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The puzzle of forestry and cervid interactions

A missing piece is in the understory

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Abstract

Shrubs of the family Ericaceae, including bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*) and heather (*Calluna vulgaris*), often dominate the understory in Eurasian boreal and cold-temperate forests. These ericaceous shrubs play crucial roles in forest ecosystems, acting as foundation species for forest communities, as well as influencing carbon cycles and the delivery of other ecosystem services. They also provide a key food resource for various wildlife, including cervids. However, over recent decades, forestry induced changes to the tree layer is thought to have reduced habitat suitability and thus the abundance of these shrubs in Sweden. Nevertheless, the precise nature of how the overstory impacts ericaceous shrubs remains largely unquantified. This thesis investigated the impact of the forest overstory on three species of ericaceous shrubs, focusing on the tree species composition and density of forest stands distributed along a large latitudinal gradient in Sweden. We carried out biomass collections and measurements, surveys, and a three-year browsing exclosure experiment. We quantified how forest stand characteristics shaped the above-ground biomass, growth, morphology, and macro-nutritional composition of these shrubs. We determined that Norway spruce (*Picea abies*) dominated stands had comparatively less above-ground biomass of the three focal species than Scots pine (*Pinus sylvestris*) stands; their plants were also shorter, and a larger proportion of their biomass provided suitable forage for cervids (I). These shorter shrubs also provided a larger proportion of new shoot biomass (II) and had a different macronutrient composition (IV) compared to shrubs in more open stands. These findings indicate that forest owners' decisions regarding tree species composition and density have a strong influence on the biomass, morphology, and nutritional composition of these plant species in Sweden. Three years of exclusion to large cervids' browsing did not reveal differences in the plants' growth and morphology in pine dominated stands (III). In addition to providing new insights into the ecology of ericaceous shrubs, we also provide biometric functions to predict the above-ground and forage biomass of the three shrubs (I), and models to predict their production of annual shoot biomass (II). In summary, our results provide a better understanding of canopy influences on ericaceous shrubs growing in conifer forests. This thesis provides tools that can help improve the management of these shrub species, and greatly increase our ability to determine stand and landscape scale availability of this food resource for cervids. We consider our findings within the larger context of landscape scale management, and highlight the importance of ensuring the continued maintenance of these ericaceous shrubs and the diverse range of ecosystem services they provide.

Keywords: *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Calluna vulgaris*, Conifer stands, Biomass modelling, Cervid forage, Nutritional balancing, Moose, Forest management

Skogsskötsel och klövvilt i samspel – fodret i fältskiktet är en viktig pusselbit

Abstract

Risväxter som tillhör familjen Ericaceae dominerar ofta fältvegetationen i nordliga skogar. Exempel på sådana arter är blåbär (*Vaccinium myrtillus*), lingon (*V. vitis-idaea*) och ljung (*Calluna vulgaris*). Dessa risväxter tillhandahåller ett stort antal ekosystemtjänster och fungerar även som en viktig födokälla för olika viltarter, inklusive hjortdjur. Skogsbrukets påverkan på trädskiktet under de senaste årtiondena verkar dock ha minskat habitatkvaliteten för dessa buskar och därmed deras förekomst i Sverige, men exakt hur trädskiktet påverkar dem är inte klargjort. Denna avhandling behandlar hur blåbär, lingon och ljung påverkas av trädskiktet, med fokus på trädartsblandning och grundyta, längs en latitudinell gradient i Sverige. Genom biomassainsamlingar, skogliga inmätningar och genomförandet av ett treårigt hägnförsök, kvantifierade vi hur skogens egenskaper påverkar risväxternas ovanjordiska biomassa, tillväxt, morfologi och näringsinnehåll. Vi fann att blåbär, lingon och ljungbuskar i bestånd dominerade av gran (*Picea abies*) hade jämförelsevis mindre biomassa än buskar i tallskogar (*Pinus sylvestris*); den täta granskogens risväxter var också kortare och en större andel av deras biomassa utgjordes av foder för hjortdjur (I). Dessa relativt små buskar bestod också av en större andel ny skottbiomassa (II) och hade dessutom ett annorlunda näringsinneåll (IV) jämfört med buskar som växte i mer öppna bestånd. Dessa resultat visar att skogsägares beslut angående sina skogars trädartssammansättning och täthet har en stark inverkan på tillväxt, morfologi och näringsinnehåll hos dessa risväxter. Tre års skydd från hjortdjurens betande visade inga skillnader på växternas tillväxt och morfologi i talldominerade bestånd (III). Förutom att leverera ny kunskap om ekologin hos de tre risväxtarterna tillhandahåller vi också biometriska funktioner för att prediktera deras totala ovanjordiska biomassa och foderbiomassa (I), och modeller för att förutsäga produktionen av årlig skottbiomassa (II). Sammanfattningsvis ger våra resultat en bättre förståelse för trädskiktets påverkan på blåbär, lingon och ljungbuskar som växer i barrskogar. Denna avhandling tillhandahåller också verktyg som kan hjälpa till att förbättra förhållandena för dessa risväxter och därmed en mångfald av ekosystemtjänster i svenska skogar.

