How do stand composition and cervid densities influence the forest floor vegetation in a multi-cervid species context?

Clémentine Leemans

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Abstract

The cover of forest floor vascular plants has been decreasing in Sweden over recent decades. Cervid rely heavily on this vegetation for food. With this study, I showed that habitat type highly influences the quality and quantity of the forest floor vegetation. In general, Scots pine forests (Pinus sylvestris) had a higher density of ericaceous shrubs (Vaccinium spp and Calluna spp; family Ericaceae) than Norway spruce forests (Picea abies), deciduous and mixed forests. Bilberry shrubs (Vaccinium myrtillus) found in Scots pine forests were taller. In accordance with previous studies done in Scots pine forests only, I observed across several different types of forests that bilberry shrubs were shorter in areas where fallow deer (Dama dama) were present at higher densities. But yearly shoots were longer in areas where moose (Alces alces) were present at higher densities. Norway spruce plantations had low abundance of ericaceous shrubs, grasses and forbs, deciduous forests also had low abundance of ericaceous shrubs but supported high abundance of grass and forbs. The decrease in forest floor cover that has been observed in Sweden is remediable with changes in the choices of forest type.

Keywords Alces alces, Cervus elaphus, Dama dama, Capreolus capreolus, cervid, Vaccinium myrtillus, Pinus sylvestris, Picea abies, browsing, forest floor cover

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1. Introduction

The numbers and distributions of different ungulates are increasing across Europe. This increase means that ecosystems that have multiple ungulate species, with partially overlapping diets, are becoming more and more common (Apollonio et al., 2010; Linnell et al., 2020). A better understanding of those interspecies interactions could be a key element in mitigating human-wildlife conflicts. For example to limit negative interactions with the forestry industry. Indeed, cervid browsing on Scots pine (*Pinus sylvestris*) can cause damage which prevents the plants from growing straight and being valuable for timber (Gill, 1992; Herfindal et al., 2015).

Ericaceous shrubs *(Vaccinium spp* and *Calluna spp;* family *Ericaceae)* also represent an important proportion of the cervid's diets. It is possible that competition occurring at the forest floor vegetation level is resulting in a change in the diet of moose (*Alces alces*) (Spitzer et al., 2020). Indeed, cervid herbivory can have a big impact on the biomass abundance (Tremblay et al., 2006), mean height and density of the forest floor vegetation (Speed et al., 2014). Smaller deer species that are often present at higher densities could be reducing the food availability for moose, forcing them to feed more on commercially important young trees (Spitzer et al., 2021). This means that ensuring high abundance of food at the forest floor layer could prove to be a more effective way of limiting cervid damage on Scots pine than just controlling cervid numbers.

1.1. Bite size hypothesis

Browsing by cervid can modify several aspects of the forest floor vegetation. High cervid densities can have a negative impact on the forest floor plant densities (Parlane et al., 2006; Tremblay et al., 2006) and biomass (Melis et al., 2006), especially in regenerating clear-cuts which can lead to a change in forest floor vegetation composition in the long term (Tremblay et al., 2006). Cervid can also influence the forest floor vegetation composition, for example by increasing the proportion of grasses and sedges (Gill, 1992), which moose only consume in very small quantities (Spitzer et al., 2020).

A lot of attention has been given to cervid foraging on trees but less so on ericaceous shrubs when they actually represent an important part of their diets (Spitzer et al., 2020). Herbivore feeding behaviour can be influenced by different aspects of forage availability. Those can be either plant density within the landscape, shoot density per individual plant or available bite size (i.e., length of shoots thinner than 4 mm in diameter) (Gross et al., 2017). A study done in Finland on bilberry (*Vaccinium myrtillus*) bushes showed that after different levels of branches harvesting by humans, the number of new shoots produced afterwards did not differ in number between the different treatments but the dry weight of the new shoots did decrease progressively as the harvesting increased (Tolvanen et al., 1994).

In the case of moose, it could actually be the size of available bilberry shoots that is driving them away from areas where smaller species of cervid are present at higher densities.

Indeed, in winter, moose, red deer and roe deer largely overlap in the tree species they feed on, but moose have been shown to browse on larger diameter tree twigs than red deer and roe deer (Nichols et al., 2015). Also, in a controlled experiment where varying numbers of tree shoots were placed at different distances, moose tended to select larger, less numerous bite sizes than smaller cervid species

especially when patch size and density decreased (Shipley, 2017). Moose could be dependent on bigger bite sizes to sustain a higher daily food intake, which is needed due to their larger body size (Nichols et al., 2015).

Forest types also controls the structure of bilberry shrubs (Tolvanen, 1995), by modifying the height of the shrubs, the length and weight of the shoots, the number of shoots that each shrub produce (Maubon et al., 1995; Woziwoda et al., 2019). This is due to varying levels of light availability, temperature and soil pH under stands of different composition.

The type of forest, as well as the cervid densities, influence the height of bilberry bushes, their densities and the length of the yearly shoots. This could in turn influence moose behaviour and create competition between the different cervid species.

1.2. Forest type

The composition of the forest floor vegetation and thus cervid forage availability varies with habitat (Bjørneraas et al., 2011; Härkönen and Heikkilä, 1999). Studies have shown that dwarf shrubs, eudicotyledons in general and grasses are more abundant under Scots pine forest than Norway spruce forest (*Picea abie*s), resulting in more food resources for herbivores (Bäcklund et al., 2015; Miina et al., 2009; Petersson et al., 2019). Vascular plant biodiversity however is higher under Norway spruce (Petersson et al., 2019). In North America, a decline in the quantities of shrubs over the last 30 years as well as varying current availability has been shown to be correlated with decreasing numbers in the moose population (Schrempp et al., 2019).

Scots pine forests in Sweden are increasingly being replaced with Norway spruce. This change can have an impact on the forest floor layer composition (A. Felton et al., 2020), which in turn can impact cervids that feed on those plants. The reduced plant cover in Norway spruce forest understory can be explained by the fact that, at similar age and stem densities, light availability is much lower under Norway spruce forest than under Scots pine. Comparing the effect of tree species on the forest floor vegetation has mainly been done between Norway spruce and Scots pine forests as they represent over 80% of Sweden's commercial forests. However, deciduous trees such as oak (*Quercus robur*), beech (*Fagus sylvatica*) and birch (*Betula spp.*) are often mixed within coniferous forests in the south of Sweden, and their effect on the forest floor vegetation is less well studied (Hedwall et al., 2016).

Numerous other factors of course also influence the abundance and composition of the forest floor layer, such as forest age, tree density (Hedwall et al., 2013), the forest regeneration method (e.i., clear-cut or not), soil type (Miina et al., 2009), canopy coverage (Bäcklund et al., 2015; Parlane et al., 2006) and previous land use (Petersson et al., 2019).

The effect on the forest floor vegetation of deciduous trees mixed within coniferous forests however is uncertain. Some studies show that it could have a negative impact on abundance (Miina et al., 2009), while others show that mixed forests could have a positive effect on biodiversity (Cavard et al., 2011). Some authors suggest that this increase in biodiversity and coverage could be due more to the decrease in canopy coverage which leads to an increase in the amount of light that reaches the ground rather than purely to the added broadleaf tree species (Cavard et al., 2011; Hedwall et al., 2019).

1.3. Aim

The aim of this study was to assess how the height of bilberry bushes as well as their yearly shoot lengths vary depending on different habitats and to varying densities of four cervid species: moose, red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and roe deer (*Capreolus capreolus*).

The difference in abundance of key food items for those cervid between several forest habitat types was also investigated.

2. Material and methods

2.1. Site description.

The study took place in Södermanland county, north of Nyköping, in Sweden. It is at an elevation of 50 metres above sea level, receives on average 615 mm of precipitation per year and has a mean annual temperature of 7 ° C (SMHI, 2021).

The study area is in the hemiboreal vegetation zone (Ahti et al., 1968). The landscape is dominated by a mix of farmland and productive forests, with farmland covering about 40% of the surface. The dominating tree species are planted Norway spruce (hereafter spruce) and Scots pine (hereafter pine) but deciduous trees such as oak, beech, alder (*Alnus glutinosa*), aspen (*Populus tremula*), rowan (*Sorbus spp.*) and birch also occur (Pfeffer, 2021). The forest floor vegetation is composed mainly of forbs, grasses and ericaceous shrubs such as bilberry, cowberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*).

Four cervid species are present in the area: moose, red deer, fallow deer and roe deer. Moose, red deer and roe deer are native to Sweden while fallow deer were introduced through large estates. They have a low dispersion capacity which leads to them having a fragmented but locally very dense population (Apollonio et al., 2010). Harvest levels (number of animals hunted yearly in the area per 1000 hectares) differ greatly among the four cervid species in the study area (table 1).

Table 1: Harvest per 1000 hectares providing a density index for the area. Älgförvaltningsområde (ÄFO) 1 in Södermanland, Sweden

fallow deer	70
moose	1.1
red deer	2.25
roe deer	4.57

Data extracted from: https://rapport.viltdata.se/statistik/

2.2. Data collection

Data was collected along transects. Transect started near the centre of 1 by 1 kilometre squares on which pellet recordings are taken yearly by the Beyond Moose research project. The sites (start of the transects) were placed approximately 3 kilometres apart, placed in a grid (figure 1). The transects were 500 metres long and were directed in the four cardinal directions from the centre of the squares. Three types of measurements were taken along them: forage availability, bilberry height and pellet counts.

