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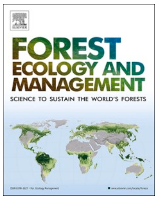

From simple metrics to cervid forage: Improving predictions of ericaceous shrub biomass

Laura Juvany [a,*], Per-Ola Hedwall [a], Adam Felton [a], Karin Öhman [b], Märtha Wallgren [c,d], Christer Kalén [e,f], Anders Jarnemo [g], Henrik Johansen [a], Annika Felton [a]

[a] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (SLU), PO Box 190, SE-234 22 Lomma, Sweden
[b] Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umeå SE-901 83, Sweden
[c] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå SE-901 83, Sweden
[d] Forestry Research Institute of Sweden, Uppsala Science Park, SE-751 83 Uppsala, Sweden
[e] Swedish Environmental Protection Agency, Stockholm 106 48, Sweden
[f] National Forest Agency, P.O. Box 343, 501 13 Borås, Sweden
[g] School of Business, Innovation and Sustainability, Halmstad University, P.O. Box 823, SE-301 18 Halmstad, Sweden

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ABSTRACT

Common understory vegetation species such as the ericaceous shrubs bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*) and heather (*Calluna vulgaris*), are key forage plant species for moose and other large herbivores, as well as fulfilling many additional ecosystem functions and services. Here we developed models to predict above-ground biomass of these ericaceous species in coniferous forests, using data on their percentage cover, height, and different stand characteristics. We also built models to understand how the aforementioned variables affect the proportion of the shrubs commonly utilized as forage by large herbivores. We found that the percentage cover of shrubs was the most important explanatory variable when predicting above-ground biomass, explaining 51%, 47% and 71% of the variation (marginal R^2) in bilberry, cowberry and heather biomass, respectively. By adding ramet height to the model with percentage cover, the variation explained increased to 77% for bilberry, 75% for cowberry and 87% for heather. The best outcome for candidate models was obtained by adding stand site index and spruce basal area to the model, improving the variation explained in bilberry to 83%, to 81% for cowberry, and 91% for heather. When modelling the proportion of the shrubs commonly utilized as forage by large herbivores, stand site index and spruce basal area often played important roles. Some of the best fitting models for forage biomass explained 51% of the variation in bilberry, 59% in cowberry and 30% in heather. Site location did not have a major role in improving the variability explained in either type of model, which indicated the applicability of the models regardless of study location. Our models therefore have a high potential to be implemented in forestry decision support systems. Their inclusion should provide better large-scale estimations of forage resources, aiding forest management, and thereby taking an important step forward to determine the ecosystem carrying capacity of large herbivores.

1. Introduction

Shrubs of the family Ericaceae, including bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*) and heather (*Calluna vulgaris*), are abundant plant species in Eurasian boreal and temperate forest ecosystems (Nilsson & Wardle, 2005). As foundation species (sensu Dayton (1972)), these plants play key roles in many ecosystem processes and services in boreal forests, via their enhancement of recreational values (Lindhagen & Bladh, 2013), provision of food to vertebrates and invertebrates (Hertel et al., 2018; Hanula et al., 2015; Selås, 2001), role in the carbon cycle (Hensgens et al., 2020; Nilsson & Wardle, 2005), and as important components of plant biodiversity.

Additionally, recent findings from Sweden show that these ericaceous shrubs (from here on shrubs) constitute large proportions of the annual dietary intake of moose (*Alces alces*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) (Spitzer, 2019). For example, these shrubs can represent as much as 40% of the diet of moose during spring and autumn in Central Sweden (Cederlund

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* Corresponding author.
E-mail address: laura.juvany.canovas@slu.se (L. Juvany).

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et al. (1980), using rumen macroscopy), 28% of the diet during winter in southern Sweden (A.M. Felton et al. (2020), rumen macroscopy), and 25–50% of the diet spanning all seasons, encompassing localities both in the South and North of Sweden (Spitzer (2019), faecal pellet DNA metabarcoding). Importantly, when the availability of, or access to, these shrubs is limited, cervids (members of the family Cervidae) may replace them by consuming biomass from other woody plant species. For example, in areas where competition from other deer species limits the availability of bilberry and cowberry, moose increase their browsing on Scots pine (*Pinus sylvestris*) (Spitzer et al., 2021), potentially leading to higher damage levels on this economically important tree species. Production trees are more likely to be damaged by red deer in areas where the cover of shrubs is limited (Jarnemo et al., 2014; Brooker et al., 2006). Despite browsing impacts on timber trees being a major concern in Sweden (Wallgren et al., 2013) and other parts of Europe (Spake et al., 2020; Putman et al., 2011), we still lack the tools needed to evaluate and predict biomass of ericaceous forage within forest landscapes. In this regard, understanding how forestry affects forage biomass is a key component in managing the combined browsing damage of several cervid species in such regions. This is especially the case in countries, like Sweden, where production forests comprise the vast majority of forest area (A. Felton et al. 2020).

The most widely available indicator of shrubs prevalence in Sweden's production forests is percentage cover estimates, e.g. from the national forest inventory (NFI). These data are often used, for example, to monitor the status of ericaceous species over time (Jonsson et al., 2021). It is important to note, however, that a plant's percentage cover may be only loosely correlated with its biomass, as percentage cover only provides a two-dimensional picture of the plant's prevalence. For example, bilberry shrubs may fully cover a patch of forest ground but still offer proportionally smaller amounts of forage for cervids, if the shrubs are of short stature and poor in the production of annual shoots. If better estimates could be made of the availability of shrub forage, then an important step would be taken towards estimating cervid carrying capacity of forest landscapes.

Some studies have developed functions to estimate above-ground biomass of understory shrubs, such as Lehtonen et al. (2016), Elzein et al. (2011) or Kuusipalo (1983), who successfully developed functions for the total biomass of shrubs in boreal and subalpine regions by combining data on percentage cover and/or shrub height. Here we use a similar approach to develop above-ground biomass equations for bilberry, cowberry and heather with the aim to predict how much of the biomass of these three species provide potential forage for cervids at varying browsing intensities. From hereon we refer to this proportion of the plant as the "forage biomass". In contrast to previous studies, our aim was also to improve the models to predict biomass by, in addition to cover, include data also on forest stand related characteristics, such as tree species composition, tree basal area, stand mean age and site index. Previous studies have shown that such forest stand characteristics significantly influence the cover (Eldegard et al., 2019; Hedwall et al., 2013) and biomass (Frolov et al., 2022; Lehtonen et al., 2016) of shrubs. Due to eco-physiological differences, we expected to see a variation among the three shrub species in terms of which aspects of the forest environment are important for improving biomass predictions. We also included a latitudinal gradient in our sample sites to capture varying environmental contexts and increase the generality of our models. In combination, our study thereby takes a novel step forward in the quest to estimate cervid carrying capacity.