Keywords: *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Calluna vulgaris*, Tallskogar, Biomassa-modeller, Klövviltsfoder, Näringsbalansering, Älg, Skogsskötsel

Dedication

To Henrik

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Juvany, L.*, Hedwall, P. O., Felton, A., Öhman, K., Wallgren, M., Kalén, C., Jarnemo, A., Johansen, H., and Felton, A. M. (2023). From simple metrics to cervid forage: Improving predictions of ericaceous shrub biomass. *Forest Ecology and Management*, 544, 121120. https://doi.org/10.1016/j.foreco.2023.121120

II. Juvany, L.*, Felton, A. M., Felton, A., Sayn, A., Kalén, C., Jarnemo, A., and Hedwall, P. O. Assessing the effect of forest stand characteristics on the annual growth of ericaceous shrubs in boreal forests (manuscript)

III. Juvany, L.*, Hedwall, P. O., Felton, A., Wallgren, M., Sayn, A., Johansen, H., Hofmeester, T. R., Jarnemo, A., and Felton, A. M. Growth and morphology of ericaceous shrubs in areas with different cervid densities: An exclosure experiment (manuscript)

IV. Felton, A. M.*, Juvany, L., Hedwall, P. O., Felton, A., Erbrech, J., Sayn, A., Morel, J., Wallgren, M., Jarnemo, A., Schönbeck, L., and Spitzer, R. Forest structure drives the macronutrient composition of *Vaccinium* winter forage for deer (submitted)

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*Corresponding author.

The contribution of Laura Juvany Canovas to the papers included in this thesis was as follows:

I. **L.J.**, P.O.H., and A.M.F. developed the research design and methodology; **L.J.** and H.J. conducted field- and lab work; **L.J.** performed statistical analyses; **L.J.** interpreted results and wrote the manuscript together with co-authors. A.M.F., P.O.H., A.F., C.K. and A.J. formulated the original idea.

II. **L.J.**, P.O.H., and A.M.F. developed the research design and methodology; **L.J.** and A.S. conducted field- and lab work; **L.J.** and A.S. performed statistical analyses; **L.J.** interpreted results and wrote the manuscript together with co-authors. A.M.F., P.O.H., A.F., C.K. and A.J. formulated the original idea.

III. **L.J.**, P.O.H., T.R.H. and A.M.F. developed the research design and methodology; **L.J.,** H.S., A.S. and A.M.F. conducted field- and lab work; **L.J.** and A.S. performed statistical analyses; **L.J.** interpreted results and wrote the manuscript together with co-authors. A.M.F., P.O.H., A.F., C.K. and A.J. formulated the original idea.

IV. A.M.F, **L.J.**, P.O.H., R.S. and A.S. developed the research design and methodology; **L.J.,** A.M.F., A.S., J.M. and J.E. conducted field- and lab work; **L.J.,** A.S., J.E. and J.M. performed statistical analyses; A.M.F. and **L.J.** interpreted results and wrote the manuscript together with co-authors. A.M.F., P.O.H., A.F. and A.J. formulated the original idea.

Abbreviations

C:N	Carbon to nitrogen ratio
NIRS	Near-infrared spectroscopy
ADF	Acid-detergent fibre
ADF-N	Insoluble nitrogen within the ADF fraction
aNDF	Amylase and sodium sulfite treated neutral-detergent fibre
WSC	Water soluble carbohydrates
TNC	Non-structural carbohydrates
TCH	Total carbohydrates
AP	Available protein

1. Introduction

The majority of the forest area in Sweden is managed for wood production. Sweden is the fifth largest exporter of timber products worldwide, despite accounting for only 1% of the world's total forest area (SFIF, 2023). Forest management relies mostly on clear-cutting and reforestation through planting (Kuuluvainen *et al.*, 2012), where monocultures of the two native coniferous species Scots pine (*Pinus sylvestris,* from here on pine) and Norway spruce (*Picea abies,* from here on spruce) make up 80% of Sweden's standing forest volume (Roberge *et al.*, 2023). The reduced diversity in the tree species that form the canopy layer, and the increase of practices such as soil scarification, fertilization, and harvesting at stand ages considerably younger than the trees' biological lifespans, have contributed to a decreasing environmental variation in Sweden's forests. These effects are putting the biodiversity and resilience of forest ecosystems at risk (Felton A. *et al.*, 2020).