Three rounds of measurements were performed in 2020. The first round of measurements was carried out in April, and all three types of measurements were taken. The second round was carried out in May and June, measuring bilberry height and pellet counts. The third round was carried out in July and August, measuring forage availability and bilberry height. As we only measured about half of the sites in April, the data collected during that month was not used here.
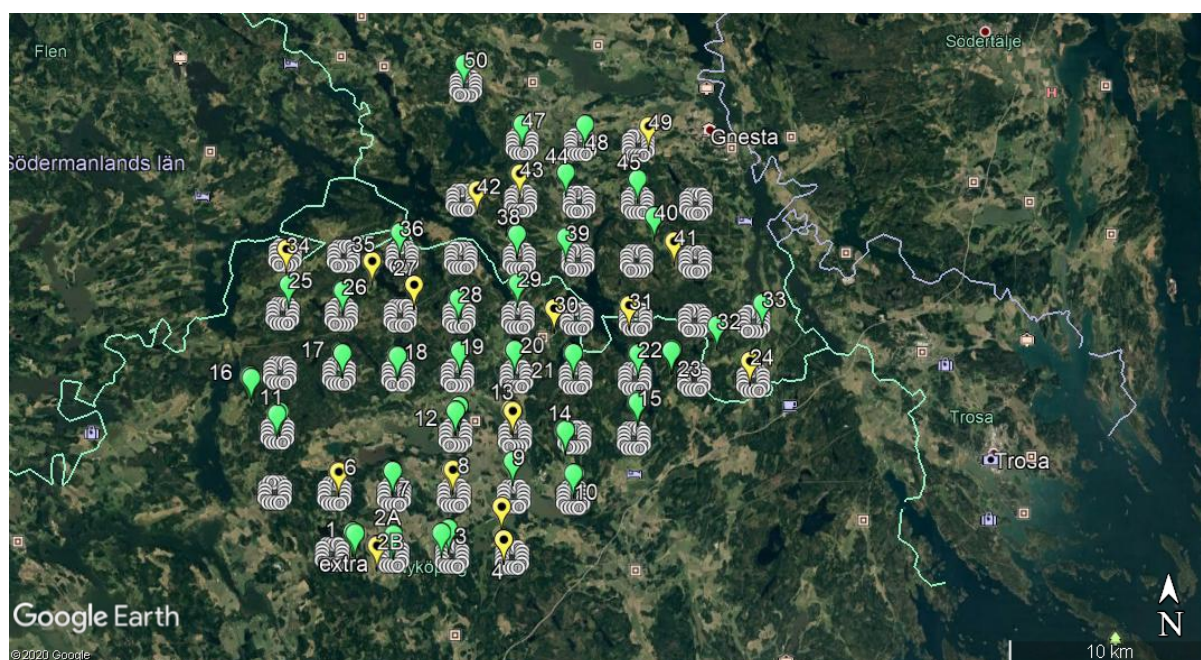
Figure 1: Map of the study area, showing the grid disposition of the square transects. The green and yellow pins show the start of the measurements transects (sites). The grey bullets placed in squares show the 16 point where pellet data was collected by the Beyond Moose research project.

2.2.1. Forage availability data collection

Food availability was measured using a modification of the step-point method (Coulloudon et al., 1999, Evans and Love, 1957) that allows for the quantification of food items. It shows great repeatability between samplers and is able to cover large areas (Evans and Love, 1957). Every 5 metres (paced off by steps) along the transects, a pole with a diameter of 2.5 centimetres was placed vertically on the ground and every living plant type that was touching it was recorded (table 2). Those food categories were chosen because they have been shown to be major food items used by the four cervid species. Habitat type, based on the environment within a 10 metre radius, was also recorded (table 3).

Table 2: Summary of the food types that were used in the analysis

Abbreviation	Food type[1]	Details
Srb	Ericaceous shrubs	Bilberry (*Vaccinium myrtillus*), Heather (*Calluna vulgaris*) and Cowberry (*Vaccinium vitis-idaea*)

1 *Plants in other categories were also recorded but only the ones that are of main interest as food resources for the cervids according to (Spitzer et al., 2021) were kept*

Fo	Forbs	Herbaceous plants that are not graminoids or cryptogams
Gf	Graminoid	Graminoids in forest
RASE	Rowan, Aspen, Willow and Oak	*Sorbus aucuparia, Populus tremula, Salix spp., Quercus robur* and *Quercus petreae*

Table 3: Summary of the different habitat types recorded, based on the environment within a 10 meter radius

Abbreviation	Habitat type	Details
Al	Agricultural land	Crops and grass fields
Ccp	Planted clear-cut	With seedlings up to three metres
Ccu	Unplanted clear-cut	Freshly cut or scarified land
Cfm	Mixed coniferous forest	Less than 70 % of pine and spruce respectively
Cfp	Coniferous forest of pine	Over 70 % of pine
Cfs	Coniferous forest of spruce	Over 70 % of spruce
Df	Deciduous forest	Over 70 % of deciduous trees
M	Mire	Includes different types of wetlands
Mf	Mixed forest	Less than 70 % coniferous and deciduous trees, respectively
U	Urban	Roads and habitations
W	Water	Lakes and rivers
E	Edges	Habitat that falls right between two of the previous habitats

2.2.2. Bilberry data collection

Bilberry shrub height and shoot length were measured every 20 metres along the transects. The height of the closest bilberry bush to the pole and within a 3.5 metre diameter from it was measured as well as the length of the longest shoot of the year present on the bush. If no bilberry bush was present in this diameter, the first bilberry bush within the next 20 metres was measured.

2.2.3. Pellet data collection

Two types of pellet data were used for my analyses. Firstly, data already collected by the research project Beyond Moose in March and April of 2020. This data was collected at 16 points along the 1 by 1 kilometre square transects. Secondly, data that I collected along the same transects as our other measurements, every 100 metres. In both cases, the dung piles were counted following the FOMA protocol (Edenius, 2012): roe deer and fallow deer dung piles were counted in a 1.78 m radius (10 m²) while moose and red deer were counted in a 5.64 m radius (100 m²). Piles were counted if they had more than 20 pellets for moose and more than 10 pellets for the other cervid. Fallow deer dung piles were differentiated from roe deer's by counting the number of individual pellets, over 45 being recorded as fallow and under 45 as roe.

2.3. Statistical analysis

The data was analysed in R version 4.0.5 (R Core Team 2021).

For the pellet count data collected by the Beyond Moose research project, sites where a minimum of 10 points out of the 16 had been sampled were selected. Indices for each of the four cervid species were calculated for the whole square tract by dividing the total number of piles counted by the area sampled. The indices of the pellet data that I collected, were calculated in a similar manner, albeit at the transect level.

For the bilberry shrub height analyses, the habitats that contained no or very few bilberry shrubs, such as urban areas and water bodies, were first removed. Seven different habitats were kept: planted and unplanted clear-cuts, mixed coniferous forests, pine forests, spruce forests, deciduous forests and mixed forests. Linear models with mixed effect were run with either the bilberry bush height or the length of the yearly shoot as the dependent variable, the habitat and the different cervid densities as the independent variables and the transects nested within the sites as random factors. This was performed with the lmer function in the lme4 package (version 1.1-27.1 (Bates et al., 2015)).

I initially tried to include measurement points where no bilberry shrubs were found within the habitats of interest, marked as zero in the analysis. This would have allowed to include a measure of density at the same time. However, this meant the model had a zero inflated distribution which proved to be complicated to analyse. A two part model could potentially be used to analyse the data in this way further, this consists in first a binary model followed by a model with a continuous distribution conditioned upon the result of the first model (Min and Agresti, 2002). However, this was deemed too complicated here. Therefore, for the rest of the analysis, the data points where no bilberry bushes were found were removed, to avoid having a zero inflated distribution.

A Tukey post-hoc test was carried with the glht function in the multcomp R package (version 1.4-17 (Hothorn et al., 2008)) to look further at the differences between the habitats.

As the intake of bilberry by the different cervid species varies during the year (Spitzer, 2019), the data collected in May-June was tested separately from the data collected in July-August. The same tests were completed in parallel on the pellet data that I collected and on the Beyond Moose project dataset (table 4).

Table 4: Summary of the linear mixed effect models performed. Eight different linear mixed effect models where used with varying collection period, source for the pellet data and dependent variable.

		Dependent variable	Explanatory variables	Random variable
May-June data	Pellet data collected by me	Bilberry height	Habitat, moose pellet index, red deer pellet index, fallow deer pellet index, roe deer pellet index	Transects nested within sites
		Yearly shoot length		
	Beyond Moose project pellet data	Bilberry height		
		Yearly shoot length		
July-August data	Pellet data collected by me	Bilberry height		
		Yearly shoot length		
	Beyond Moose project pellet data	Bilberry height		
		Yearly shoot length		

To evaluate the differences in abundance of the food types of interest between the different habitats a generalized linear mixed effect model was employed (glmer function in the lme4 package,version 1.1-27.1 (Bates et al., 2015)). With each food item of interest used in turn as the dependent variable. Habitat was set as the independent variable and the site as a random factor. The data was analysed under a binary form (Royle et al., 2003) and a Tukey post-hoc test was also used to look at the differences between the habitats (glht function in the multcomp package, version 1.4-17 (Hothorn et al., 2008)).

3. Results

The data was collected at 46 different sites. In May-June, 663 plots were surveyed for dung pellet piles, a summary of the number of pellet piles recorded can be found in table 5. 1885 bilberry bushes were also measured. In July-August, 1722 bilberry bushes were measured and 16001 plants from the four different food categories were recorded with the pole method.