2. Materials and methods

2.1. Study areas

Data on the cover and above-ground biomass of bilberry, cowberry and heather were collected during July and August of 2019 in three sites with a latitudinal spread across Sweden: one site within the northern boreal forest region (NB), one at the limit between the boreal and the hemiboreal (HB), and one within the southern range of the hemiboreal biome (SB) (Fig. 1, A). With this choice we included a north-to-south climatic and environmental context gradient (Table 1). In the north, greater snow depth can decrease shrub availability during the winter season, whereas in the south, milder weather conditions that should allow for year-round shrub availability, may be countered by higher levels of consumption from a more diverse cervid community (Spitzer, 2019). A total of 36 forest stands (all on mineral soils, sizes between 1.54 and 11.27 Ha) were sampled, 12 in each site, which varied in tree species composition spanning different mixtures of both Scots pine (hereafter "pine") and Norway spruce (*Picea abies*, hereafter "spruce"). We also selected stands to capture differences in site productivity and dominance of bilberry, cowberry and heather. Stands were divided into four age categories in relation to their stage in the rotation period: early (between 7 and 18 years), young (19–39 years), middle (40–70 years) and late (>71 years old). Three forest stands per site represented each age category (Appendix 1). These 36 forest stands provided us with the bulk of the data used in this study. Within a stand, 2–3 circular plots were selected (Fig. 1, B), not to represent the stands' overstory, but to capture as much variation as possible occurring at the understory level within the stand. The abundance of the understory determined the time needed to complete the sampling, and out of the 36 stands sampled, 14 stands only had 2 plots. There was at least a 24 m distance between the centres of plots, so they would not overlap, and stand edges and strip roads were avoided. In each plot we collected both tree layer data and understory vegetation data.

In addition, to determine what proportion of the shrubs' above-ground biomass is normally utilised by free-ranging cervids in Sweden, we collected data on browsed bite diameters at the beginning of spring of 2020 and 2021, measuring the diameter of bites after winter foraging. We selected two sites, one with relatively high cervid population densities (HC) and one with lower cervid densities (LC) (Fig. 1, A). The ungulate populations in these two areas have been monitored since 2012 and 2015 respectively, using dung pellet counts along multiple 4 km square transects ("tracts") (for study site description and details about pellet count, see Spitzer (2019)). Based on existing estimates of cervid population densities, from 76 tracts in LC (with moose, roe deer, red deer, fallow deer, and sporadically reindeer (*Rangifer tarandus*) in winter) and 50 tracts in HC (with the same four main species), we selected 10 tracts in each of the two locations that captured the variation in ungulate densities within each area (Spitzer, 2019). We selected one forest stand as close as possible to each tract that was dominated by pine (at least 60% of stand basal area) and was 45–70 years old. This allowed us to focus our collection of bite diameter data on the gradient in cervid browsing pressure, while keeping stand characteristics as similar as possible and with favourable conditions to have extensive shrub cover.

2.2. Data collection

2.2.1. Tree layer

The tree species was recorded, and diameter at breast height (DBH, 1.3 m from the ground) was measured for all living trees taller than 1.3 m, in a 5.64 m (100 m^2) radius plot for the youngest stand age category (5–15 years), and within a 10 m (314 m^2) radius for the other three stand age categories (Fig. 1, C). We determined the age at 1.3 m (hereon BH age) and measured the height of the tree with the largest DBH in two plots per stand. If the largest tree was not suitable (e.g. damaged or crooked stem), we selected the next biggest tree.

2.2.2. Ericaceous shrubs data collection and sample processing

The sampling was carried out after the peak of the growing season in each site, from the beginning of July until mid-August of 2019 from south to north. In this way plants could recover from previous potential winter browsing and we avoided the time for leaf senescence in bilberry.

All three studied plant species are clonal and grow single shoots

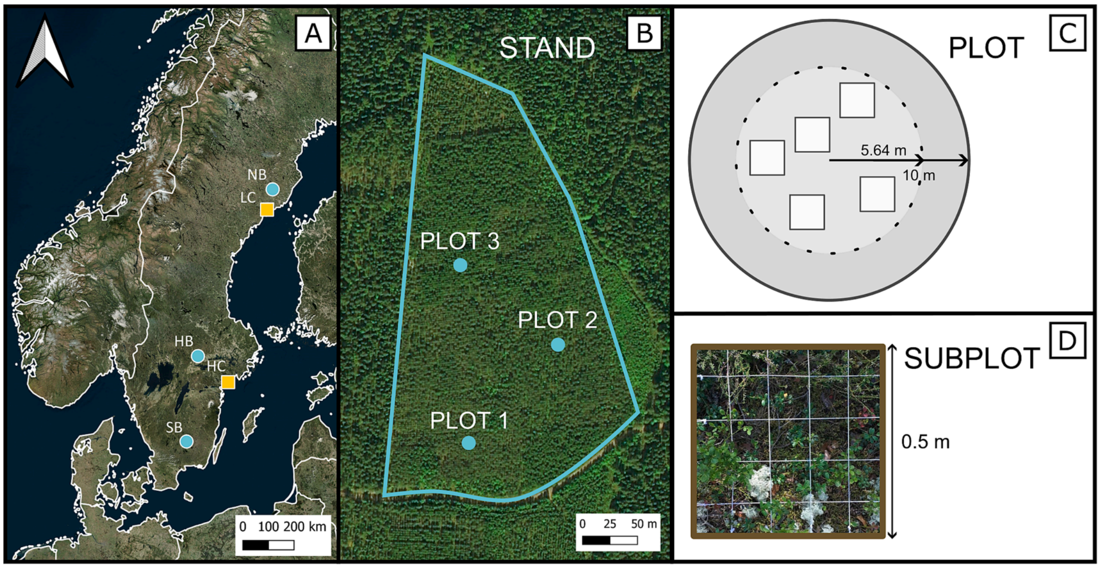

Fig. 1. Locations of the five study sites in Sweden in panel A. Dots (blue) indicate the location of sites where data on cover and above-ground biomass of bilberry, cowberry and heather was taken in the northern boreal region (NB), hemiboreal region (HB) and the southern hemiboreal region (SB). Squares (yellow) indicate the location of the sites where data on bite diameter of the three plant species was taken, in the north (low cervid population density (LC)), and south (high cervid population density (HC)). In panel B, an example of a selected stand and the 3 located plots (note that in some stands only two plots were sampled). The plot dimensions are shown in panel C. Overstory data were collected within a 10 m radius circular plot, and understory data in a 5.64 m radius plot (for our youngest stand category both types of data were collected within the 5.64 m radius plot), which included 5 randomly distributed quadrates of 0.25 m^2 (panel D), in which the shrub data were collected.

Table 1
Elevation and climate data at the three study sites NB (northern boreal), HB (hemiboreal biome) and SB (southern hemiboreal biome). All values are averages from the reference period 1961–1990, sourced from the Swedish Meteorological and Hydrological Institute (SMHI, 2022). Name of the closest weather station is given in brackets for each study site.

Site	Elevation (m)	Mean annual temperature (C)	Annual snow cover (days)	Mean yearly rainfall (mm)	Length of vegetation period (days)
NB (Vindeln-Sunnansjönäs)	237	1.6	150–175	587.5	147
HB (Lindesberg)	70	5.3	100–125	677.6	184
SB (Berg)	250	5.5	75–100	662.9	187

(ramets) from underground rhizomes (Woziwoda et al., 2019; Tolvanen, 1995; Mohamed & Gimingham, 1970). We used ramet as the unit to study these plant species, due to the difficulty determining separate individuals.