One notable outcome of forest management is the reported decline in the cover of ericaceous shrubs in Fennoscandian forests (Hedwall & Brunet, 2016; Hedwall *et al.*, 2013; Miina *et al.*, 2009). The family Ericaceae has a nearly world-wide distribution and includes more than 4000 described species (Christenhusz & Byng, 2016). This is a morphologically diverse group of flowering plants that includes bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*). Over the past half century, the cover of these shrub species has declined by approximately 15% in the boreal region of Sweden, and by as much as 50% in the hemiboreal region (Hedwall *et al.*, 2019a).

These declines in ericaceous shrub cover are closely associated to the alterations in the forest overstory, where denser and darker forests (Roberge *et al.*, 2023; Sandström *et al.*, 2016) are causing a decrease in light availability in the understory, and a shift in plant species composition towards more shade-tolerant species (Hedwall *et al.*, 2019b). The widely used clear-cutting method has also been found to be detrimental for ericaceous shrubs in the short- (Atlegrim & Sjöberg, 1996) and long-term (Hedwall *et al.*, 2013). Ericaceous shrubs need a recovery time of between 80 and 100 years following clear-cutting, meaning that the current forest rotation periods do not provide sufficient time for the shrubs to fully recover. At the same time, the historical increase in air-borne nitrogen deposition is likely another driver of this decrease (Hedwall *et al.*, 2019a), as it diminishes the competitive ability of the ericaceous shrubs compared to more nutrient-demanding plants such as forbs and graminoids (Bobbink *et al.*, 2010). In addition, nitrogen deposition, together with fertilization that may be used as part of forest management practices, can promote tree growth, indirectly contributing to decreased light availability in the understory (Hedwall *et al.*, 2019a; From *et al.*, 2016). Climate change is yet another factor that has contributed to the observed decline in ericaceous shrubs, where not only the increase in temperature, but also the decrease in snow cover, could have already severely affected the prevalence of ericaceous shrubs (Kreyling *et al.*, 2012). In the coming years, climate change is expected to further reduce the distribution of ericaceous shrubs in Europe (Puchałka *et al.*, 2023). These declines not only raise concerns with respect to the future conservation status of the ericaceous shrub species themselves, but also the resultant impacts on other aspects of forest biodiversity and ecosystem services.

Ericaceous shrubs are important components of forest ecosystems, being widespread and dominant in large parts of boreal forests (Økland, 1996). These species provide multiple benefits to these ecosystems, and due to their large representation, are considered foundation species (*sensu* Dayton (1972), Hedwall *et al.* (2014)). Additionally, ericaceous shrubs play key roles in many forest ecosystem processes, from their role in carbon cycles (Hensgens *et al.*, 2020; Nilsson & Wardle, 2005), and the shelter provided for other plants (Brooker *et al.*, 2006) and wildlife such as capercaillie (*Tetrao urogallus*) and bank voles (*Clethrionomys glareolus*) (Selås *et al.*, 2021; Storch, 1993). There are also many species that depend on ericaceous shrubs as a food resource. For example, the fruit production of bilberry has been found to be a key component of the diets of brown bears (*Ursus arctos*) in Scandinavia, where body weights of females and yearlings increases linearly with bilberry abundance (Hertel *et al.*, 2018). This food resource is also important for species such as capercaillie (Selås, 2001) and grey-sided voles (*Craseomys rufocanus*) (Dahlgren *et al.*, 2007). Furthermore, berries produced by the two *Vaccinium* species have high economical and societal values due to the importance of berry picking in Scandinavian countries (Sténs & Sandström, 2013).

Besides the benefits mentioned above, the increasingly understood role that ericaceous shrubs play in the diets of large herbivore communities (cervids, members of the family Cervidae), has put them further under the spotlight. The browse provided by ericaceous shrubs constitute a major part of the diet of moose *Alces alces*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and fallow deer *Dama dama* in northern Europe (Schrempp *et al.*, 2019; Obidziński *et al.*, 2013; Barančeková *et al.*, 2010; Krojerová-Prokešová *et al.*, 2010; Wam *et al.*, 2010; Mysterud *et al.*, 1997; Hjeljord *et al.*, 1990; Cederlund *et al.*, 1980). For example, ericaceous shrubs may represent 50% or more of the cervids' annual diets in areas of Sweden with limited snow depth (Spitzer, 2019). Due to their dietary importance, declines in the abundance of ericaceous shrubs raise concerns that cervids may alter their foraging patterns to consume other woody plant species, which may in-turn exacerbate some of the drivers of the shrubs' decline. The potential for such a feedback arises because browsing impacts on economically important tree species has been a major concern in Sweden, where pine has been identified as more vulnerable to browsing (Felton *et al.*, 2022; Pfeffer *et al.*, 2022; Wallgren *et al.*, 2013) than spruce (but see Jarnemo *et al.* (2014)). This difference in browsing susceptibility and risk of damage has been identified as one of the contributing factors to the ongoing trend of people replacing pine stands with spruce in southern Sweden (Felton *et al.*, 2020; Petersson, 2019), the region where the decline of the ericaceous shrubs is more pronounced (Hedwall *et al.*, 2019a).