Table 5: Summary of the number of plots surveyed as well as the number of pellet piles counted for each cervid species, including the pellet data that I collected as well as for the Beyond Moose project pellet data

	Plots surveyed	Fallow deer pellet piles	Moose pellet piles	Red deer pellet piles	Roe deer pellet piles
Pellet data collected by me	663	507	10	58	75
Beyond Moose project pellet data	655.75	427	111	53	82

Each forest habitat is present at different abundance within the landscape. Figure 2 shows the proportions of each of the habitats of interest within the study sites. Forests comprising of a mix of deciduous and coniferous trees were the most common. Purely deciduous forests were not very frequent while both types of clear-cuts considered together represented over ten percent of occurrences.
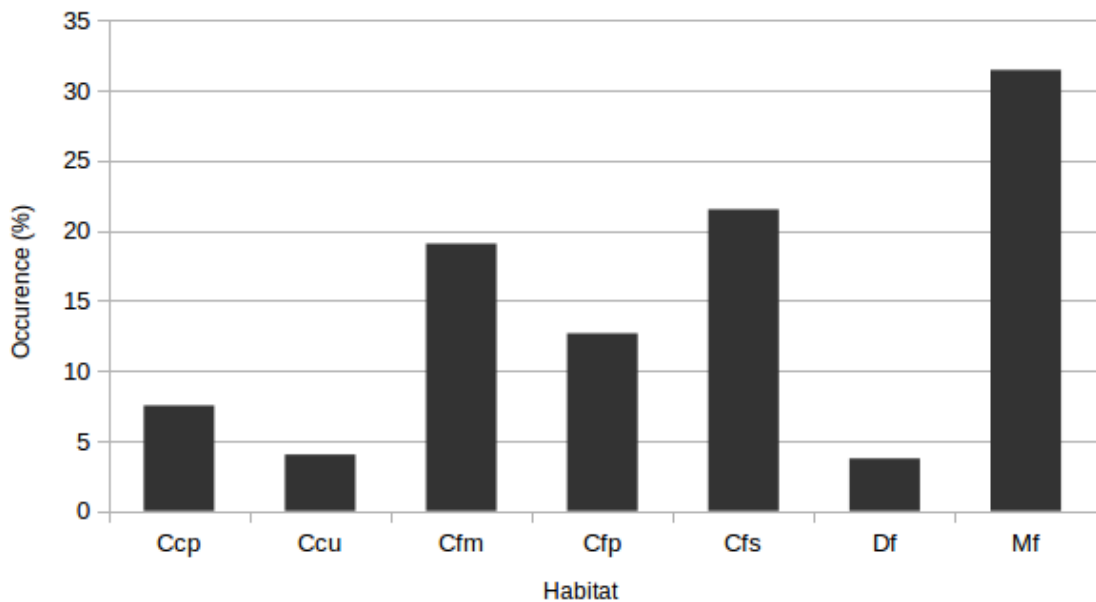
Figure 2: Proportions of occurrences of the different forest stands of interest. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

3.1. Bilberry height and shoot length

3.1.1. Relationship between bilberry characteristics and stand composition

A study of the generalized variance-inflation factors (appendix A5) for the linear mixed effect models showed that none were above the threshold value of two, which indicates that there was no significant multicollinearity between the different explanatory variable.

During both measurement periods, habitat type had a significant effect on the height of the bilberry bushes (table 6) and on the length of the yearly shoot (table 7).

Table 6: p-values of the linear mixed effect models made with bilberry height as the dependent variable

	Intercept	Habitat	Fallow deer index	Roe deer index	Moose index	Red deer index
May-June, Pellet data collected by me	< 2.2e-16 ***	6.64e-14 ***	0.002173 **	0.610331	0.409952	0.829242
May-June, Beyond Moose project	< 2.2e-16 ***	6.6472e-11 ***	0. 07305	0.43626	0.67990	0.02100 *
July-August, Pellet data collected by me	< 2.2e-16 ***	4.699e-12 ***	0.005162 **	0.312721	0.124685	0.333127

July August, Beyond Moose project	< 2.2e-16 ***	1.247e-08 ***	0.4443	0.1776	0.5687	0.1042

Table 7: p-values of the linear mixed effect models made with the length of the yearly shoot as the dependent variable

	Intercept	Habitat	Fallow deer index	Roe deer index	Moose index	Red deer index
May-June, Pellet data collected by me	< 2e-16 ***	< 2.2e-16 ***	0.2099	0.5824	0.1394	0.1427
May-June, Beyond Moose project	< 2.2e-16 ***	< 2.2e-16 ***	0.7866	0.1921	0.5806	0.1637
July-August, Pellet data collected by me	< 2.2e-16 ***	0.0002635 ***	0.0969722 .	0.5819716	0.6933939	0.6318997
July August, Beyond Moose project	< 2.2e-16 ***	0.001687 **	0.502346	0.644400	0.004756 **	0.631375

The subsequent Tukey post-hoc tests that were performed (appendix A1 and A2), showed that bilberry bushes in spruce forest have a similar height as in clear-cuts (figure 3). The tallest bilberry bushes are found in pine forest.

There was overall little difference between the bilberry heights in May-June and July-August (figure 3). The overall mean height in May-June was 13.51 centimetres and 13.36 centimetres in July-August. There were more significant differences between habitats with the bilberry height than with the shoot lengths (figure 3 and 4).

a)
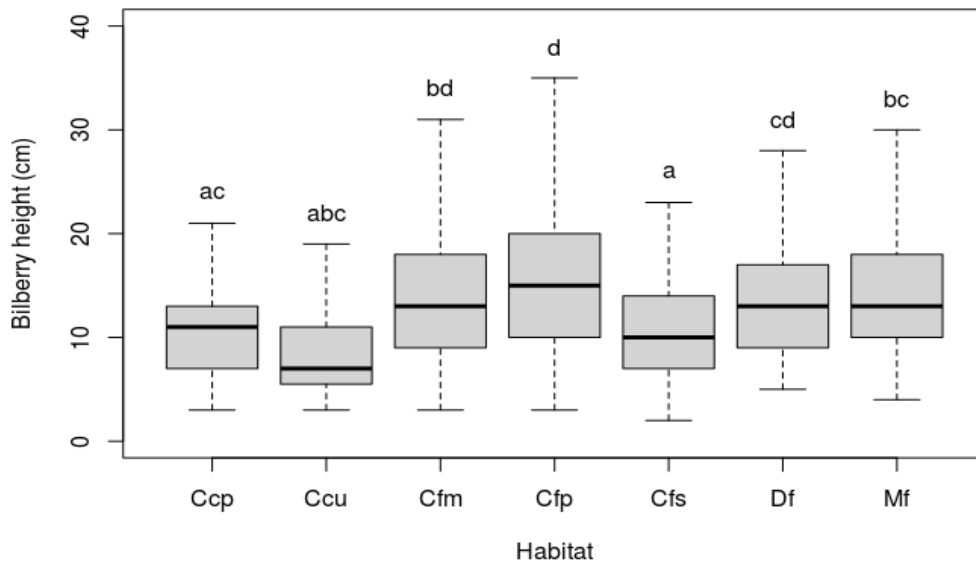
b)

Figure 3: Boxplot with Tukey test compact letter display showing the differences in height of bilberry bushes in different habitats. Habitats that have the same letter have no significant difference between them. In the boxplot, the boundary of the box indicates the 25 th percentile and 75 th percentile, the black line within the box marks the median and the whiskers below and above the box indicate the 2.5 th and 97.5 th percentiles. a) May-June measurements; b) July-August measurements. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

For the shoot lengths, however, the results of the Tukey post-hoc tests show that different patterns can be observed between the two measurements periods (appendix A3 and A4). In May-June, some differences in length can be observed between the different habitats (figure 4a), which have been much resorbed two months later (figure 4b). Shoots in clear-cuts show a big growth between May-June and July-August compared to the other habitats. In May-June (figure 4a), clear-cuts of both types present the shortest shoots; pine, mixed and mixed coniferous forest the longest, while shoots in spruce forests are of an intermediate length. In July-August (figure 4b), shoots measured in pine and mixed forests remain significantly longer than in spruce forests ($p < 0.001$ *** and $p = 0.001$ ** respectively). But shoots in spruce forest are no longer significantly longer than in clear-cuts.
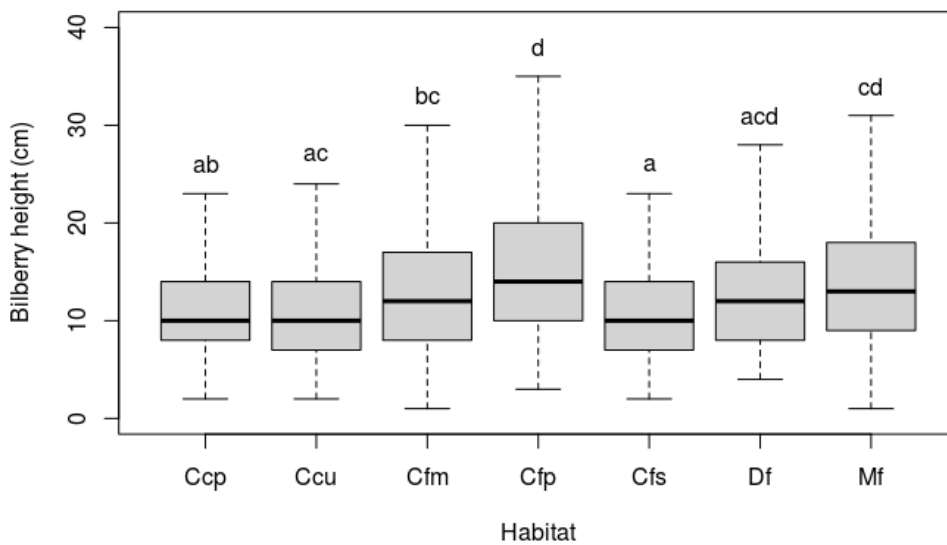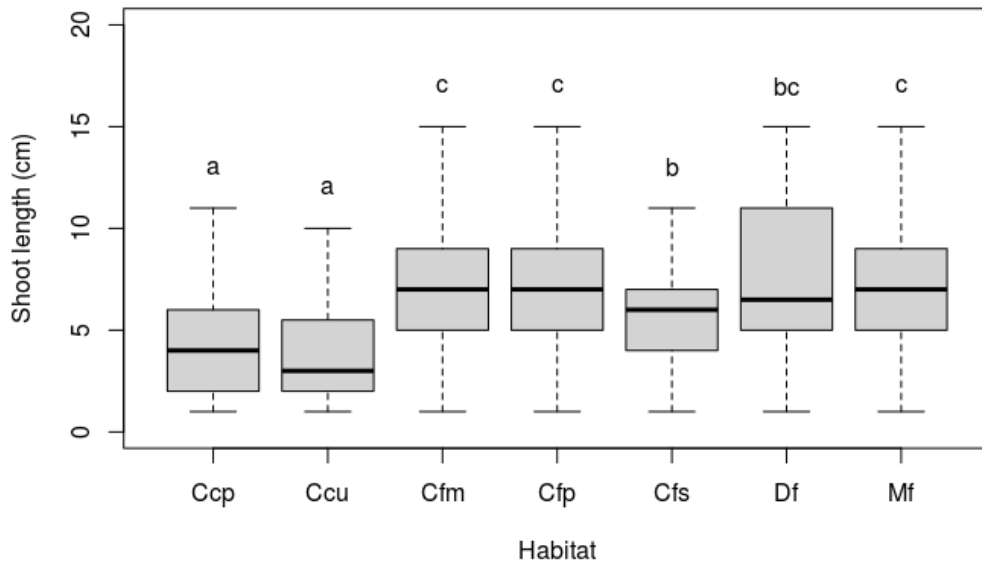
a)