In each plot, within a 5.64 m radius, we randomly selected five 0.25 m^2 square-shaped quadrates (Fig. 1, C and D) within which we visually estimated the percentage cover for each of the three shrub species and the total cover of other vascular plants. All percentage cover estimates were carried out by the same observer, after being trained and calibrated by experienced observers. In each quadrat, we also measured the top height of the two tallest ramets present per shrub species, without stretching the ramet. We collected all above-ground biomass of the three species (if present) in each of the five quadrates, by cutting each ramet at the ground level. We recorded the total fresh wet weight per species and quadrate directly after harvest and selected a bagful of ramets (average ca 50 g wet weight) per species and plot. This subsample was weighed directly after harvest and dried at the end of the day for 12 h at 103 °C, allowing us to assess the relative water content of the total biomass collected in each quadrate and calculate the dry biomass.

In addition, we selected ten representative ramets per species from the total biomass collected in each plot (i.e. of pooled material from the five squares). These ramets were used to estimate how the biomass was distributed along the ramet for each species, as determined by variation in diameter along the stem, and leaf distribution, to later build forage biomass models (Fig. 2). To avoid deterioration, these ramets were dried within 10 h of collection at 60 °C (for 24 h). We separated leaves from stems, and measured all stems with an electronic calliper, cutting and splitting them into seven diameter fractions (see Table 2 for specifications of diameter per plant species). All leaves from the ten ramets per species and plot were collated into an eighth fraction. To determine the leaves' biomass distribution along the stems, we selected one of the ten ramets per species and stand, which was split into the seven diameter classes, and each class weighed separately as stem and leaf biomass fractions. After processing, all fractions were dried at 103 °C for 12 h and each fraction weighed using a precision scale.

2.2.3. *Collection of bite diameter data to estimate forage biomass*

In each of the 10 stands in the sites LC and HC (Fig. 1, A), we selected two 10 m radius plots, similar in both overstory and understory conditions, that were representative of the whole stand. Within these plots we searched for browsed ramets of the three plant species. A ramet was considered to be browsed by a cervid if the bite surface was lightly frayed, and there was more than one stem cut at the same height, which indicated that the bite came from a large herbivore. As cowberry ramets tend to have less branching compared to the other two plant species, we considered these to be browsed even if the ramet had one single stem bite. Once an individual ramet was chosen, we measured height above ground for both the top height and at most two observed bites. If we did not find any browsed individuals within a plot, we selected browsed plants opportunistically within the stand.

During collection, we assessed the colour of each bite surface, determining it was recent (light green, pale beige, or cream = realized within a year) or older (grey = more than a year old). Using an electronic calliper, we measured the stem diameter of the ramet at the cut point of

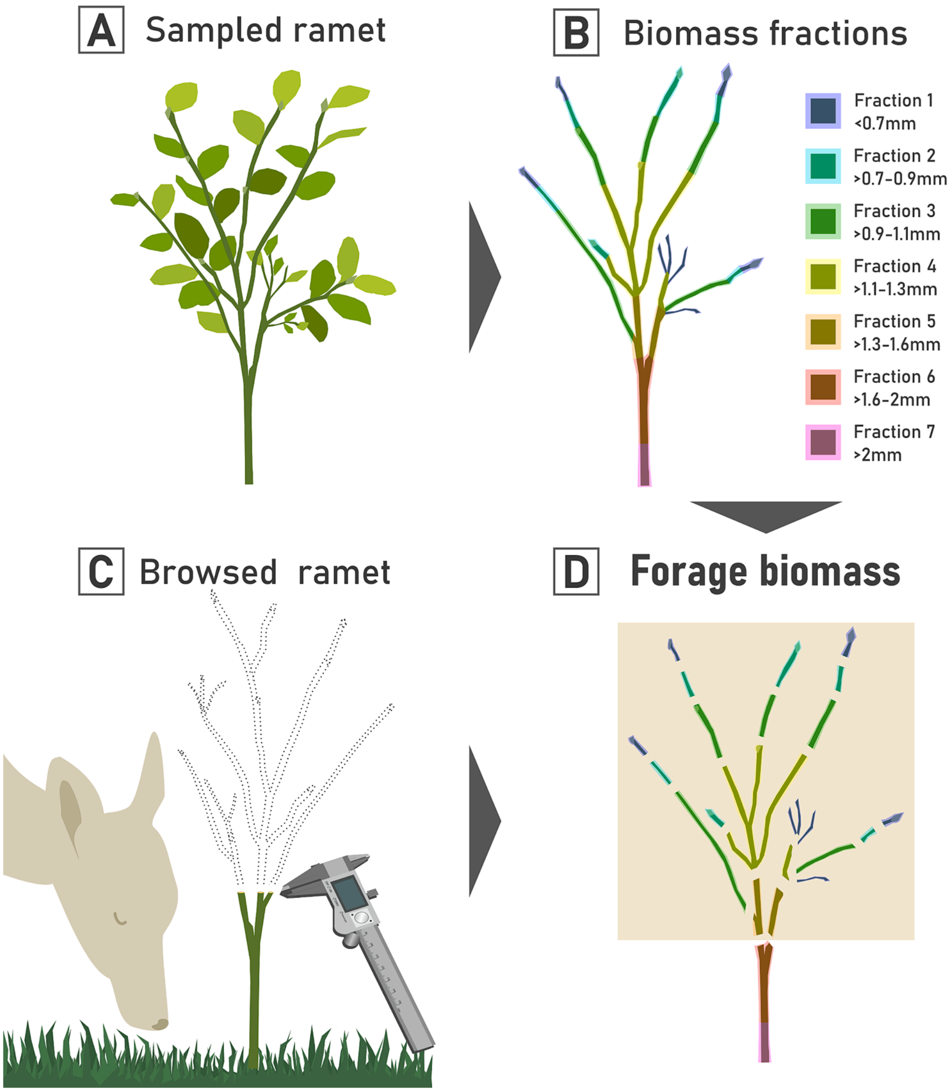

Fig. 2. We selected a subset of representative sampled ramets (A) per plot and species from our above-ground biomass collection, measured their stem diameter and split them into 7 diameter fractions (B) and calculated the biomass proportion of each fraction to the total sample biomass. To determine how much of the ramet biomass is normally used as forage by cervids, we additionally collected data on browsed ramets in sites varying in cervid population densities (Fig. 1), and measured the stem diameter of the bite surface (C). We then built models to predict the proportion of the biomass fractions (D).

Table 2
Diameters in mm of the seven diameter fractions per ericaceous shrub species.

