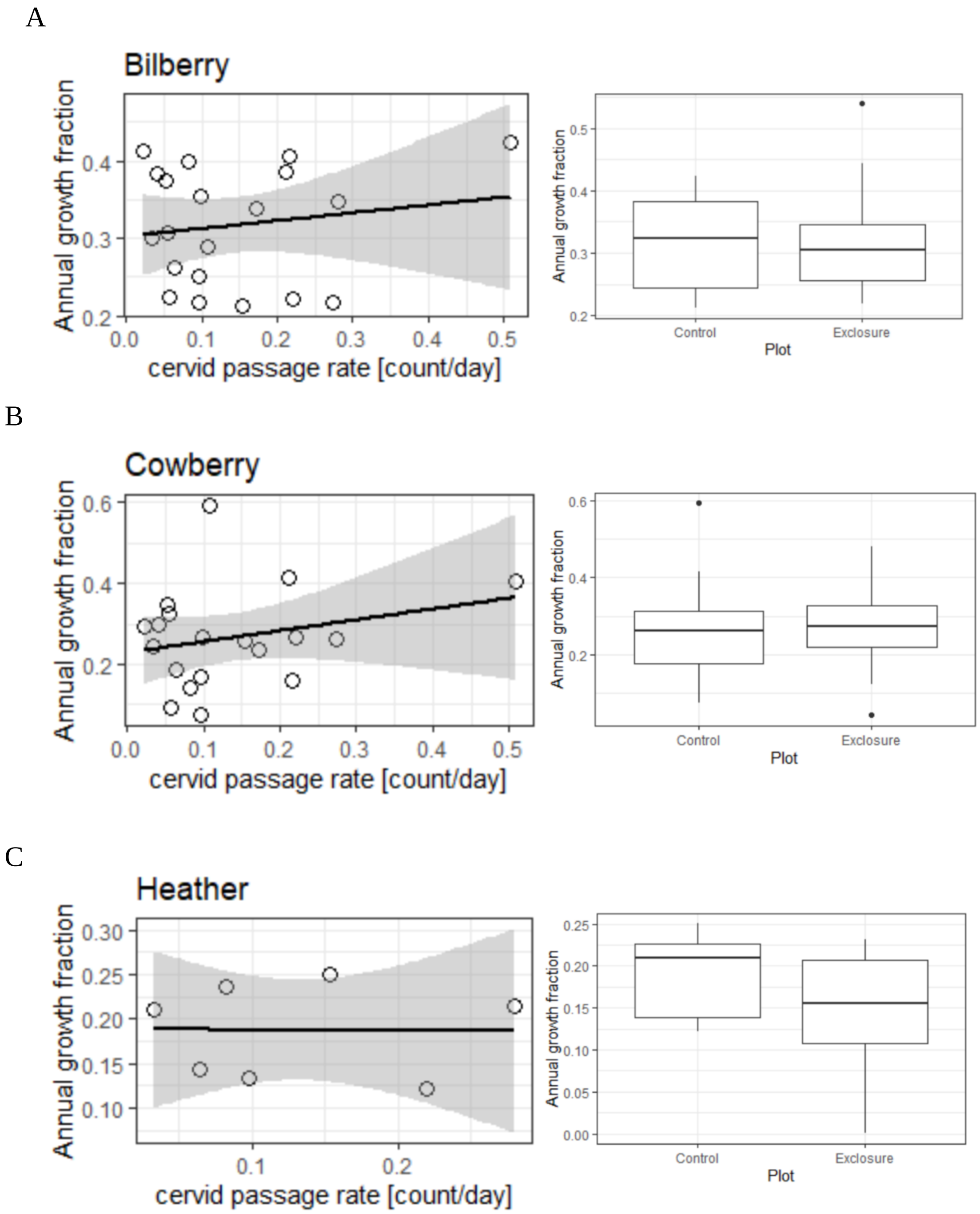


Figure 3.Relationship between cervid density and annual growth of three ericaceous shrubs (A: bilberry; B: cowberry; C; heather) growing in Swedish production forests (see also Table 2 and Table A3). Left: Regression plots where the x-axis indicates cervid passage rate (moose, red deer, fallow deer, and roe deer grouped) in front of camera traps (count/day during the growing season), and the y-axis indicates the proportion of total biomass represented by the growth fraction produced during 2020. Right: Box plots showing the difference in annual growth between exclosures and control plots.

Table 3.Results of the linear models of three ericaceous shrub species (bilberry, cowberry, and heather) in northern and central Sweden. The response variable is the annual growth fraction of the plant species, and the independent variables are small deer passage rate, moose passage rate, and plot (control versus exclosure). The passage rate was estimated using camera traps. Small deer species included were roe deer, fallow deer, and red deer. Annual growth fraction was defined as the biomass produced during the last growing season, divided by the total biomass.

	Bilberry		**Cowberry**		**Heather**	
Coefficient	*Estimates*	*p-Value*	*Estimates*	*p-Value*	*Estimates*	*p-Value*
Intercept	0.20	0.024	-0.23	0.139	-0.19	0.127
Small deer passage rate	0.07	0.833	0.83	0.188	-0.10	0.853
Moose passage rate	1.96	0.602	11.57	0.074	-10.6	0.113
Plot (Exclosure)	0.01	0.913	0.06	0.693	0.07	0.643

3.1.2. Cervid passage rate and plant morphology

There was no significant linear relationship between mean top ramet height and cervid passage rate for any of the three tested plant species in the control plots (figure 4, table 4). There was also no significant linear relationship between mean branch number and cervid passage rate for any of the two tested plant species in the control plots (figure 5, table 5).