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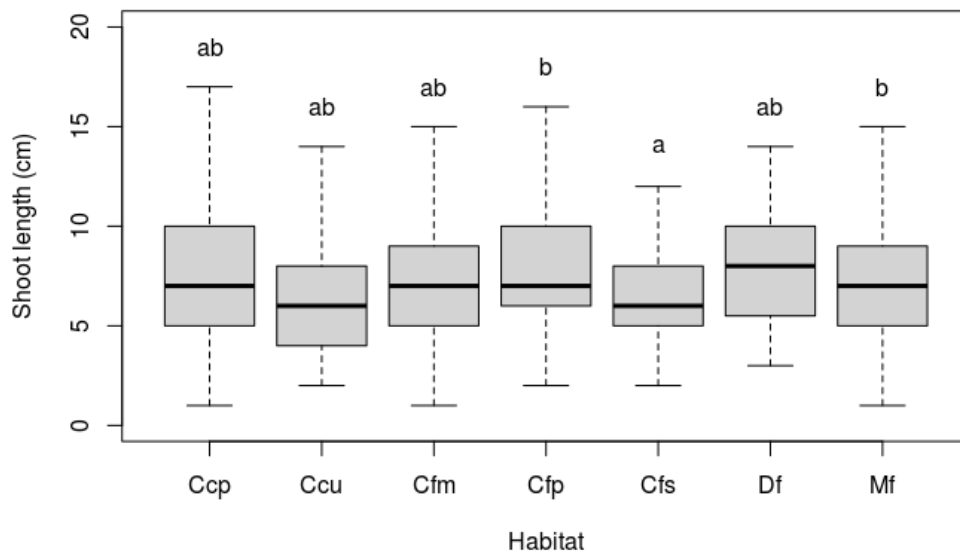
Figure 4: Boxplot with Tukey test compact letter display showing the differences in shoot length of bilberry bushes in different habitats. Habitats that have the same letter have no significant difference between them. In the boxplot, the boundary of the box indicates the 25 th percentile and 75 th percentile, the black line within the box marks the median and the whiskers below and above the box indicate the 2.5 th and 97.5 th percentiles. a) May-June measurements; b) July-August measurements. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

3.1.1. Relationship between bilberry characteristics and cervid density

As for the relationship that the different cervid species have with the bilberry height and shoot length: the linear mixed effect models showed that with the pellet data that I collected, for both the May-June and the July-August measurements, only fallow deer densities are significantly correlated with bilberry height (β = -1.0699 , p = 0.002 ** and β = -1.0188, p = 0.005 ** respectively), (table 6). In both cases, fallow deer densities are higher where bilberry shrubs are shorter (figure 5). The range in density detected was correlated with a variation in height from about twelve centimetres to five centimetres.

Figure 5: Negative relationship observed between fallow deer densities and the height of bilberry bushes. May-June measurements. The grey area represents a 95% confidence interval.

The results of the linear mixed effect models made with the Beyond Moose project pellets had two significant relationships (table 6 and 7). A positive relationship between the red deer index and the height of bilberry bushes in May-June (β = 9.9552, p = 0.021 *), (figure 6) and also a positive relationship between the moose index and the length of the longest yearly shoot (β = 5.658, p = 0.005 **), (figure 7). The density range for the red deer was correlated with a change in height of five centimetres whereas the moose was correlated with a change in shoot length of two centimetres.