Diameter fraction	Species *Bilberry stem diameter (mm)*	*Cowberry stem diameter (mm)*	*Heather stem diameter (mm)*
1	<0.7	<0.7	<0.5
2	>0.7–0.9	>0.7–0.8	>0.5–0.6
3	>0.9–1.1	>0.8–0.9	>0.6–0.9
4	>1.1–1.3	>0.9–1.1	>0.9–1.1
5	>1.3–1.6	>1.1–1.3	>1.1–1.5
6	>1.6–2	>1.3–1.5	>1.5–2
7	>2	>1.5	>2

each bite in two directions forming a cross (Fig. 2, C), noting the largest diameter. During the data collection in 2020, all measured ramets in the field were harvested, dried for 24 h at 60 °C, and the diameter of their bites measured again. We carried out a paired samples *t*-test and found differences in the bite diameter between fresh and dried ramets for the three plant species (paired samples *t*-test; bilberry ($n = 393$): $t = -4.87$, $df = 392$, $p < 0.001$; cowberry ($n = 278$): $t = -5.01$, $df = 274$, $p < 0.001$; heather ($n = 265$): $t = -5.07$, $df = 264$, $p < 0.001$). Although statistically different, the mean difference between dry and fresh diameters for all three species was only 0.03 mm, which we deem normal within measurement error. We therefore considered the differences in diameter between dry and fresh ramets negligible. Consequently, during the data collection in spring of 2021 the bite diameter was only measured on fresh samples.

2.3. *Calculations of plot and stand variables*

We calculated the total basal area per plot and the contribution to it by each tree species present in the plots (10 m radius). To estimate the age of the stand we calculated the average of the age values measured from the tree cores. Site index (the height in m at 100 years age) was calculated per stand following the equations in Elfving and Kiviste (1997), using the height and total age obtained for the biggest trees in two out of three plots, and obtaining an average per stand. As age was measured from a core sample taken at BH, we estimated total age taking into account latitude and general fertility characteristics of each area, as in Hägglund and Lundmark (2003).

2.4. *Statistical analysis*

All statistical analysis were carried out in R version 4.2.1 (RCoreTeam, 2021). Code is available in https://github.com/laurajuvany/VacciniumBiomass.

2.4.1. Above-ground biomass models

The plot-level relationship between stand variables and the log-transformed dry biomass (natural logarithm) per m^2 of each species of shrub were modelled using linear mixed models (LMM) as implemented in the glmmTMB function in the glmmTMB package with Gaussian distribution and identity link (Magnusson et al., 2017). We carried out a collinearity test (Spearman correlation coefficient > 0.6) for the candidate explanatory variables to build the models: log percentage cover of plant species, mean height of the species, site (NB, HB and SB), site index, mean stand age and total, pine, spruce and deciduous plot basal area. For all three plant species, total basal area and pine basal area were strongly correlated, and in the case of heather, pine basal area was negatively correlated with stand site index. In those cases, none of the strongly correlated variables were included in the same model. For bilberry and heather, we identified that percentage cover and height of the plant were strongly correlated. In this case these two variables were still included in the same candidate model, but the respective coefficients must be interpreted with care due to this collinearity. After this, we built different candidate models (Table 3) which included the same variables for the three plant species. The intercept was excluded from all models to force predictions through the origin. Stand and plot number were included as nested random intercept variables following our design. Site was included as a random variable in some of the models. Coefficients of determination (conditional and marginal R^2) were calculated using the function r2 in the performance package (Lüdecke et al., 2021) as developed by Nakagawa et al. (2017). Our model evaluation did not reveal any patterns when plotting the residuals against predicted values and against each predictor or when plotting the predicted values against the measured biomass per shrub species (Appendix 2).

2.4.2. Determination of forage biomass from bite diameter

We calculated the mean, median, maximum and minimum bite diameter, and the 10%, 50% and 90% quantile from all bites measured per stand, HC and LC site and year. We then carried out a two-way analysis of variance (ANOVA) and pair-wise Tukey HSD test, to determine if there were differences in bite diameter between sites, sampling years and their interaction (Table 4).

2.4.3. Forage biomass models

Because the bite diameter measurements showed us that diameter fraction 7 generally had a larger stem diameter than the mean maximum of observed bites (see section 3.2) we did not include it in further analysis. We calculated the proportion of each diameter fraction from 1 to 6 in relation to the total biomass of the ramet and used this as our dependent variable in the models. From hereon we refer to these proportions as forage biomass fractions.

We built generalized linear mixed models (GLMMs) using the glmmTMB function in the glmmTMB package with beta error distribution and logit link to model the relationship between the explanatory variables and the proportion of each diameter class per plant species. We included the following explanatory variables in the models: associated fraction identity (from one to six), total, pine and spruce basal area, stand site index, mean age of the stand, mean shrub height and percentage cover of the shrub species. Before building the models, we identified which variables had a strong correlation (Spearman correlation coefficient > 0.6). For all three plant species we determined that total basal area, pine basal area and mean stand age were strongly correlated, as well as mean stand age and stand site index. For bilberry we also found that cover percentage and mean height were strongly correlated. For heather, mean age was strongly correlated with stand site index. Correlated variables were never included together in the same model.

Fraction ID (1–6) was included as an explanatory variable, but also in interaction with all the other explanatory variables included in each model. This allowed us to capture the effect of each explanatory variable on the individual fractions as well as their overall effect on all forage biomass fractions combined (sum of the proportions of fractions one to six). Plot nested in stand was included as a random intercept effect for bilberry and cowberry. Site was also included as a random intercept effect if it was excluded as an explanatory variable in the model. The same model structure indicated singular fit for heather, and accordingly, the random effects had to be excluded from the models of this species.

We determined model candidates per species as starting points for model selection, taking into account the collinearity between variables. We used the function dredge from the MuMIn package (Barton & Barton, 2015) to explore all possible model combinations and selected the model with the lowest AIC (see Appendix 3 for bilberry, 4 for cowberry and 5 for heather). Coefficients of determination (conditional and marginal R^2) were calculated using the function r2 in the performance package (Lüdecke et al., 2021) as developed by Nakagawa et al. (2017). If an interaction was present, we carried out a type III ANOVA test on the model. If the interaction was significant ($P < 0.05$), we re-specified the model to get individual slopes and P-values for the continuous variable within fraction. We then chose 3 models from all presented candidate models per species: the model with the lowest AIC; the model with the lowest AIC among those including ramet height; and the one among those who did not include ramet height and study site. By presenting additional models without height and site we gave a more flexible option to make the models easier to implement. Our model evaluation did not reveal any patterns when plotting the residuals against predicted values and against each predictor or when plotting the predicted values against the measured biomass proportions per shrub species.

Table 3

Candidate models for the relationship between biomass, and percentage cover and height of bilberry, cowberry and heather, as well as variables describing forest structure and site productivity. Sample size is indicated within brackets, consisting of the number of 0.25 m^2 quadrates in which each shrub species was present. All 7 models were built using the same variables for each of the studied plant species.