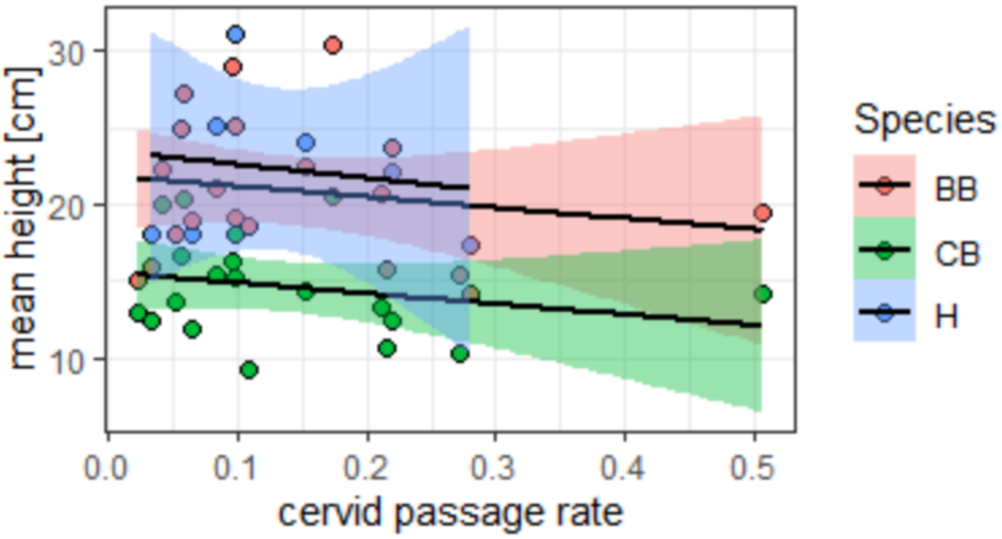


Figure 4.Relationship between mean top height of bilberry (BB, pink), cowberry (CB, green), and heather (H, blue) and cervid passage rate in two study sites in northern and central Sweden.

Table 4.Relationship between top ramet height (mean cm per stand) of three ericaceous shrub species (bilberry, cowberry, and heather) and cervid passage rate (linear regression model). Data was collected in northern and central Sweden during the growing season of 2020. The passage rate was estimated using camera traps. Cervid species included were roe deer, fallow deer, red deer, and moose.

	Bilberry height [cm]		**Cowberry height [cm]**		**Heather height [cm]**	
Coeffcient	*Estimates*	*P-Value*	*Estimates*	*P-Value*	*Estimates*	*P-Value*
Intercept	21.87	**<0.001**	15.55	**<0.001**	23.46	**0.002**
Cervid passage rate	-7.01	0.461	-6.84	0.331	-8.84	0.734
Observations	20		19		7	

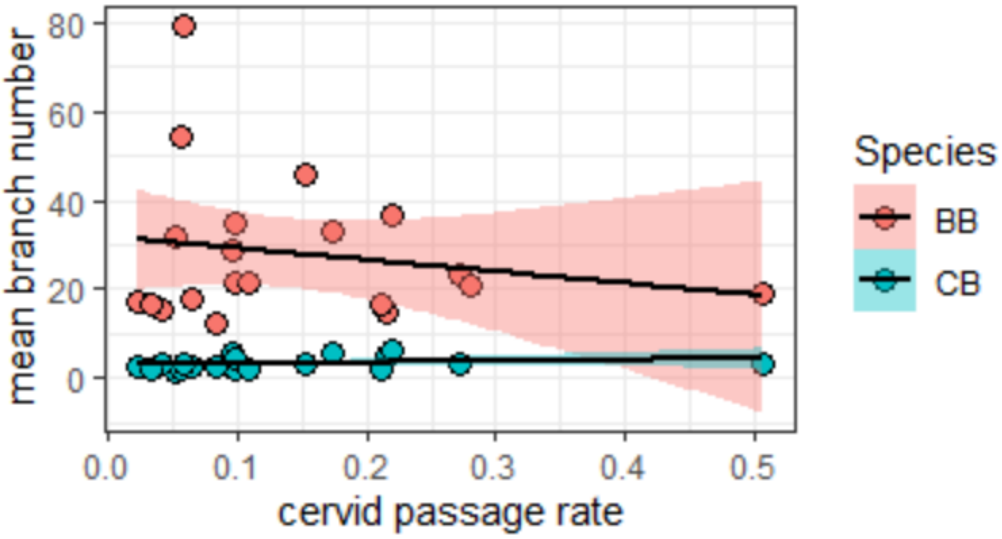


Figure 5.Relationship between the mean number of branches of bilberry (BB; pink), and cowberry (CB; blue) and cervid passage rate in two sites in northern and central Sweden.

Table 5. Relationship between the number of branches (mean number per stand) of two ericaceous shrub species (bilberry and cowberry) and cervid passage rate (linear regression model). Data was collected in northern and central Sweden at the end of the growing season of 2020. The passage rate was estimated using camera traps. Cervid species included were roe deer, fallow deer, red deer, and moose.

	Bilberry branch nr		**Cowberry branch nr**	
Coeffcient	*Estimates*	*P-Value*	*Estimates*	*P-Value*
Intercept	31.80	**<0.001**	2.87	**<0.001**
Cervid passage rate	-26.32	0.427	3.03	0.281
Observations	20		19	

3.2. Landscape survey: Forestry-related variables as predictors of annual growth of ericaceous shrubs in Sweden

The landscape survey analyzed the annual growth fractions of bilberry, cowberry, and heather in relation to the forestry-related variables dominant tree species, basal area, stand age/time since clear-cutting, and C/N ratio.