There was no relationship between roe deer distribution and bilberry height or shoot length (tables 6 and 7).
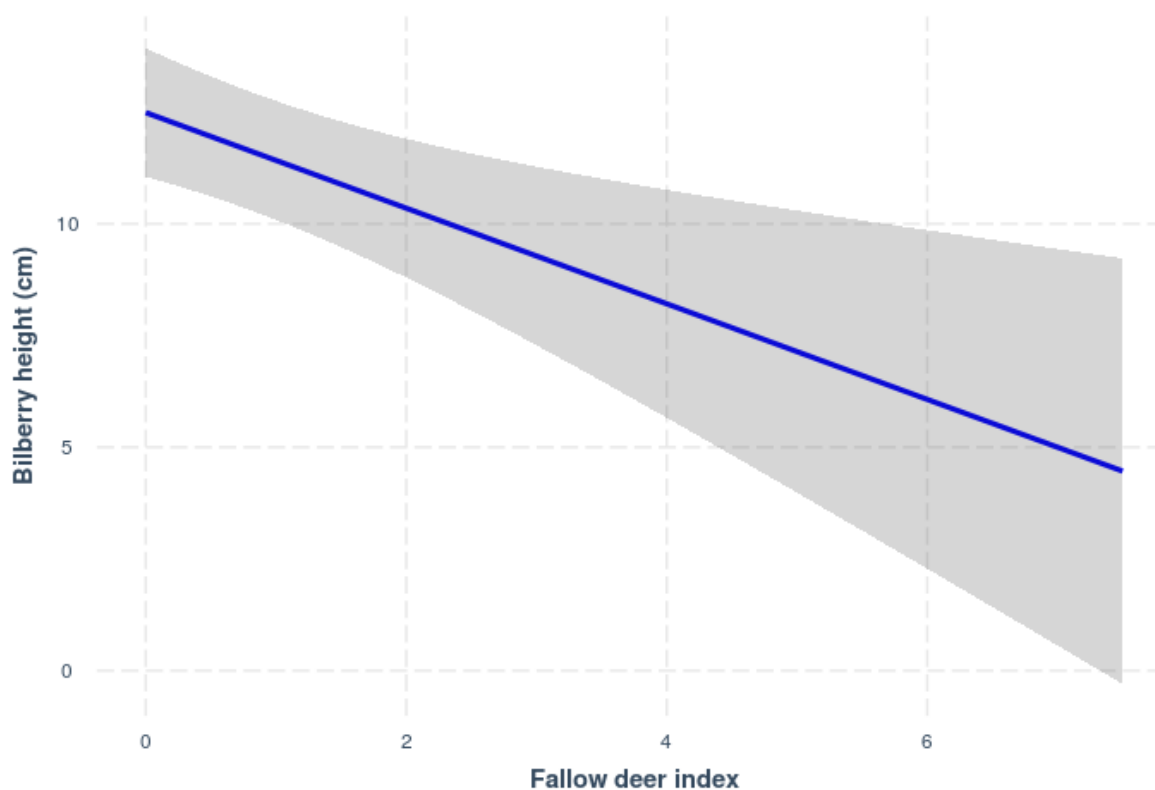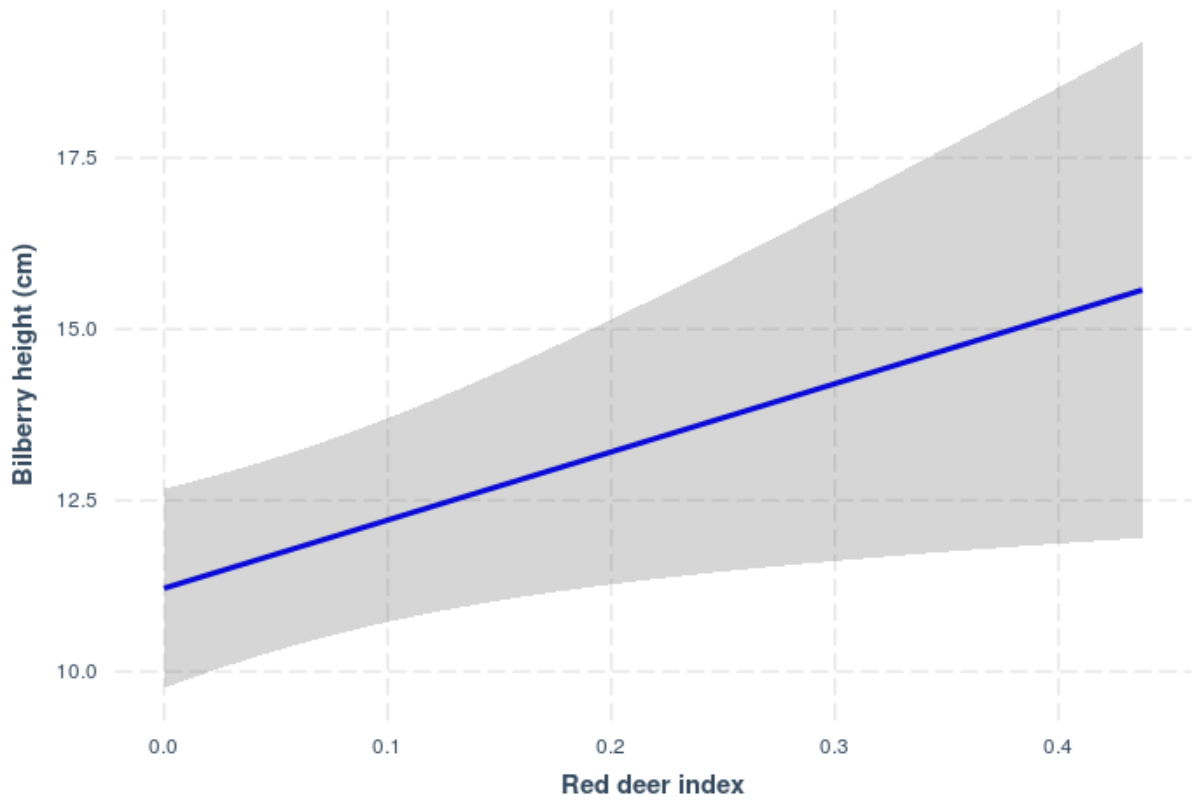
Figure 6: Positive relationship observed between red deer densities and the height of bilberry bushes. May-June measurements. The grey area represents a 95% confidence interval.
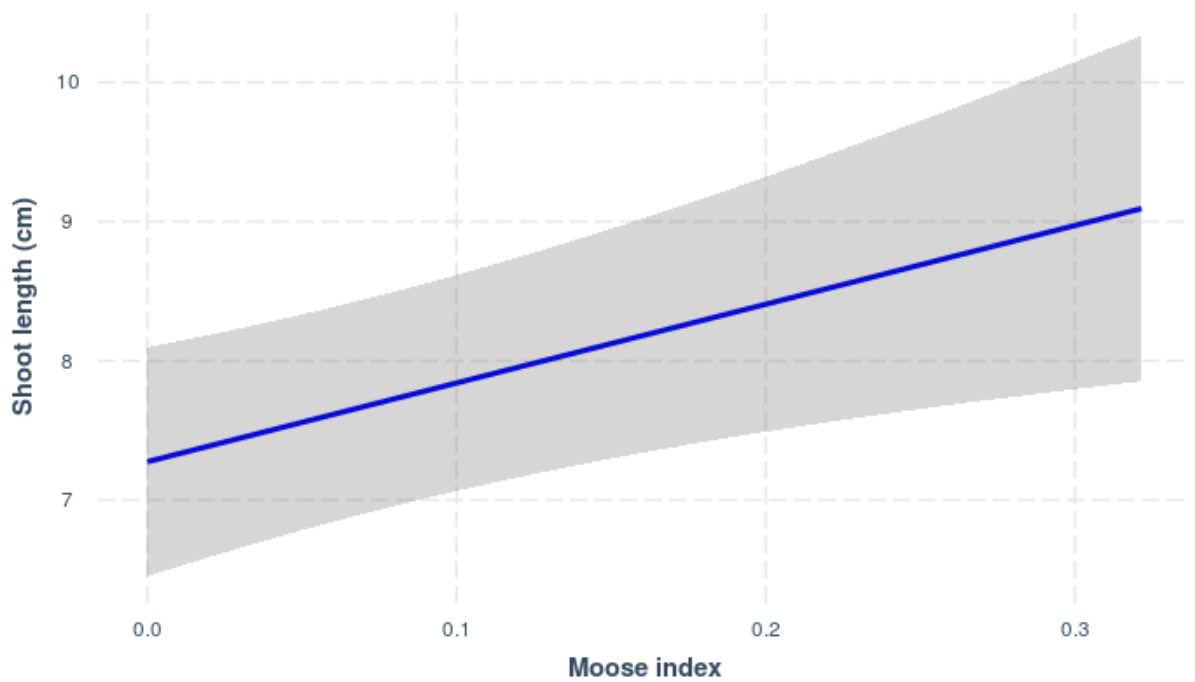
Figure 7: Positive relationship observed between moose densities and the length of bilberry shoots. July-August measurements. The grey area represents a 95% confidence interval.

As a further study, a Pearson correlation was also used to look at the relation between the height of bilberry bushes and the length of each bush's longest shoot.

Bilberry height and shoot length are very highly significantly positively correlated to each other, both in May-June (r (1615) = 0.485301, $p < 2.2e-16$***) and July-August (r (1626) = 0.5306633, $p < 2.2e-16$***) (figure 8), but bilberry height has a wider range.
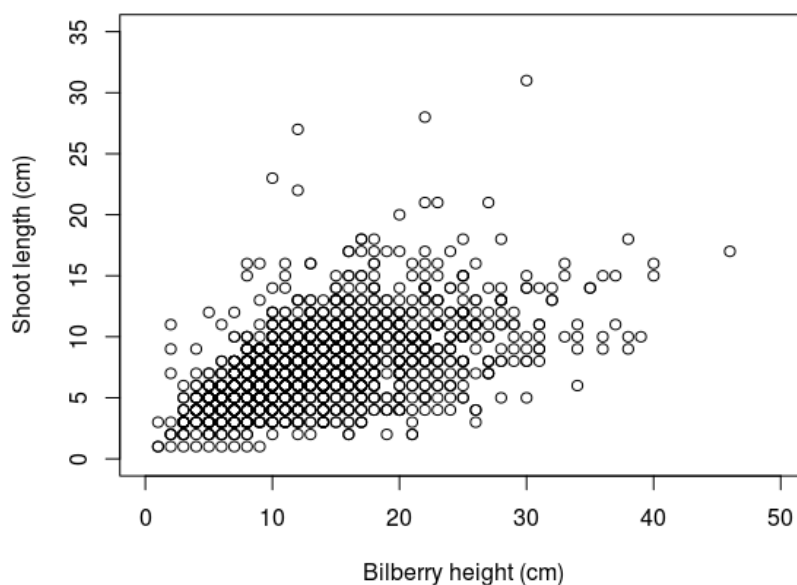
Figure 8: Scatter plot showing the correlation between the height of bilberry bushes and the length of their longest shoot. July-August measurements.

3.2. Food availability in relation to habitat type

The linear mixed effect model made with the forage types as the dependent variable and the forest type as the explanatory variable showed that forest type had a significant effect on abundance for all four of the studied food groups (table 8).

Table 8: Results of the general linear mixed effect models made with the four different food items as dependent variables, habitat as the explanatory variable and transect nested within site as the random variable.

	Df	F value	P-value
Ericaceous shrubs	6	77.215	$p < 2.2e-16$ ***
Grasses	6	57.045	$p < 2.2e-16$ ***
Forbs	6	47.181	$p < 2.2e-16$ ***
RASE	3	7.9066	$p = 1.217e-05$ ***

Subsequent Tukey post-hoc tests were performed to look at the differences between the different habitats (appendix A6 to A9). Pine forests show the highest abundance of ericaceous shrubs, with the pole touching one of them around 45 percent of the time it is placed down (figure 9a). In clear-cuts, spruce and deciduous forests however, the shrubs are present less than ten percent of the time. Mixed coniferous forests and mixed forests are at an intermediate level.

Deciduous forests have the highest abundance of both grasses and forbs (figure 9b and 9c). Spruce forests however are present in the lowest abundance statistical group for grass, forbs and ericaceous shrubs. The three types of coniferous forests show globally a lower abundance of grass and forbs than the other habitats.