Independent variable	Units	Range in inventory data						Models						
		Bilberry (n = 379)		Cowberry (n = 359)		Heather (n = 98)								
		Min	Max	Min	Max	Min	Max	1	2	3	4	5	6	7
Percentage plant cover	%	0.1	83.0	0.1	76.0	0.1	96.0	x		x	x	x	x	x
Percentage plant cover in SB	%	0.1	83.0	0.1	51.0	0.1	92.0		x					
Percentage plant cover in HB	%	0.2	81.0	0.1	76.0	1.0	96.0		x					
Percentage plant cover in NB	%	0.5	63.0	0.1	62.0	0.2	59.0		x					
Total basal area	m^2/Ha	0.02	70.71	0.02	70.71	0.09	42.68			x				
Pine basal area	m^2/Ha	0	35.46	0	35.46	0	35.46				x			
Spruce basal area	m^2/Ha	0	50.14	0	50.14	0	19.80				x	x		
Site Index	m	20	36	20	36	20	36					x		
Mean age	years	7	169	7	169	10	132						x	
Mean plant height	cm	1.2	50.4	3.7	46.8	5.2	66.4							x

Table 4

Linear mixed models describing the relationship between bilberry (table 4.1), cowberry (table 4.2) and heather (table 4.3) biomass and cover, as well as other explanatory variables. The response variable is the natural logarithm of dry biomass in grams per m^2.

4.1 Bilberry

	Coefficient	Bilberry cover	Bilberry cover SB	Bilberry cover HB	Bilberry cover NB	Total basal area	Pine basal area	Spruce basal area	Site Index	Mean stand age	Bilberry height	ICC	Marginal R^2 / Conditional R^2	AIC
Model 1	*Estimates*	1.05										0.92	0.51 / 0.96	798.6
	Conf. Int (95%)	1.00–1.09												
	Statistic	42.93												
	P-Value	**<0.001**												
Model 2	*Estimates*		1.12	0.97	1.15							0.91	0.54 / 0.96	787.8
	Conf. Int (95%)		1.03–1.21	0.90–1.03	1.06–1.24									
	Statistic		24.94	30.21	24.77									
	P-Value		**<0.001**	**<0.001**	**<0.001**									
Model 3	*Estimates*	1.02				0.04						0.86	0.69 / 0.96	738.1
	Conf. Int (95%)	0.97–1.06				0.03–0.05								
	Statistic	44.06				8.99								
	P-Value	**<0.001**				**<0.001**								
Model 4	*Estimates*	1.01					0.05	0.02				0.85	0.72 / 0.96	734.1
	Conf. Int (95%)	0.97–1.06					0.04–0.07	−0.00–0.04						
	Statistic	44.09					8.44	1.83						
	P-Value	**<0.001**					**<0.001**	0.067						
Model 5	*Estimates*	1						−0.03	0.06			0.6	0.83 / 0.93	623
	Conf. Int (95%)	0.95–1.04						−0.05–−0.02	0.05–0.06					
	Statistic	47.75						−4.67	19.23					
	P-Value	**<0.001**						**<0.001**	**<0.001**					
Model 6	*Estimates*	1.02								0.02		0.85	0.72 / 0.96	730
	Conf. Int (95%)	0.97–1.06								0.01–0.02				
	Statistic	44.3								9.76				
	P-Value	**<0.001**								**<0.001**				
Model 7	*Estimates*	0.81									0.06	0.76	0.77 / 0.95	679.9
	Conf. Int (95%)	0.75–0.87									0.05–0.07			
	Statistic	26.09									11.03			
	P-Value	**<0.001**									**<0.001**			

4.2 Cowberry

	Coefficient	**Cowberry cover**	**Cowberry cover SB**	**Cowberry cover HB**	**Cowberry cover NB**	**Total basal area**	**Pine basal area**	**Spruce basal area**	**Site Index**	**Mean stand age**	**Cowberry height**	**ICC**	**Marginal R^2 / Conditional R^2**	**AIC**
Model 1	*Estimates*	1.02										0.91	0.47 / 0.95	728.3
	Conf. Int (95%)	0.96–1.08												
	Statistic	34.9												
	P-Value	**<0.001**												
Model 2	*Estimates*		0.96	1.03	1.05							0.91	0.47 / 0.95	730.4
	Conf. Int (95%)		0.85–1.07	0.95–1.11	0.97–1.14									
	Statistic		17.46	24.91	24.11									
	P-Value		**<0.001**	**<0.001**	**<0.001**									
Model 3	*Estimates*	1.01				0.04						0.84	0.64 / 0.94	670.9
	Conf. Int (95%)	0.95–1.06				0.03–0.05								
	Statistic	36.57				8.61								

(*continued on next page*)

Table 4 (*continued*)

	P-Value	**<0.001**				**<0.001**								
Model 4	*Estimates*	1					0.05	0.02				0.83	0.66 / 0.94	669.5
	Conf. Int (95%)	0.95–1.05					0.04–0.06	0.00–0.05						
	Statistic	36.32					7.6	2.23						
	P-Value	**<0.001**					**<0.001**	**0.026**						
Model 5	*Estimates*	1						−0.02	0.05			0.54	0.81 / 0.91	574.1
	Conf. Int (95%)	0.95–1.05						−0.04–−0.01	0.05–0.06					
	Statistic	39.5						−3.05	16					
	P-Value	**<0.001**						**0.002**	**<0.001**					
Model 6	*Estimates*	1.01								0.02		0.83	0.68 / 0.95	666.8
	Conf. Int (95%)	0.95–1.06								0.01–0.02				
	Statistic	36.64								8.95				
	P-Value	**<0.001**								**<0.001**				
Model 7	*Estimates*	0.9									0.06	0.75	0.75 / 0.94	617.3
	Conf. Int (95%)	0.84–0.96									0.05–0.07			
	Statistic	30.39									11.71			
	P-Value	**<0.001**									**<0.001**			

4.3 Heather

	Coefficient	**Heather cover**	**Heather cover SB**	**Heather cover HB**	**Heather cover NB**	**Total basal area**	**Pine basal area**	**Spruce basal area**	**Site Index**	**Mean stand age**	**Heather height**	**ICC**	**Marginal R^2 / Conditional R^2**	**AIC**
Model 1	*Estimates*	1.26										0.81	0.71 / 0.95	259.1
	Conf. Int (95%)	1.08–1.44												
	Statistic	13.55												
	P-Value	**<0.001**												
Model 2	*Estimates*		1.27	1.23	1.26							0.82	0.70 / 0.95	262.9
	Conf. Int (95%)		1.08–1.47	1.00–1.46	0.99–1.52									
	Statistic		12.93	10.31	9.21									
	P-Value		**<0.001**	**<0.001**	**<0.001**									
Model 3	*Estimates*	1.2				0.05						0.75	0.74 / 0.94	234.2
	Conf. Int (95%)	1.08–1.33				0.03–0.06								
	Statistic	18.58				5.19								
	P-Value	**<0.001**				**<0.001**								
Model 4	*Estimates*	1.23					0.04	0.08				0.71	0.76 / 0.93	234.6
	Conf. Int (95%)	1.09–1.37					0.01–0.06	0.03–0.13						
	Statistic	16.89					3.06	3.09						
	P-Value	**<0.001**					**0.002**	**0.002**						
Model 5	*Estimates*	1.04						0	0.06			0.28	0.91 / 0.94	154.9
	Conf. Int (95%)	0.96–1.12						−0.03–0.03	0.05–0.07					
	Statistic	26.3						−0.14	12.41					
	P-Value	**<0.001**						0.886	**<0.001**					
Model 6	*Estimates*	1.22								0.01		0.73	0.77 / 0.94	233.4
	Conf. Int (95%)	1.09–1.34								0.01–0.02				
	Statistic	18.68								5.24				
	P-Value	**<0.001**								**<0.001**				
Model 7	*Estimates*	0.99									0.05	0.52	0.87 / 0.94	212.6
	Conf. Int (95%)	0.87–1.11									0.03–0.06			
	Statistic	16.02									8.2			
	P-Value	**<0.001**									**<0.001**			