3.2.1. Bilberry

The annual growth fraction of bilberry was negatively associated with both increasing basal area per plot (figure 6A), as well as by increasing time after clear-cutting (stand age) (figure 6B). However, it was only in spruce-dominated forests where the effect was significant (table 6). At the lowest basal area and the earliest time point tested, the annual growth fraction was higher in spruce-dominated stands than in pine-dominated stands.

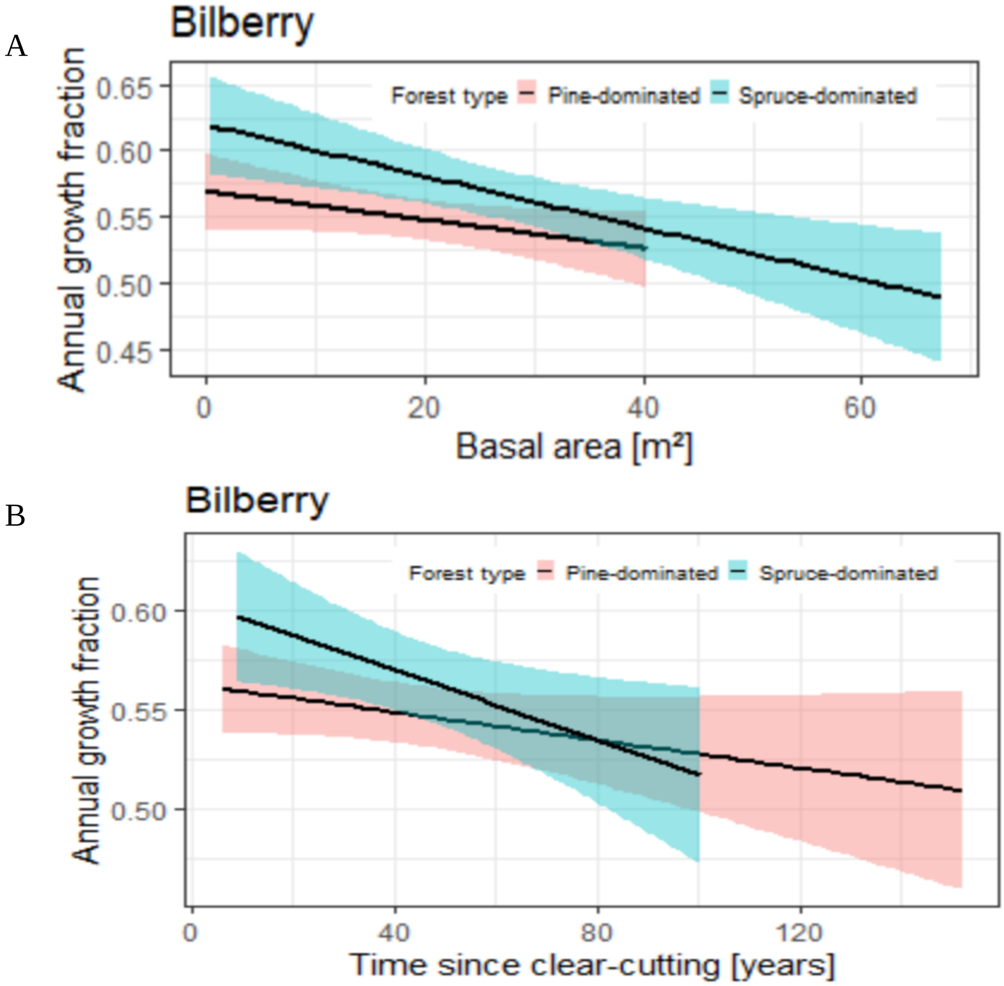


Figure 6.Annual growth fraction of bilberry over A: basal area and B: time since clear-cutting in pine- (pink) versus spruce- (blue) dominated forests in Sweden.

Table 6. GLMMs for the response of the annual growth fraction of bilberry to different explanatory variables. For each model, estimates and p-values are given for each variable included in the model.

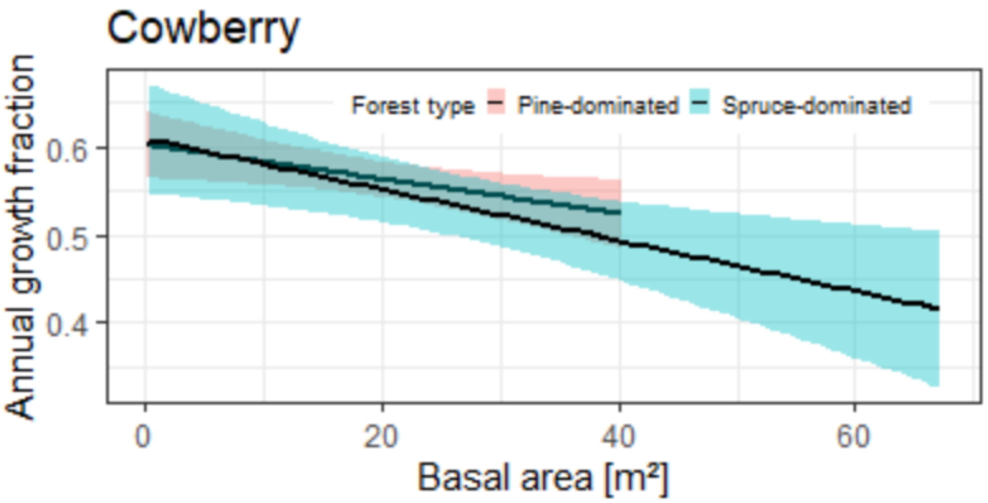
Bilberry

	Model incl. basal area		**Model incl. age**	
Variables	*Estimates*	*P-Value*	*Estimates*	*P-value*
Intercept	0.302	0.021	0.189	0.128
dom. tree species (Spruce)	0.208	**0.026**	0.177	**0.047**
Pine*basal area	-0.004	0.102		
Spruce*basal area	-0.007	**<0.001**		
Pine*Age			-0.002	0.128
Spruce*Age			-0.004	**0.006**

3.2.2. Cowberry

The annual growth fraction of cowberry was negatively associated with both increasing basal area per plot (figure 7A) and by increasing time since clear-cutting (figure 7B) in spruce-dominated stands. In terms of basal area, both pine and spruce-dominated forest stands show a significant effect on the annual growth fraction of cowberry (table 7). For the time since clear-cutting (age), this effect is significant only in spruce-dominated forests.