Abundance of RASE (rowan, aspen, salix and oak) was much higher in planted clear-cuts than in spruce, deciduous and mixed forests (figure 9d).

a)

b)

c)

d)
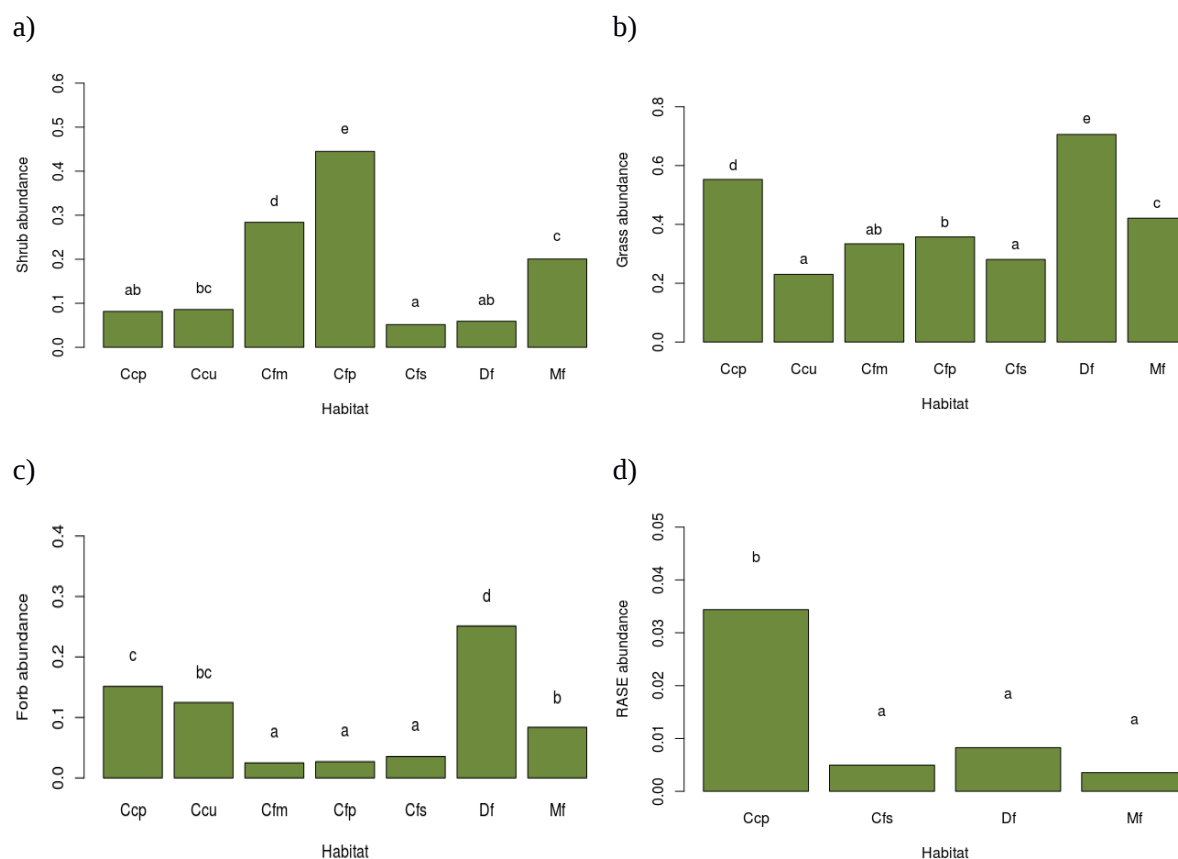
Figure 9: Relative abundance of the food items in the different habitats. The ordinate axis represents the proportion of occurrences of the food item of interest for each habitat. For example, if a certain habitat has an abundance of 0.1, it means that in that habitat, the pole – when placed down - was touching the food item of interest in ten percent of the cases. a) Ericaceous shrubs; b) grasses; c) forbs; d) RASE. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

4. Discussion

4.1. Bilberry interactions

Overall, habitat significantly influenced bilberry shrubs density (table 8), height (table 6) and shoot length (table 7). Those are important aspects by which herbivores perceive the forage quantity and quality in their environment (Edenius et al., 2002; Beest et al., 2010). Our study sites was located in the hemiboreal vegetation zone. Clear-cuts and spruce forest there generally had the smallest bilberry bushes and shortest shoots, pine forest the tallest bushes and longer shoots with mixed forests having intermediate height and length.

It has been shown that moose, at least for trees, prefer bigger twigs (Jónsdóttir et al., 1991; Nordengren and Ball, 2005; Shipley and Spalinger, 1995). My results seem to suggest the same thing for bilberry shoots, with moose being present at higher densities where shoots are longer (figure 7). Whereas their distribution was not correlated with bilberry height (table 6), despite yearly shoot length and bilberry height being correlated to each other (figure 8).

My results showed that shoot length was mostly dependent on the habitat type (table 7). Shoot length could also have been reduced where densities of cervid were high as shown by previous studies (Hegland et al., 2005). But my results did not show such significant results. A larger data set is necessary to clarify whether the negative non-significant trend I observed between fallow deer densities and shoot length (p = 0,097) is of ecological relevance or not. But one could also argue that even if the cervid do reduce shoot length, if they are distributed according to an ideal free distribution with respect to shoot length, the effect of their browsing would then not be detectable

Previous studies show that in areas where smaller cervid species are present in high densities, moose consume less Vaccinium and more pine, which offer a bigger bite size (Spitzer et al., 2021). Thus, a reduction in the shoot length, due either to a modification of the habitat or to the browsing pressure of other cervid, might not only lead to a reduced density of moose but rather to a modification in their diet. This means that in this case, the effect of the reduction of shoot length on moose density might have been underestimated. It could be interesting to look at interactions between pine damage and bilberry bushes characteristics.

My results also showed that high densities of fallow deer were correlated with smaller bilberry bushes. Those results point in the same direction as a previous study done with red deer (Melis et al., 2006). It seems that fallow deer, which can have a locally very dense population, are heavily browsing bilberry bush and maintaining them at a lower height than they otherwise would. My red deer results however went the opposite way than this study, with more red deer being present where bushes were taller. However, the red deer densities present on the island in that study were much higher than at our study sites. Or this could be the result of other factors influencing red deer behaviour and distribution. But it could also highlight the importance of studying interspecies interactions in ecosystems with multiple species competing for the same resources (Weisberg and Bugmann, 2003).

Fallow deer live in groups and have locally very dense populations with very low dispersion capacity. Moose, however, are mostly solitary and travel longer distances (Olsson et al., 2011; Torres et al., 2011). This possibly explains the differences in results between the pellet data that were collected in

this study and the Beyond Moose project pellets. Indeed, observations at the right scale are important to detect biological processes (Herfindal et al., 2015; Pfeffer, 2021; Weisberg and Bugmann, 2003). With our pellet data, the density indices were calculated at the transect level, close to where bilberries were measured whereas the density indices in the Beyond Moose project were calculated for the whole square surrounding the four transects at each site. The density indices calculated at the transect level might have been better than the bigger Beyond Moose project squares to detect the heterogeneous use of the landscape and locally very dense browsing by fallow deer. Moose however are much more mobile during their foraging bouts so a bigger scale was maybe more appropriate.

My study does not allow us to distinguish cause from effect. Is fallow deer browsing contributing to a reduced height in bilberry bushes or is their distribution related to other factors in the environment that are correlated with bilberry height? The same could be asked for the relation between shoot length and moose densities. Is it a consequence of this shoot length or of another factor in the landscape such as food availability in the surrounding fields and clear-cuts, varying hunting pressure, or the presence of urban areas (Áhlik et al., 2009; Dressel et al., 2018; van Beest et al., 2010)? But other studies have previously shown that cervid can influence plant structure and height (Côté et al., 2017; Speed et al., 2014) such as a study with fewer bias factors, done in only pine stands of similar age that also shows the negative effect of fallow deer on bilberry height (Spitzer et al., 2021). Furthermore, a study done on moose kept in enclosures has determined that, with tree shoots placed along different feeding stations, they preferred longer shoots (Shipley and Spalinger, 1995).

4.2. Availability of important food items from the forest floor layer

Despite spruce and pine forests representing, countrywide, over 80 percent of commercial forest cover, my results showed that in our study area pure pine or spruce stands together represented only 34 percent of coverage. When mixed coniferous forests and coniferous forests with deciduous trees included are included, we reach 84 percent - much closer to the national average (figure 2).

My results showed no increased abundance of grass and forbs in stands with a mix of pine and spruce compared to pure stand. The introduction of deciduous trees, on the other hand, led to a significant increase in grass and forbs. As for ericaceous shrubs, mixed stands showed intermediate abundance compared to pure stands.

Fallow and red deer are mixed feeders, consuming some woody browse, especially in the winter, as well as a range of grasses and forbs. Roe deer and moose, in contrast, are more browsers. Previous studies show that coniferous forests are preferred habitats for moose compared to deciduous forests (Bjørneraas et al., 2011; Olsson et al., 2011) and that they generally use spruce forests below availability and pine forests above availability (Härkönen and Heikkilä, 1999). Which makes sense as according to the optimal foraging theorem, herbivores should spend more time in areas of high forage quality to maximise food intake (Milligan and Koricheva, 2013).

Mixed coniferous forests had reduced bilberry cover compared to purely pine stands, but did not have an increase in forbs and grass. Whereas mixed deciduous and coniferous forests also had reduced bilberry cover and height but they did gain in forbs and grass (figure 9). Mixed forests could thus be beneficial for moose as a recent study in nutritional ecology shows that they benefit from having a wide range of food resources to have a balanced intake of macronutrients (A. M. Felton et al., 2021).

Forest floor vegetation cover has been decreasing in the past decades in Sweden (Hedwall et al., 2013). My results support other research that shows that the replacement of pine forest by spruce has a negative impact on the forest floor vegetation (A. Felton et al., 2020). In addition to that, food availability in spruce stands could currently be higher due to residual biodiversity (Petersson et al., 2019). Indeed, areas where spruce is replacing pine or grass fields in first generation could have a higher abundance of plants than if spruce forest succeeded to spruce. In this configuration food availability in spruce forests could become even lower than what it currently is.

The replacement of pine forests by spruce is mostly done to benefit from the rapid growth of spruce and to prevent damage to young trees as young spruce trees are less susceptible to damage by herbivores than pine (Beest et al., 2010). Nonetheless, other factors should also be taken into consideration while making those decisions: pine forests are better appreciated for their recreational values, they are more resilient in the face of climate change by being more resistant to storms and drought, and pines are not affected by diseases that currently plague spruce (A. Felton et al., 2020). Moreover, the beneficial value of pine forests and mixed forests over spruce due to the increase in shrubs quantity and quality for cervid could also be included in the reflection, especially since the gradual rarefaction of pine stands and the decreased availability of bilberry shrubs in spruce might be adding browsing pressure on the remaining pine (Bergqvist et al., 2014).