3. Results

3.1. Above-ground biomass models

The percentage cover of bilberry, cowberry and heather was the most important explanatory variable in predicting the above-ground biomass of these plant species (Table 4, model 1: 0.96 conditional R^2 for bilberry, 0.95 for cowberry and heather; 0.51 marginal R^2 for bilberry, 0.47 for cowberry and 0.71 for heather, see also Appendix 2 for graphs showing observed vs. predicted (back transformed) model results for each shrub species). Including site as a fixed effect instead of a random effect (Table 4, model 2), did not substantially improve the models (0.54 marginal R^2 for bilberry, 0.47 for cowberry and 0.70 for heather). Forest stand characteristics, in addition to cover, improved the prediction ability of our models. Total basal area had a positive effect on the biomass of all three species (Table 4, model 3: 0.69 marginal R^2 for bilberry, 0.64 for cowberry and 0.74 for heather), as did the basal area of pine in combination with spruce basal area (Table 4, model 4: 0.72 marginal R^2 for bilberry, 0.66 for cowberry and 0.76 for heather). However, total basal area and pine basal area were tightly correlated in our data, making it impossible to discern which of these two variables was responsible for the positive effect. The best performing model did not include either total or pine basal area. Instead, the best performing model for all three species included site index, which had a positive effect on the biomass of all three plant species, and spruce basal area, which had a significant negative impact on the biomass of bilberry and cowberry, and no significant effect on heather biomass (Table 4, model 5: 0.83 marginal R^2 for bilberry, 0.81 for cowberry and 0.91 for heather). Mean age of the stand was found to positively affect the biomass of the three plant species (Table 4, model 6: 0.72 marginal R^2 for bilberry, 0.68 for cowberry and 0.77 for heather). Combining plant height and percentage cover also improved model predictions when compared to model 1 (Table 4, model 7: 0.77 marginal R^2 for bilberry, 0.75 for cowberry and 0.87 for heather, see also Appendix 2 for observed against predicted back transformed model results for each shrub species).

3.2. Bite diameter

Across both sampling occasions we measured a total of 788 bites by cervids in bilberry, 528 in cowberry and 561 in heather (Appendix 6). For bilberry, most of the bites we found had a diameter between 1.23 (10% quantile) and 2.05 mm (90% quantile), the latter is close to the thicker limit of fraction 6 (2 mm). For cowberry most bites were found between 0.74 (10% quantile) and 1.18 mm (90% quantile), and the latter falls close to the thicker limit of fraction 5 (1.3 mm). Most of the measured heather bites were found between 0.53 (10% quantile) and 1.10 mm (90% quantile), the latter being close to the thicker limit of fraction 4 (1.1 mm).

The two-way ANOVA for bilberry (Fig. 3, A, Appendix 7), showed that the mean bite diameter was significantly different between sites ($F = 6.66$, $P = 0.010$); being larger in HC (Tukey HSD $P < 0.001$), and also different between years ($F = 13.90$, $P < 0.001$), as well as being larger in 2020 compared to 2021 in LC ($P = 0.019$). For cowberry (Fig. 3, B), we found a significant interaction between site and sampling year ($F = 10.64$, $P = 0.001$), and bite diameter was different between sites ($F = 136.13$, $P < 0.001$); being larger in HC ($P < 0.001$), and between sampling years ($F = 21.14$, $P < 0.001$), as well as being larger in LC in 2021 ($P < 0.001$). For heather (Fig. 3, C), we found a significant interaction between site and sampling year ($F = 7.09$, $P = 0.008$) and no significant differences between sites ($F = 0.95$, $P = 0.331$), whereas bite diameter was larger in 2020 in LC ($P < 0.001$).

3.3. Forage biomass models

3.3.1. Forage biomass fraction models for bilberry

From the 18 full models (Appendix 3) model 3 had the lowest AIC score (-1245.5, conditional $R^2 = 0.53$, Appendix 8, see also Appendix 9 for graph showing observed vs. predicted back transformed model results). This model included the variables: fraction ID ($P < 0.001$ for the ANOVA test), spruce basal area ($P = 0.023$), site index ($P < 0.001$) and the interaction between ramet height and fraction ($P < 0.001$). Both spruce basal area and stand site index had a positive effect on the forage biomass proportion. Ramet height had a positive effect on biomass in fractions 4 ($P = 0.011$), 5 ($P < 0.001$) and 6 ($P < 0.001$), and no significant effect on fractions 1, 2 and 3 ($P = 0.081$–0.918). Model 6 was the model with the lowest AIC score (-1220.0, $R^2 = 0.54$) among the models that did not contain the variable ramet height. It incorporated the variables fraction ($P < 0.001$), pine basal area ($P = 0.037$), the interaction between site and fraction ($P < 0.001$), and the interaction between cover of bilberry and fraction ($P < 0.001$). Pine basal area had a negative effect on the forage biomass proportion. Cover had a positive effect on biomass in fractions 4 ($P = 0.050$), 5 ($P < 0.001$) and 6 ($P < 0.001$), and no significant effect on biomass in fractions 1, 2 and 3 ($P = 0.323$–0.507). Model 2 had the lowest AIC score (-1209.2, $R^2 = 0.51$) among those models that did not contain the variables height and site. It included fraction ($P = 0.178$), spruce basal area ($P = 0.077$), the interaction between stand site index and fraction ($P = 0.002$), and the interaction between cover and fraction ($P < 0.001$). Cover had a positive effect on biomass in fractions 5 ($P < 0.001$) and 6 ($P < 0.001$), and no effect on fractions 1 to 4 ($P = 0.090$–0.451). Site index had a positive effect on biomass in fractions 1 ($P = 0.032$), 2 ($P = 0.021$) and 4 ($P = 0.011$), negative effect on fraction 6 ($P = 0.046$), and non-significant effects on 3 ($P = 0.258$) and 5 ($P = 0.892$).