A



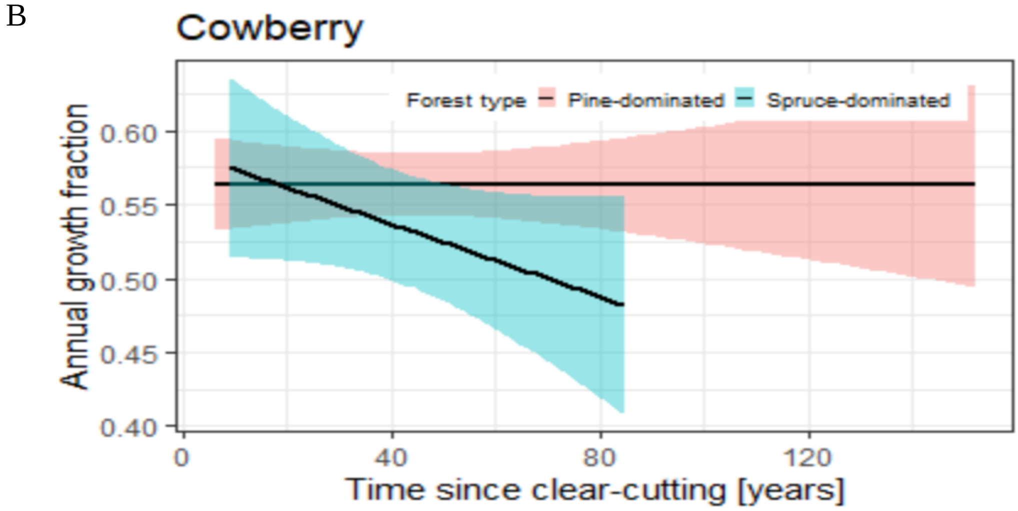


Figure 7. Annual growth fraction of cowberry over A: basal area and B: time since clear-cutting in pine- (pink) versus spruce- (blue) dominated forests in Sweden.

Table 7. GLMMs for the response of the annual growth fraction of cowberry to different explanatory variables. For each model, estimates and p-values are given for each variable included in the model.

Cowberry

	Model incl. basal area		**Model incl. age**	
Variables	*Estimates*	*P-Value*	*Estimates*	*P-Value*
Intercept	0.36	0.070	$2.586e^{-01}$	**0.001**
dom. tree species (Spruce)	0.036	0.796	$8.551e^{-02}$	0.550
Pine*basal area	-0.008	**0.043**		
Spruce*basal area	-0.012	**<0.001**		
Pine*Age			$-8.757e^{-05}$	0.951
Spruce*Age			$-4.992e^{-03}$	**0.037**

3.2.3. Heather

Both basal area per plot (figure 8A) and time since clear-cutting (figure 8B) were significantly associated with the annual growth fraction of heather. The effects, however, had opposing directions when comparing pine- versus spruce-dominated forest stands. In pine-dominated stands, the increasing basal area had a significant negative effect on the annual growth fraction, whereas there was a significant positive effect in spruce-dominated stands (table 8). Similarly, time since clear-cutting (here: age) had a significant negative effect on the annual growth fraction in pine stands, whereas it had a significant positive effect in spruce-dominated stands (table 8). Furthermore, at a low basal area (<10m²) and little time since clear-cutting (<20 years), the annual growth fraction was higher in pine- than in spruce-dominated stands. Note that we did not find heather in spruce stands older than 49 years.