4.3. Caveats

Fewer measurements were taken in unplanted clear-cuts and in deciduous forests than in the other habitats, as shown in figure 2. To better understand the differences highlighted by the different tests that were performed, it should be remembered that the sensitivity of a test depends on the standard deviations of the sampled means and thus on the standard deviation of the population and on the sample size :

$$\sigma_m = \sigma / \sqrt{(n)}$$

With σ_m the standard deviation of the sample mean, σ the standard deviation of the population and n the sample size. The sample sizes in unplanted clear-cuts and in deciduous forests were smaller than in the other habitats. The standard deviation of their sampled means was indeed much bigger than the other groups which explains why they generally had fewer significant differences with other habitats.

A study comparing pellet classification by humans to DNA identifications has shown that human identification can be inaccurate, with misidentification mostly occurring between roe deer, red deer and fallow deer. Experienced observers were shown to make fewer mistakes than novices, which I was (Spitzer et al., 2019). Camera traps could be a good alternative for more accurate species identification (Pfeffer et al., 2017).

Pellet counting usually occurs early in spring, when the snow has melted but before plant coverage is too high. Our pellet data was potentially collected too late in the year, leading to pellets being likely missed due to the vegetation. For example, our pellet data contained very few occurrences of moose pellets compared to the Beyond Moose project dataset, with only 10 pellet piles found in over 600 plots sampled.

Some habitat categories covered a relatively wide array of habitats. Planted clear-cut for example could range from an open recently scarified terrain with 30 centimetres high saplings to densely packed three meter tall trees. Mixed forests were also of several different types: they could consist of spruce plantations with alder mixed within them, or oaks and pines together, or either spruce or pine plantation where birch has naturally regenerated after the clear-cutting. Differences in forest floor composition and abundance could have been overlooked due to these different combinations being grouped together.

Many other factors could have been taken into account that might have affected bilberry height and forest floor composition that I didn't measure: age of tree stand, regeneration method, soil type,...

The amount of young trees counted with the pole method was relatively low compared to food items from lower strata. It is perhaps not the best method for trees. For the other food items this method did allow us to sample large areas and it removes much of the bias brought by human perception that other methods have

4.4. Conclusion

My results showed that forest type had a major impact on the composition, coverage and quality of the forest floor vegetation. Scots pine forest had a higher abundance of bilberry, which were taller and with longer shoots than Norway spruce forests. Forests with coniferous and deciduous species mixed together brought good abundance of forbs, grasses and bilberry, which could be good to provide a varied diet for cervid species.

High fallow deer numbers were associated with smaller bilberry bushes, while higher moose densities were correlated with longer bilberry shoots. It would be interesting to study further the effect that high densities of fallow deer can have on the forest floor vegetation as their distribution continues to expand. And also research, perhaps in a more controlled environment, how moose feeding habits are influenced by available shoot length.

The decrease of the forest floor vegetation cover that has been happening over the past decades in Sweden can be remedied through different silvicultural practices. Forestry management decisions should be taken while considering all the ecosystem services that forests can bring and not solely for wood production.

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6. Appendix

Table A1: Result of the Tukey post-hoc test done on the linear mixed effect model with bilberry height as the dependent variable and habitat as the grouping, explanatory variable. May-June measurements, pellet data collected by me. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Ccu - Ccp == 0	-1.1572	1.3448	-0.860	0.97426
Cfm - Ccp == 0	2.1320	0.7226	2.950	0.04224 *
Cfp - Ccp == 0	3.5737	0.7408	4.824	< 0.001 ***
Cfs - Ccp == 0	-0.5773	0.7154	-0.807	0.98146
Df - Ccp == 0	2.9077	1.2027	2.418	0.16794
Mf - Ccp == 0	1.7310	0.7180	2.411	0.17024
Cfm - Ccu == 0	3.2892	1.2253	2.684	0.08751 .
Cfp - Ccu == 0	4.7309	1.2482	3.790	0.00235 **
Cfs - Ccu == 0	0.5799	1.2230	0.474	0.99898
Df - Ccu == 0	4.0649	1.5594	2.607	0.10695
Mf - Ccu == 0	2.8882	1.2333	2.342	0.19823
Cfp - Cfm == 0	1.4416	0.4994	2.887	0.05046 .
Cfs - Cfm == 0	-2.7094	0.4914	-5.514	< 0.001 ***
Df - Cfm == 0	0.7756	1.0737	0.722	0.98960
Mf - Cfm == 0	-0.4011	0.4678	-0.857	0.97477
Cfs - Cfp == 0	-4.1510	0.5369	-7.732	< 0.001 ***
Df - Cfp == 0	-0.6660	1.0825	-0.615	0.99563
Mf - Cfp == 0	-1.8427	0.5015	-3.674	0.00378 **
Df - Cfs == 0	3.4850	1.0691	3.260	0.01566 *
Mf - Cfs == 0	2.3083	0.4810	4.799	< 0.001 ***

	Estimate	Std. Error	z value	Pr(>|z|)
Mf - Df == 0	-1.1767	1.0556	-1.115	0.91214

Table A2: Result of the Tukey post-hoc test done on the linear mixed effect model with bilberry height as the dependent variable and habitat as the grouping, explanatory variable. July-August measurements, pellet data collected by me. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Ccu - Ccp == 0	0.8909	1.1618	0.767	0.9860
Cfm - Ccp == 0	1.4052	0.8097	1.735	0.5606
Cfp - Ccp == 0	3.8385	0.8493	4.519	< 0.001 ***
Cfs - Ccp == 0	-0.3755	0.8280	-0.454	0.9992
Df - Ccp == 0	1.9211	1.2380	1.552	0.6858
Mf - Ccp == 0	2.6083	0.7765	3.359	0.0118 *
Cfm - Ccu == 0	0.5143	0.9841	0.523	0.9983
Cfp - Ccu == 0	2.9476	1.0131	2.909	0.0484 *
Cfs - Ccu == 0	-1.2664	1.0094	-1.255	0.8563
Df - Ccu == 0	1.0302	1.3727	0.750	0.9875
Mf - Ccu == 0	1.7175	0.9525	1.803	0.5141
Cfp - Cfm == 0	2.4333	0.5510	4.416	< 0.001 ***
Cfs - Cfm == 0	-1.7807	0.5426	-3.282	0.0155 *
Df - Cfm == 0	0.5159	1.0727	0.481	0.9989
Mf - Cfm == 0	1.2032	0.4376	2.749	0.0756 .
Cfs - Cfp == 0	-4.2140	0.6119	-6.887	< 0.001 ***
Df - Cfp == 0	-1.9174	1.0960	-1.749	0.5514
Mf - Cfp == 0	-1.2301	0.5178	-2.376	0.1874
Df - Cfs == 0	2.2966	1.0923	2.103	0.3213

	Estimate	Std. Error	z value	Pr(>|z|)
Mf - Cfs == 0	2.9839	0.5007	5.960	< 0.001 ***
Mf - Df == 0	0.6872	1.0472	0.656	0.9939

Table A3: Result of the Tukey post-hoc test done on the linear mixed effect model with shoot length as the dependent variable and habitat as the grouping, explanatory variable. May-June measurements, pellet data collected by me. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Ccu - Ccp == 0	-0.3529	0.5977	-0.590	0.9965
Cfm - Ccp == 0	2.3390	0.3200	7.309	< 0.001 ***
Cfp - Ccp == 0	2.4517	0.3279	7.476	< 0.001 ***
Cfs - Ccp == 0	1.4558	0.3171	4.591	< 0.001 ***
Df - Ccp == 0	2.6282	0.5326	4.935	< 0.001 ***
Mf - Ccp == 0	2.5720	0.3180	8.089	< 0.001 ***
Cfm - Ccu == 0	2.6919	0.5454	4.936	< 0.001 ***
Cfp - Ccu == 0	2.8046	0.5550	5.053	< 0.001 ***
Cfs - Ccu == 0	1.8087	0.5448	3.320	0.0131 *
Df - Ccu == 0	2.9811	0.6929	4.302	< 0.001 ***
Mf - Ccu == 0	2.9249	0.5488	5.330	< 0.001 ***
Cfp - Cfm == 0	0.1127	0.2225	0.507	0.9985
Cfs - Cfm == 0	-0.8832	0.2186	-4.040	< 0.001 ***
Df - Cfm == 0	0.2892	0.4761	0.608	0.9959
Mf - Cfm == 0	0.2330	0.2088	1.116	0.9118
Cfs - Cfp == 0	-0.9959	0.2379	-4.187	< 0.001 ***
Df - Cfp == 0	0.1765	0.4800	0.368	0.9998
Mf - Cfp == 0	0.1203	0.2235	0.538	0.9979

	Estimate	Std. Error	z value	Pr(>|z|)
Df - Cfs == 0	1.1725	0.4743	2.472	0.1480
Mf - Cfs == 0	1.1163	0.2142	5.212	< 0.001 ***
Mf - Df == 0	-0.0562	0.4688	-0.120	1.0000