3.3.2. Forage biomass fraction models for cowberry

For cowberry, out of 12 full GLMM models (Appendix 4), model 1 had the lowest AIC score (-1149.9, conditional $R^2 = 0.64$, Appendix 10 see also Appendix 11 for graph showing observed vs. predicted back transformed model results). This model included the variables: fraction ID ($P < 0.001$), percentage cover ($P = 0.054$) and the interaction between fraction and site ($P < 0.001$), ramet height ($P < 0.001$) and spruce basal area ($P = 0.003$). Height had a positive effect on biomass in fraction 6 ($P < 0.001$) and no effect on the other fractions ($P = 0.053$–0.273). Spruce basal area had a positive effect on biomass in fraction 2 ($P = 0.012$), negative on fraction 5 ($P = 0.014$) and no effect on fraction 1, 3, 4 and 6 ($P = 0.088$–0.848). Model 3 (-1133.4, $R^2 = 0.60$) was the model with the lowest AIC among those that did not include the variable ramet height. It included fraction ($P < 0.001$), the interaction between site and fraction ($P < 0.001$) and the interaction between spruce basal area and fraction ($P = 0.002$). Spruce basal area had a negative effect on biomass in fraction 5 ($P = 0.007$) and 6 ($P = 0.040$), and no effect on fractions from 1 to 4 ($P = 0.037$–0.622). Model 4 (-1115.5, $R^2 = 0.59$) was the next best fitting model among those that did not contain height or study site. It included the variables fraction ($P < 0.001$), the interaction between spruce basal area and fraction ($P = 0.003$), and the interaction between stand site index and fraction ($P < 0.001$). Spruce basal area had a negative effect on biomass in fraction 4 ($P = 0.034$) and 5 ($P = 0.002$), and no significant effects on fraction 1, 2, 3 and 6 ($P = 0.103$–0.364). Site index had a positive effect on biomass in fraction 1 ($P = 0.002$), negative on fraction 3 ($P = 0.010$), and no significant effect on fraction 2, 4, 5 and 6 ($P = 0.078$–0.837).

3.3.3. Forage biomass fraction models for heather

From 12 full GLM models (Appendix 5), model 1 had the lowest AIC score (-741.9, marginal $R^2 = 0.33$ Appendix 12, see also Appendix 13 for graph showing observed vs. predicted back transformed model results). This model included the variables: fraction ID ($P < 0.001$), ramet height ($P = 0.012$), the interaction between spruce basal area and fraction ($P <$

0.001) and the interaction between fraction and study site ($P < 0.001$). Spruce basal area had a negative effect on biomass fraction 6 ($P < 0.001$). Ramet height had a negative effect on the forage biomass proportion. Model 6 (-739.8, marginal $R^2 = 0.33$) was the next best fitting model among those that did not contain ramet height. It included the variables fraction ($P < 0.001$), pine basal area ($P = 0.041$), the interaction between spruce basal area and fraction ($P < 0.001$), and the interaction between site and fraction ($P < 0.001$). We found that site and spruce basal area showed the same response as for model 1, and pine basal area had a positive effect on the forage biomass. Model 4 (-724.7, marginal $R^2 = 0.30$) did not include height and study site but had the highest AIC from all the obtained models. This model only included the interaction between spruce basal area and fraction ($P = 0.005$), with a positive effect on biomass in fraction 5 ($P = 0.036$), negative on 6 ($P = 0.001$), and no effects on fractions 1 to 4 ($P = 0.123$–0.982).

4. Discussion

The key finding of this study is that not only can we model above-ground biomass of the three foundation understory plant species bilberry, cowberry and heather growing in boreal and hemiboreal forests, but also predict the proportion that provides forage for wild cervids. To our knowledge this has not been done before and we believe it improves our abilities to estimate current biomass and predict future development of this key resource (see Monzingo et al. (2022) for similar results using other plant species). Furthermore, we show that these models can be improved further by including specific stand characteristics, determined by forest management, in addition to the plant's percentage cover. Our models can also take into consideration variable cervid browsing levels, and are thus dynamic with respect to both browsers and forest management. We discuss the best fitting models for the above-ground biomass, followed by the forage biomass models and their effects on individual diameter fractions, focussing on the most important independent variables included.

Whereas percentage cover was the best predictor for modelling above-ground biomass of the three studied plant species (marginal R^2 values of 0.51 for bilberry, 0.47 for cowberry and 0.71 for heather), there were a number of additional variables that can be used to improve predictions. Ramet height was found to be a highly explanatory variable when used in combination with cover to determine biomass, increasing the marginal R^2 to 0.77 for bilberry, 0.75 for cowberry and 0.87 for heather. Whereas stem thickness could also have important effects on shrub biomass, we showed that our two variables were sufficient on their own to realistically predict biomass. This result also indicates that overstory tree data is not crucial (though beneficial, see below), when estimating the biomass of these three shrub species. Notably, Elzein et al. (2011) also predicted above-ground biomass of bilberry and cowberry in alpine regions only using data of their percentage cover and ramet height, obtaining high coefficients of determination (0.80 adjusted R^2 for bilberry and 0.59 for cowberry).

The aim of this study was not to tease out the ecological relationships between biomass and site characteristics, but to include such variables to improve biomass predictions. Of the forest stand related variables that were included in our analyses, the best fitting models for the three shrub species included spruce basal area and site index (marginal R^2 of 0.83 for bilberry, 0.81 for cowberry and 0.91 for heather), in addition to shrub percentage cover. In our models, site index had a positive linear influence on the amount of biomass. This partly confirms previous findings that site fertility plays a major ecological role for ericaceous shrubs (Miina et al., 2021; Hedwall et al., 2013). However, over larger ranges of site fertility than were included in our data, the response can be unimodal (Hedwall et al., 2013) with a decrease in biomass at high fertility. A comparison between our results and the ones presented by Hedwall et al. (2013) is however speculative, as they investigated the direct effect of fertility on cover, whereas we model the additional effect of fertility on the cover-biomass relationship. Spruce basal area had a significant negative effect on the above-ground biomass of both bilberry and cowberry (due to covariation between total basal area and pine basal area in our data, their effects (both positive) on above-ground biomass could not be separated). While an increase in basal area generally means a decrease in light availability, the tree species composition plays a major role in this relationship (Eldegard et al., 2019). Compared to pine dominated forests, spruce forests are known to create darker environments (Petersson et al., 2019), which can be negative for these understory plant species resulting in less cover (Hedwall et al., 2013; Miina et al., 2009) and biomass (Kuusipalo (1983) and this study). Although we did not measure light availability directly in these stands, there is strong evidence for negative correlation between spruce basal area and understory light levels (Petersson et al., 2019). Surprisingly, we did not find the same effect of spruce basal area on heather biomass. Previous studies have shown that heather cover increases with increasing light availability (Gaudio et al., 2011). Notably, in our data heather was only found in those spruce stands occurring at lower ranges of basal area (see Table 3), and plots with zero-occurrence were not included in the analyses, which possibly caused this lack of a relationship.