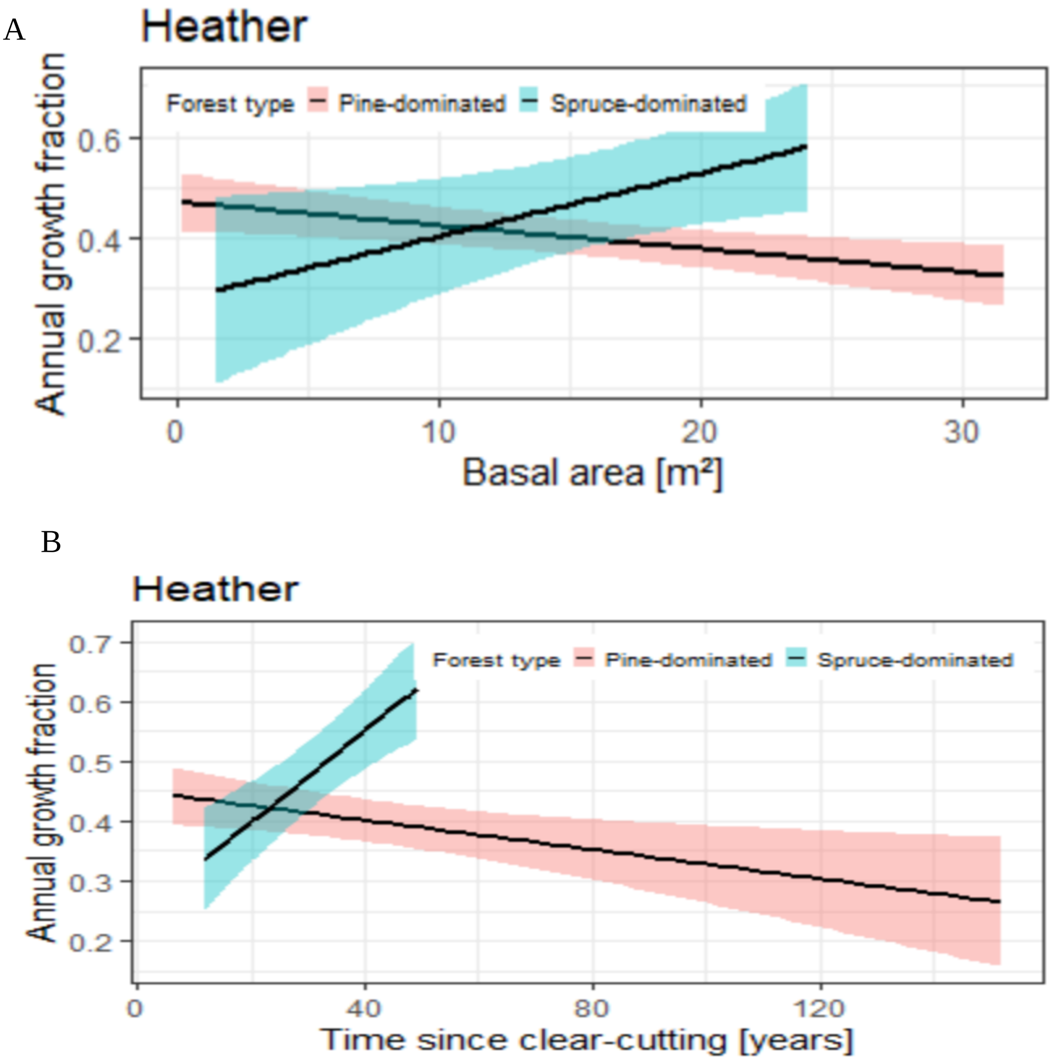


Figure 8. Annual growth fraction of Heather over A: basal area and B: time since clear-cutting in pine- (pink) versus spruce- (blue) dominated forests in Sweden.

Table 8. GLMMs for the response of the annual growth fraction of heather to different explanatory variables. For each model, estimates and p-values are given for each variable included in the model.

Heather

	Model incl. basal area		**Model incl. age**	
Variables	*Estimates*	*P-Value*	*Estimates*	*P-Value*
Intercept	-0.007	0.988	-0.260	0.550
dom. tree species (Spruce)	-0.849	**0.013**	-0.831	**0.006**
Pine*basal area	-0.020	**0.001**		
Spruce*basal area	0.052	**0.002**		
Pine*age			-0.005	**0.005**
Spruce*age			0.031	**<0.001**

3.2.4. C/N ratio of pine- or spruce-dominated forest stands

The C/N ratio of the soil samples taken at all plots differed between pine- and spruce-dominated forest stands. In pine-dominated stands, the C/N ratio is significantly (p= 0.012) higher than in spruce-dominated stands in the areas tested (Vindeln, Siljansfors, and Asa) (figure 9). Both the carbon and the nitrogen percentage are significantly higher in spruce-dominated stands (table 9).

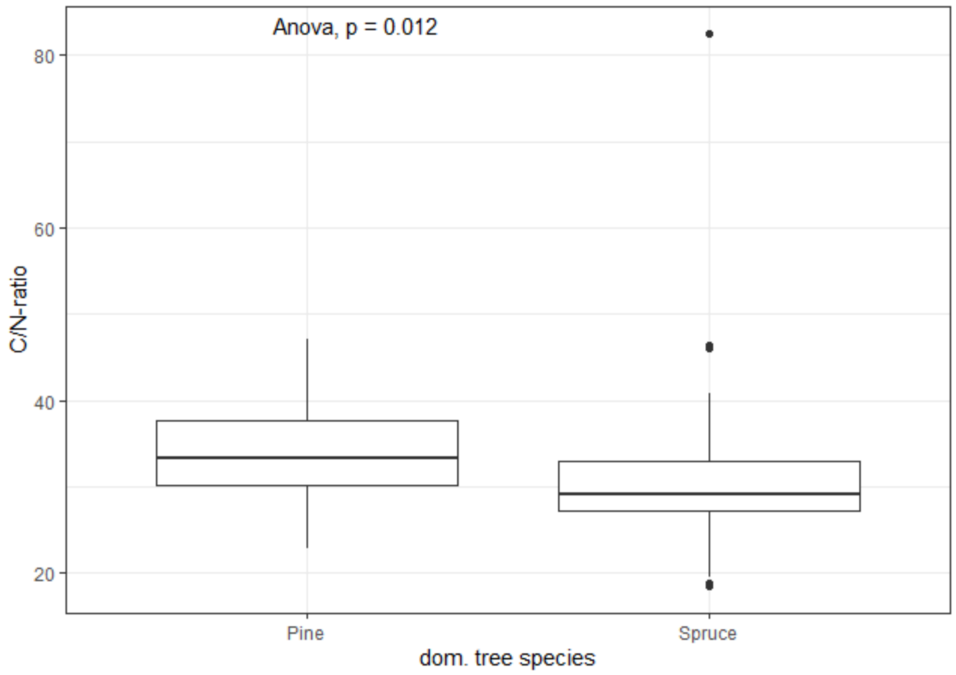
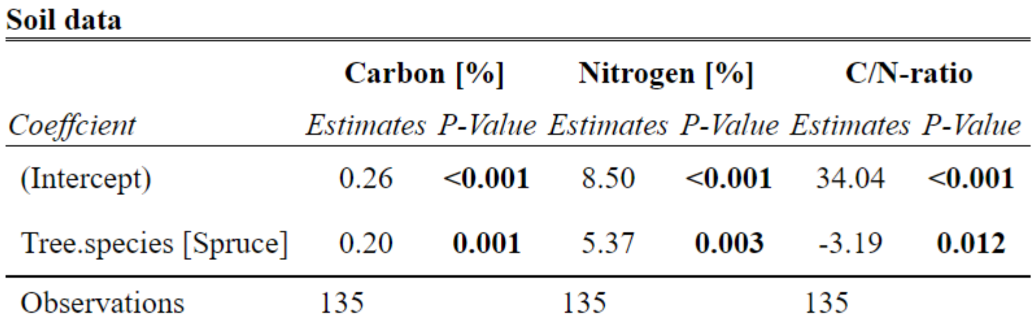