Table A4: Result of the Tukey post-hoc test done on the linear mixed effect model with shoot length as the dependent variable and habitat as the grouping, explanatory variable. July-August measurements, pellet data collected by me. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Ccu - Ccp == 0	-0.85806	0.61163	-1.403	0.77870
Cfm - Ccp == 0	-0.34264	0.42175	-0.812	0.98111
Cfp - Ccp == 0	0.27314	0.44241	0.617	0.99562
Cfs - Ccp == 0	-1.12097	0.43216	-2.594	0.11265
Df - Ccp == 0	0.28257	0.64935	0.435	0.99939
Mf - Ccp == 0	-0.06633	0.40500	-0.164	1.00000
Cfm - Ccu == 0	0.51542	0.51940	0.992	0.94918
Cfp - Ccu == 0	1.13119	0.53486	2.115	0.31470
Cfs - Ccu == 0	-0.26292	0.53310	-0.493	0.99875
Df - Ccu == 0	1.14062	0.72283	1.578	0.66901
Mf - Ccu == 0	0.79173	0.50399	1.571	0.67357
Cfp - Cfm == 0	0.61577	0.29103	2.116	0.31414
Cfs - Cfm == 0	-0.77834	0.28624	-2.719	0.08163 .
Df - Cfm == 0	0.62520	0.56452	1.108	0.91572
Mf - Cfm == 0	0.27631	0.23189	1.192	0.88438
Cfs - Cfp == 0	-1.39411	0.32132	-4.339	< 0.001 ***
Df - Cfp == 0	0.00943	0.57667	0.016	1.00000

Mf - Cfp == 0	-0.33947	0.27308	-1.243	0.86197
Df - Cfs == 0	1.40354	0.57525	2.440	0.16223
Mf - Cfs == 0	1.05464	0.26472	3.984	0.00109 **
Mf - Df == 0	-0.34890	0.55166	-0.632	0.99501

Table A5: Generalised variance inflation factors (GVIF) from the mixed effect linear models with yearly shoot length and bilberry height as the dependent variable and habitat as well as the different cervid indices as the explanatory variables

	May-June data				July-August data			
	Beyond Moose project pellet data		Pellet data collected by me		Beyond Moose project pellet data		Pellet data collected by me	
	Yearly shoot length	Bilberry height	Yearly shoot length	Bilberry height	Yearly shoot length	Bilberry height	Yearly shoot length	Bilberry height
Habitat	1.02729	1.02071	1.03130	1.02613	1.02859	1.01654	1.04495	1.03300
Fallow deer index	1.04206	1.04093	1.02754	1.02557	1.03515	1.02864	1.03077	1.02726
Roe deer index	1.02097	1.01957	1.04234	1.04044	1.02968	1.02168	1.03651	1.03409
Moose index	1.03536	1.03500	1.02724	1.02736	1.00603	1.00738	1.01737	1.01366
Red deer index	1.02206	1.01994	1.08467	1.08249	1.03087	1.02498	1.05573	1.05420

Table A6: Result of the Tukey post-hoc test done on the general linear mixed effect model with shrub abundance as the dependent variable and habitat as the grouping, explanatory variable. July-August measurements. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Ccu - Ccp == 0	0.38734	0.24901	1.556	0.6756
Cfm - Ccp == 0	1.27069	0.16416	7.741	< 0.001 ***
Cfp - Ccp == 0	1.84803	0.16746	11.035	< 0.001 ***
Cfs - Ccp == 0	-0.53737	0.18695	-2.874	0.0513 .

	Estimate	Std. Error	z value	Pr(>|z|)
Df - Ccp == 0	-0.48628	0.28284	-1.719	0.5630
Mf - Ccp == 0	0.78041	0.16006	4.876	< 0.001 ***
Cfm - Ccu == 0	0.88336	0.21043	4.198	< 0.001 ***
Cfp - Ccu == 0	1.46069	0.21362	6.838	< 0.001 ***
Cfs - Ccu == 0	-0.92471	0.22797	-4.056	< 0.001 ***
Df - Ccu == 0	-0.87362	0.30974	-2.820	0.0594 .
Mf - Ccu == 0	0.39307	0.20663	1.902	0.4374
Cfp - Cfm == 0	0.57733	0.08989	6.423	< 0.001 ***
Cfs - Cfm == 0	-1.80806	0.12394	-14.588	< 0.001 ***
Df - Cfm == 0	-1.75697	0.24654	-7.126	< 0.001 ***
Mf - Cfm == 0	-0.49028	0.07935	-6.179	< 0.001 ***
Cfs - Cfp == 0	-2.38539	0.12908	-18.480	< 0.001 ***
Df - Cfp == 0	-2.33430	0.24811	-9.408	< 0.001 ***
Mf - Cfp == 0	-1.06761	0.08732	-12.227	< 0.001 ***
Df - Cfs == 0	0.05109	0.26274	0.194	1.0000
Mf - Cfs == 0	1.31778	0.11974	11.005	< 0.001 ***
Mf - Df == 0	1.26669	0.24331	5.206	< 0.001 ***

Table A7: Result of the Tukey post-hoc test done on the general linear mixed effect model with grass abundance as the dependent variable and habitat as the grouping, explanatory variable. July-August measurements. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Ccu - Ccp == 0	-1.42782	0.16042	-8.900	< 0.001 ***
Cfm - Ccp == 0	-1.07901	0.10732	-10.055	< 0.001 ***
Cfp - Ccp == 0	-0.84254	0.11461	-7.352	< 0.001 ***

	Estimate	Std. Error	z value	Pr(>|z|)
Cfs - Ccp == 0	-1.30811	0.10746	-12.173	< 0.001 ***
Df - Ccp == 0	0.61350	0.16350	3.752	0.00303 **
Mf - Ccp == 0	-0.54878	0.09873	-5.558	< 0.001 ***
Cfm - Ccu == 0	0.34880	0.14798	2.357	0.19797
Cfp - Ccu == 0	0.58528	0.15444	3.790	0.00252 **
Cfs - Ccu == 0	0.11971	0.14825	0.807	0.98209
Df - Ccu == 0	2.04132	0.18956	10.769	< 0.001 ***
Mf - Ccu == 0	0.87903	0.14317	6.140	< 0.001 ***
Cfp - Cfm == 0	0.23648	0.08781	2.693	0.08930 .
Cfs - Cfm == 0	-0.22910	0.07941	-2.885	0.05314 .
Df - Cfm == 0	1.69252	0.14771	11.458	< 0.001 ***
Mf - Cfm == 0	0.53023	0.07012	7.561	< 0.001 ***
Cfs - Cfp == 0	-0.46558	0.09016	-5.164	< 0.001 ***
Df - Cfp == 0	1.45604	0.15174	9.596	< 0.001 ***
Mf - Cfp == 0	0.29375	0.08130	3.613	0.00495 **
Df - Cfs == 0	1.92162	0.14847	12.942	< 0.001 ***
Mf - Cfs == 0	0.75933	0.07076	10.731	< 0.001 ***
Mf - Df == 0	-1.16229	0.14105	-8.240	< 0.001 ***

Table A8: Result of the Tukey post-hoc test done on the general linear mixed effect model with forbs abundance as the dependent variable and habitat as the grouping, explanatory variable. July-August measurements. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Ccu = Clear-cut unplanted, Cfm = Coniferous forest mixed, Cfp = Coniferous forest pine, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Ccu - Ccp == 0	-0.1129	0.2199	-0.513	0.9985
Cfm - Ccp == 0	-2.0136	0.2055	-9.798	< 0.001 ***

	Estimate	Std. Error	z value	Pr(>|z|)
Cfp - Ccp == 0	-1.9366	0.2283	-8.483	< 0.001 ***
Cfs - Ccp == 0	-1.5257	0.1830	-8.336	< 0.001 ***
Df - Ccp == 0	0.8055	0.1981	4.067	< 0.001 ***
Mf - Ccp == 0	-0.6497	0.1469	-4.423	< 0.001 ***
Cfm - Ccu == 0	-1.9008	0.2435	-7.806	< 0.001 ***
Cfp - Ccu == 0	-1.8238	0.2651	-6.880	< 0.001 ***
Cfs - Ccu == 0	-1.4129	0.2266	-6.236	< 0.001 ***
Df - Ccu == 0	0.9183	0.2388	3.846	0.0022 **
Mf - Ccu == 0	-0.5369	0.2006	-2.676	0.0986 .
Cfp - Cfm == 0	0.0770	0.2436	0.316	0.9999
Cfs - Cfm == 0	0.4879	0.2049	2.381	0.1960
Df - Cfm == 0	2.8191	0.2195	12.843	< 0.001 ***
Mf - Cfm == 0	1.3639	0.1734	7.866	< 0.001 ***
Cfs - Cfp == 0	0.4109	0.2281	1.801	0.5313
Df - Cfp == 0	2.7421	0.2395	11.450	< 0.001 ***
Mf - Cfp == 0	1.2869	0.2008	6.410	< 0.001 ***
Df - Cfs == 0	2.3312	0.1998	11.666	< 0.001 ***
Mf - Cfs == 0	0.8760	0.1481	5.915	< 0.001 ***
Mf - Df == 0	-1.4552	0.1652	-8.809	< 0.001 ***

Table A9: Result of the Tukey post-hoc test done on the general linear mixed effect model with RASE (rowan, aspen, willow and oak) abundance as the dependent variable and habitat as the grouping, explanatory variable. July-August measurements. Habitat abbreviations correspond to: Ccp = Clear-cut planted, Cfs = Coniferous forest spruce, Df = Deciduous forest, Mf = Mixed forest

	Estimate	Std. Error	z value	Pr(>|z|)
Cfs - Ccp == 0	-1.5191	0.5314	-2.858	0.0211 *
Df - Ccp == 0	-1.9628	0.6820	-2.878	0.0200 *

Mf - Ccp == 0	-2.3343	0.4796	-4.867	< 0.001 ***
Df - Cfs == 0	-0.4437	0.7156	-0.620	0.9236
Mf - Cfs == 0	-0.8153	0.4607	-1.769	0.2813
Mf - Df == 0	-0.3715	0.6897	-0.539	0.9481

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