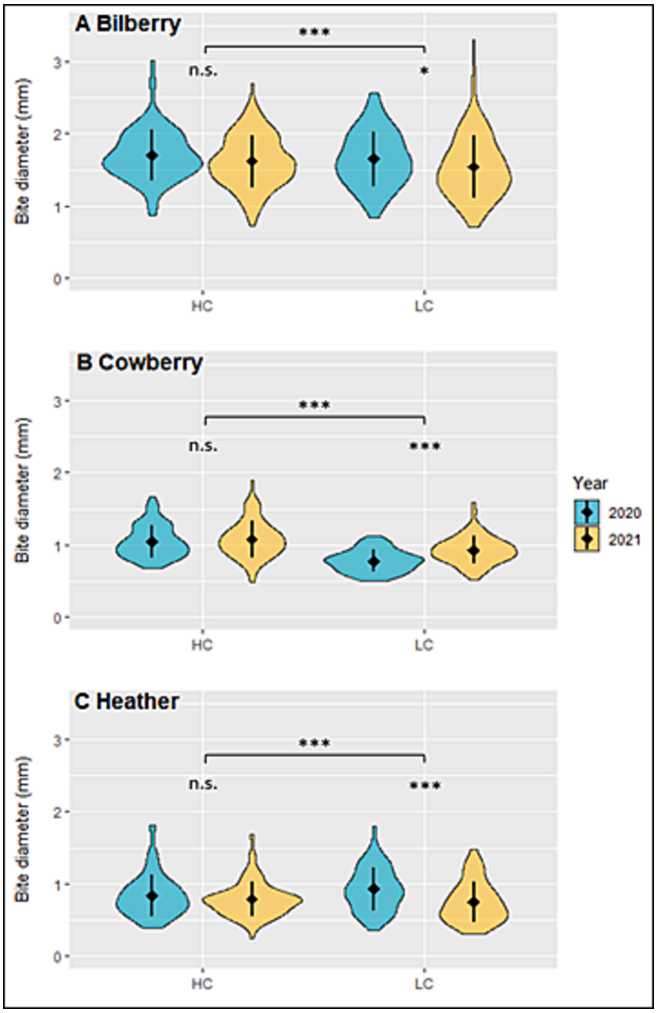

Fig. 3. Violin graphs showing the means and distributions of the measured diameter bites on stems of bilberry (A), cowberry (B) and heather (C), in the high cervid density (HC) and low cervid density (LC) locations, carried out in 2020 and 2021. "***" is $P < 0.001$, "*" is $P \leq 0.05$ and "n.s." is $P > 0.05$ from a two-way analysis of variance (ANOVA) and pair-wise Tukey HSD test with interaction effect (Appendix 7).

We also determined that study location did not substantially improve the models when added to cover (change in marginal R^2 was: $\Delta 0.103$ for bilberry, $\Delta 0.00$ for cowberry and Δ-0.01 for heather). Most likely, percentage cover is already capturing some of the between-site variation, which makes it a strong variable for predictions of above-ground biomass of shrubs regardless of their location.

Browsing intensity has an influence on the plants' ramet height and reproductive success (e.g. bilberry, Hegland et al. (2005)). Although ericaceous species are known to be highly resilient when it comes to normal levels of browsing (Angelstam et al., 2017; Tolvanen, 1994), the potential effect of browsing on the plants in our study should not be disregarded, and could have influenced both their biomass, and the distribution of biomass among fractions. For example, if our sites were located in regions with high browsing pressure, this could result in biomass underestimation, and potentially bias our models. However, we didn't identify a large number of browsed ramets in study locations NB, HB and SB. It is important nonetheless to consider this issue when applying the models to predict above-ground biomass of these plant species in areas with very high browsing pressure.

Although cover of ericaceous shrubs is often collected in forest inventories, the methodology to obtain cover data on ground vegetation is not universal, which can make comparison among data from different sources difficult (Alberdi et al., 2010). For example, plot sizes can vary, which may influence observer bias and the accuracy of estimations. In our study, a single observer visually estimated understory cover percentage in an area of 0.25 m^2. In contrast, the Swedish NFI uses a 100 m^2 plot, with cover estimates made by observers that vary among locations and years, requiring strict calibration. In order to implement the biomass fractions presented in this study at a larger spatial scale, differing methodologies for data collection must be compared and potentially calibrated. In this regard, caution is advised when applying the functions to other years and seasons, due to potential intra and inter-annual variation in shrub biomass.

When taking the step from predicting above-ground biomass to predicting forage biomass, a key consideration is that not all above-ground biomass is consumed. We found significant (although minor) between-site differences in the bite diameters in bilberry and cowberry, which were larger in the high cervid density area. This indicates that cervid population density influences the degree of biomass utilisation, which requires consideration if accurately estimating forage biomass at local scales. We included a dynamic aspect in our models, considering six biomass fractions that depended on the thickness of the ramets stem, that allowed their use at varying cervid densities.

Overall, in the forage biomass models for the three species (based on the proportion of each fraction to the total plants' biomass), percentage cover did not play as important a role as it did for the above-ground biomass models. Shrub height on the other hand, was present in the best fitting models for all three species. In all species, height had a positive effect on some of the thickest fractions, showing that taller plants have a larger proportion of thick stems. Specifically, we found that taller plants have a smaller biomass proportion of what we considered to be edible by cervids. The N:C ratio and palatability of the shrubs likely decreases towards the thicker parts of the plant, as observed for other foraged plant species (Shipley et al., 1999; Palo et al., 1992) edible by cervids, which in the majority of cases was below 2 mm in diameter (Fig. 3).

The basal area of spruce, and to some extent pine, were both important explanatory variables in the forage biomass models. For bilberry, we found a positive effect of spruce basal area on the forage biomass proportion, and for cowberry and heather, spruce basal area had a negative effect on some of the thicker biomass fractions. This implies that in spruce dominated forests a larger proportion of the shrubs' total biomass is within the range of what the animals normally utilise, which could make these plants more sensitive to browsing by cervids. For pine stands we found the opposite pattern in bilberry, where pine basal area had a negative effect on the forage biomass proportion. This could indicate that these shrubs are larger and have proportionally less biomass generally utilized by cervids. Spruce basal area was consistently a crucial variable in our models, having a negative impact on above-ground biomass of bilberry and cowberry. The management-driven expansion of spruce forest in Sweden may therefore have resulted in not only a decline in the two-dimensional prevalence of shrubs on the ground (Hedwall et al., 2013), but also a decline along a third spatial dimension, as indicated by the above ground biomass. This may cause wild cervids to preferably utilize forests with a different overstory composition to find shrub forage, or to switch to other sources of forage, such as tree saplings.

Presenting three candidate models per plant species allowed us to determine the additional predictive value that may be gained by including ramet height and study site. These two additional variables do come with some limitations: site restricts our predictions to the areas where our study was carried out, and measurements of ramet height are rarely collected in forest inventories. It is therefore a positive outcome for the potential future application of our models that, even though the best fitting models for all three species contained either or both of these variables, variation was explained almost as well by models lacking these two additions. For example, in bilberry, the difference between our best fitting model (model 3), and the model without height (model 6) is 2% of explained variation, and 4% when we exclude site. Ramet height is, however, an easily accessible measure in comparison to many stand variables and may therefore be recommended for inclusion in inventories of dwarf shrubs, where tree data, for example, isn't already collected.

5. Conclusions

In this study we presented models to predict above-ground and forage biomass of the shrubs bilberry, cowberry and heather. We showed that percentage cover is essential when modelling above-ground biomass of the three shrub species, and that stand site index and spruce basal area generally improve our predictions for both total above-ground biomass and forage biomass. We also showed how study site did not play a major role in explaining the variation of the above-ground and forage biomass of the three shrubs, meaning that our models have a higher likelihood of working similarly in other productive boreal forests. Because the models presented in this study are built with variables which are readily available in many large-scale forest inventories, they could potentially be included in forestry decision support systems. By doing so, our models could help researchers and managers working with various wildlife species explore the effect of different forest management alternatives on shrub availability, and thereby maintain or promote the biomass of these highly important components of forest ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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