Figure 9. C/N ratio in the soil over forest stands dominated in Scots pine or Norway spruce.

Table 9. Differences in carbon and nitrogen percentage and ratio between spruce and pine-dominated forest stands in three sites across Sweden.



Soil data

	Carbon [%]		**Nitrogen [%]**		**C/N-ratio**	
Coeffcient	*Estimates*	*P-Value*	*Estimates*	*P-Value*	*Estimates*	*P-Value*
(Intercept)	0.26	**<0.001**	8.50	**<0.001**	34.04	**<0.001**
Tree.species [Spruce]	0.20	**0.001**	5.37	**0.003**	-3.19	**0.012**
Observations	135		135		135	

4. Discussion

The key findings of this study were that the annual growth of the three ericaceous shrub species was strongly influenced by basal area and time since clear-cutting, especially in spruce-dominated forests, whereas no significant influence could be assigned to browsing pressure of local moose and small deer. Plant morphological traits also seem unaffected by cervid browsing. This means that my hypotheses about forestry-related factors can be accepted, while I have to reject my hypotheses about the impact of cervid browsing.

4.1. The exclosure study

The importance of the forest floor vegetation for browsers like small deer and moose is well established, with both macroscopy of moose rumen samples and DNA-metabarcoding of faecal samples from deer and moose proving a high proportional presence of ericaceous shrubs in the diet of Swedish browsers (A. M. Felton et al., 2020; Spitzer et al., 2021). There is also growing evidence of direct and indirect effects of herbivores on plants. For example, plant growth may be impaired due to browsing or trampling, or growth may be accelerated by nitrification of the soil with dung and urine (Hobbs, 1996). Some plants may even benefit from tissue removal as a way of growth stimulation (Owen, 1980). A study from Maschinski and Whitham (1989) shed light on the plasticity of plant responses to herbivory depending on context and plant species. Despite these findings, the exclosure study could not identify any correlations between browsing pressure and annual growth, top height, or the number of branches of ericaceous shrubs.

As figure 3 shows, the annual growth of the 2020 growing season is not only the same within and outside of the cervid exclosures for all plant species, but it is also unchanged between study stands with different cervid densities. This means that in my study, cervid browsing does not affect the annual growth of the plant species of interest over one growing season. Similarly, cervid passage did not show any effect on plant morphological traits (height and branch number).

To discern why cervid presence did not affect plant growth, it has to be taken into account that this data only provided ramet samples over one growing season. Several research efforts have given evidence for seasonal feeding differences in small deer and moose. For example, a study by Cederlund and Nyström (1981) discovered that roe deer has a seasonal adaptation of its rumen, making it digest woody plant species better in winter while feeding more on forbs in summer. Additionally, Spitzer et al. (2021) further revealed that competition over *Vaccinium* shrubs is lower in summer when smaller deer can feed on grasses and other foods that may not be available in snowy winters. They also showed that while moose had a stable, low consumption of *Vaccinium* shrubs all year round, dwarf-shrub consumption peaked in winter and early spring for the three small deer species. Despite not observing an effect of summer browsing on the plants' growth and morphology, there may well be a stronger effect in winter, when feeding competition is higher due to depletion of other food sources. Future studies could also include information about the wider context of each forest stand, such as surrounding crop fields or presence of feeding stations to account for the availability of alternative food sources.

Nevertheless, this part of the study may confirm findings from studies carried out in Sweden by Angelstam et al. (2017) and Persson et al. (2005) respectively. The former found that while deer herbivory affected deciduous tree recruitment negatively, the field layer volume was not correlated with deer index based on pellet counts and body mass. They hypothesized that heather and bilberry may not be greatly affected because they play an important role as a food source for only a limited time period annually. The latter research team revealed that forage plants may be well adapted to low to medium levels of browsing, as the annual growth of pine trees only suffered when simulated moose browsing was high, following a threshold model.

Recent assessment shows that camera trap pictures and dung pellet counts tell the same story when comparing the impact of deer occurrence on the forest floor vegetation (Sayn, 2021). Nevertheless, it has to be taken into account that this study assumes that a higher cervid passage rate recorded by the camera traps is correlated with higher browsing pressure experienced by the ericaceous shrubs in the sampling plots. As pointed out by Burton et al. (2015), assumptions about the links between relative abundance measured by the camera traps and ecological processes, such as foraging, might be a source of error. Instead, they suggest a specification of the assumptions that need to be fulfilled in order to draw these connections.

Therefore, I can conclude that cervid browsing does not affect the annual growth of dwarf shrubs over summer, at least under the levels of browsing experienced in this study. To draw conclusions for a whole year, more research is needed spanning a longer time period to capture seasonal variation.

4.2. The landscape survey

Another important aspect that is indirectly driven by cervid browsing is the conversion of pine to spruce stands in Swedish production forests after clear-cutting, especially in the south. Spruce trees have similar rotation lengths (spruce: 45-90 years; pine: 60-90 years) and can be grown under similar conditions as pine, although spruce is preferably grown on more fertile soil, whilst pine does well on poor to intermediate soil (A. Felton et al., 2020). Above all, young spruce trees are significantly less prone to browsing damage (A. Felton et al., 2020). However, several studies have found negative effects of a conversion of a pine-dominated to a spruce-dominated landscape, for example on biodiversity, ecosystem services (A. Felton et al., 2020) and understory vegetation (Petersson et al., 2019). This made a separation of my results into pine or spruce stands relevant.

Pine-dominated and spruce-dominated forests showed different patterns with regards to the relationship between basal area and time since clear-cutting, and the annual growth fraction of bilberry, cowberry, and heather. In general, basal area and time since clear-cutting had a more negative effect in spruce-dominated forests for bilberry and cowberry. These results give additional support to Petersson et al. (2019) who found that members of the *Vaccinium* genus were especially negatively impacted by replacing pine with spruce forests. They also measured the light transmission related to basal area and found that pine had a significantly higher light transmission to the forest floor compared to spruce for the same basal area. Strikingly, only in spruce forests, light availability had a positive effect on understory abundance in their study. This could explain why in my study, basal area had no significant effect on the annual growth fraction in bilberry, and only little effect on cowberry, in pine stands. Possibly, even in dense pine forests with a high basal area, light transmission is sufficient for the growth of the *Vaccinium* dwarf shrubs. Similarly, time after clear-cutting shows the same pattern as basal area since over time the canopy will close up and allow less light to reach the understory.

For heather, the pattern was inverted, with basal area and time since clear-cutting negatively affecting the annual growth fraction only in pine-dominated forests, and positively affecting it in spruce-dominated forests. Interestingly, heather samples were only found up until a basal area of around 30 m^2 per plot in pine-dominated stands, and even at a lower basal area in spruce-dominated stands whilst both bilberry and cowberry are found until a basal area of over 60 m^2. This gives support to Ritchie (1955, 1956), who compared the shade tolerance of bilberry, cowberry, and heather. He found that both bilberry and cowberry were much more shade tolerant than heather and were thus outcompeting heather at higher shade levels. He also concluded that bilberry and cowberry performed best in pine-dominated forests, which supports my findings. Furthermore, heather annual growth fraction declining with age in pine-dominated stands and not existing at all in spruce-dominated stands above 49 years of age supports the finding of Mohamed and

Gimingham (1970). They showed that the capacity of heather to regenerate vegetatively declines with age. This statement, however, assumes that the ramet tested would have a similar age to the stand in general. The fact that in spruce-dominated forests, the trend of heather annual growth fraction is initially positive with increasing basal area or time since clear-cutting could also give support to Petersson et al.'s (2019) discovery that spruce forests host higher species richness, because light availability is the main determinant of coverage, whereas in pine-dominated forests competition mainly determines species occurrence. In pine stands, heather may be outcompeted rapidly over time by the *Vaccinium* shrubs and other plant species.

Another striking result is that the bilberry annual growth fraction was higher in young spruce-dominated than in young pine-dominated forest stands (figure 6). This is not true for cowberry, and the opposite pattern can be observed in heather. One way of interpreting this result could be linking it to the difference in soil nutrition between the two forest types (figure 9). Spruce-dominated stands have a significantly lower C/N- ratio, meaning that there is more nitrogen available in relation to carbon in the soil. Furthermore, spruce-dominated stands have significantly higher carbon and nitrogen levels compared to pine-dominated stands. This could explain why the annual growth fraction is initially higher in spruce stands, at least for bilberry. Differences between bilberry, cowberry, and heather find support in Hägglund and Lundmark (1977) who describe site fertility as a measure of site productivity. Out of the species I analyzed, they ranked bilberry-dominated sites as highly fertile, closely followed by cowberry-dominated and lastly heather-dominated sites. This pattern is the same observed in my analysis, where bilberry production is favored by higher nitrogen availability, cowberry is not as affected, and heather is negatively affected. To draw final conclusions, more investigation regarding the effect of nitrogen and carbon on bilberry productivity has to be done.

4.3. Improvements and future research

Despite the findings of my study being supported by some other studies, some details could be improved in the study setup and analysis. For example, using camera pictures to capture deer densities can entail weaknesses, such as a bias of detecting bigger species like moose at further distances than smaller ones like roe deer. This problem could be solved by including a measure referred to as *effective detection distance* as introduced by T. R. Hofmeester et al. (2017). When analyzing the camera trap footage, the distance at which each species is successfully triggering the camera is measured to include a variable of sensor sensitivity to the analysis. Other shortcomings of camera trap footage could include battery dependence, inability to identify the species in the pictures, or animals passing either outside of the range of the camera or failure of the camera to be triggered (T. R. Hofmeester et al., 2019).

In terms of models, the choice of using a proportion of annual growth to total biomass enabled a comparison between stands and sites but makes the outcome more difficult to interpret. An alternative would have been to harvest all ramets within a specified area unit, however, this would have been very time-consuming and beyond the aims of my project.

Considering the large climate gradient that this study includes, future analyses could also incorporate weather/climate data, such as precipitation, hours of sunlight per day, or snow cover in winter per stand to account for those differences in all models.

4.4. Conclusions

In conclusion, my study has given yet another piece of evidence that current forestry practices, such as dense plantations of spruce trees, have severe consequences for biodiversity and important ecosystem services. This is especially important in southern Sweden, where higher deer densities drive forest owners to increasingly plant spruce to avoid browsing damage on young production trees. Forest owners or policymakers should use these studies to make better informed decisions regarding the future of Swedish production forests. For example, the loss of understory vegetation could be decelerated by reducing the conversion of former pine plantations to spruce plantations. In agreement with Hedwall et al. (2013), more thinning, or planting of tree species with more light-transmissive crowns would favor the understory. This is crucial especially now since the Swedish Forest Agency (SFA) predicts that in the future more spruce will replace pine in southern Sweden (Claesson et al., 2015).

Additionally, as Hedwall et al. (2019a) state, due to its long history of forestry, Sweden is a useful model to predict future changes in other forests in the world that may encounter more anthropogenic pressure. This means that especially studies as large scale as this one spanning several climatic conditions can be useful for other countries too.

In the future, the outcomes of this study about productivity can be combined with results about quality (via nutritional analyses) and quantity (via predicting edible biomass) of ericaceous shrubs under different forest and game management types to build models that can project forage availability.

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Appendix 1

Table A1. *Start and end date of ramet collection in four sites across Sweden at the end of the growing season 2020.*

Site	Start date	End date
Asa	16/09/20	21/09/20
Siljansfors	07/09/20	13/07/20
Öster Malma	31/08/20	04/09/20
Nordmaling	15/08/20	25/08/20
Vindeln	09/08/20	20/08/20

Appendix 2

Table A2. *Camera operability in days per location and stand with exact dates during which cameras were active.*

Location	**Stand**	**Camera set-up**	**Camera pick-up**	**Camera operability in days**
Nordmaling	1	2020-05-18	2020-08-24	97.96
	2	2020-05-21	2020-08-25	95.87
	3	2020-05-22	2020-08-22	91.96
	4	2020-05-07	2020-07-18	71.79
	5	2020-05-08	2020-08-24	108.10
	6	2020-05-13	2020-08-24	103.19
	7	2020-05-12	2020-08-15	94.76
	8	2020-05-16	2020-07-06	50.70
	9	2020-05-15	2020-07-27	72.87
	10	2020-05-06	2020-07-05	59.79
Öster Malma	1	2020-04-25	2020-09-02	129.75
	2	2020-04-20	2020-09-03	136.16
	3	2020-04-08	2020-09-03	147.16
	4	2020-04-21	2020-08-31	131.99
	5	2020-04-21	2020-09-02	69.45
	6	2020-04-23	2020-07-31	98.89
	7	2020-04-28	2020-09-01	125.93
	8	2020-04-10	2020-08-31	142.85
	9	2020-04-20	2020-09-01	133.80
	10	2020-04-27	2020-09-04	129.88

Appendix 3

Table A3. Results of the linear models of three ericaceous shrub species (bilberry, cowberry, and heather) in northern and central Sweden. The response variable is the annual growth fraction of the plant species, and the independent variables are the cervid passage rate and plot (control versus exclosure). The passage rate was estimated using camera traps. Cervid species included were roe deer, fallow deer, red deer, and moose. Annual growth fraction was defined as the biomass produced during the last growing season.

	Bilberry		**Cowberry**		**Heather**	
Coefficient	*Estimates*	*P-Value*	*Estimates*	*P-Value*	*Estimates*	*P-Value*
Intercept	0.22	**0.004**	-0.10	0.452	*-0.26*	***0.044***
Cervid passage rate	0.07	0.915	0.83	0.203	*-0.17*	*0.782*
Plot (Exclosure)	0.01	0.844	0.05	0.748	*0.00*	*0.980*
Observations	40		38		*13*	

Appendix 4

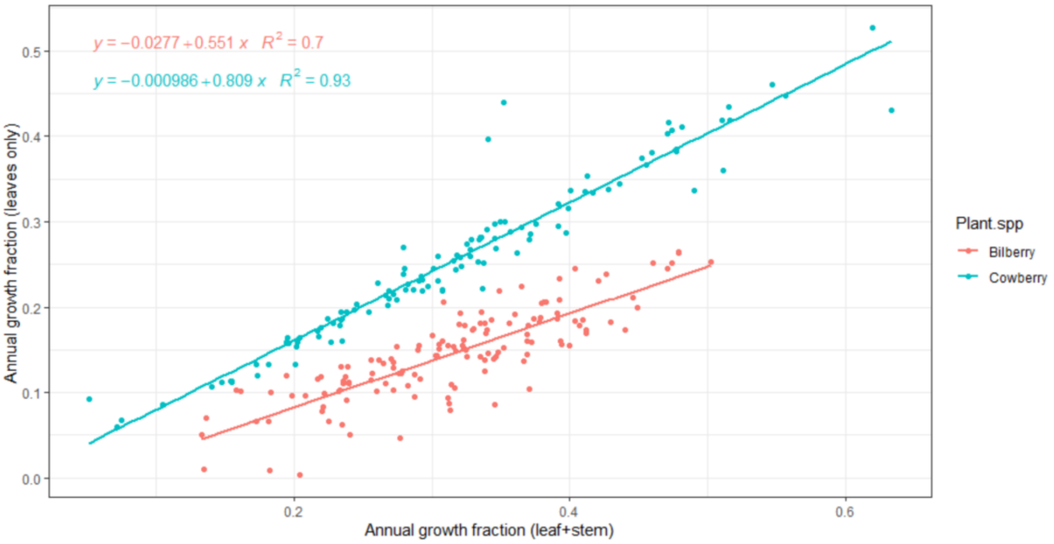

Figure A4. Annual growth fraction including leaves and stems is highly correlated to annual growth fraction only including leaves for both bilberry (red) and cowberry (blue). Formulas and R²values are indicated in the plot.