As the replacement of pine with spruce involves a shift to a tree species with a higher leaf area and lower crown (Felton *et al.*, 2020), the net result is a reduction in understory light levels and the potential suitability of large areas of production forest environments for ericaceous shrubs (Petersson *et al.*, 2019). Furthermore, throughout Sweden, the growing efficiency of forestry operations is increasing the basal area of production stands, which can likewise reduce habitat availability for the ericaceous shrubs (Felton A. *et* *al.*, 2020). However, the precise nature of how the production forest overstory impacts understory ericaceous shrubs remains largely unquantified, as is our capacity to project the resultant implications of changes to forest management on the availability of suitable understory forage for cervids. Predictions can be made, however, based on basic premises in plant ecology regarding how plants generally allocate their resources and how they respond to resource limitation. With insufficient light, ericaceous shrubs are expected to have a lower abundance, and thus lower above-ground biomass (Eldegard *et al.*, 2019). These conditions are likely to impact their annual production of new shoots, which can in-turn suppress their growth or trigger compensatory growth to cope with challenging conditions (Atlegrim & Sjöberg, 1996; Tolvanen, 1995). In clonal plant species, such resource limitation could also affect their morphology (e.g. height and number of branches), as well as the balance between carbon and nitrogen in their tissues (Bryant *et al.*, 1983). These measurable traits and responses would allow for a deeper understanding of how plants react to different overstory conditions.

In this thesis I tackle these complexities from both the plants' and cervids' perspective, and try to disentangle how the forest overstory shapes the biomass, growth, morphology and ultimately, macro-nutritional composition of the focal ericaceous shrub species. These efforts allow us to i) better understand some of the drivers underlying the shrubs' decline, ii) provide tools and recommendations for management that can be applied during the forest planning process, and iii) ultimately influence our ability to determine the impact of forest management on food availability for cervids, and thereby enable more informed decision making about cervid carrying capacity.

1.1 Thesis objectives

The overall objective of this thesis was to improve our knowledge on how forest stand related characteristics (such as stand density and tree species composition, which are the product of management decisions) influence the quantity, productivity and macro-nutritional composition of the ericaceous shrubs bilberry, cowberry and heather. The specific objectives for each paper are the following:

I. To build models for prediction of the three shrub species' above-ground biomass and forage biomass for cervids based on the shrubs' cover, plant height, and stand characteristics.
II. To understand how the growing habits of the three ericaceous shrubs are affected by forest stand characteristics.
III. To identify the effect of browsing on the growth and morphological traits of the ericaceous shrubs.
IV. To investigate if forest stand characteristics drive the macro-nutritional composition of bilberry and cowberry and how this affects the nutritional space for moose and other cervids.

2. Materials and methods

This section provides an overview of the methodology used in each paper in the thesis. For more detailed information, see the corresponding papers.

2.1 Study sites

In all four studies we aimed to incorporate a large latitudinal gradient. Study sites N (north Sweden, Vindeln, boreal region), C1 (central Sweden, Grimsö, boreal region), C2 (central Sweden inland, Siljansfors, boreal region) and S (south Sweden, Asa, temperate region), covered a wide environmental and climatic variation (Figure 1). Forest stands were selected within these areas incorporating a variation in tree species composition (pine or spruce), forest density, stand fertility and time since stand-replacing disturbance. Sites LC (Nordmaling) and HC (Öster Malma) are located within the boreal and temperate zone respectively. These sites are different in terms of their cervid population densities (Cromsigt *et al.*, 2023), with HC having relatively high densities and LC low. However, the two areas have a similar cervid species composition, consisting of moose, roe deer, red deer and fallow deer. The stands we selected in these two areas were all pine dominated and aged between 41 and 82 years, which provided favourable conditions for shrub development (with high light availability (Eldegard *et al.*, 2019) and recovery time after stand-replacing disturbance (Hedwall *et al.*, 2013)). Studies in each paper were carried out in the following study sites:

- Paper I: sites N, C1 and S; we sampled in 36 forest stands (12 in each site). Sites HC and LC were used to determine bite diameter of browsed shrubs, sampling in 20 stands (10 in each).
- Paper II: sites N, C2 and S; we sampled in 47 forest stands (15 in N and 16 in C2 and S, respectively).

- Paper III: sites LC and HC; we sampled in 20 forest stands (10 in each).
- Paper IV: sites N, LC, C2, HC and S (we used the same selected stands from paper II and III).

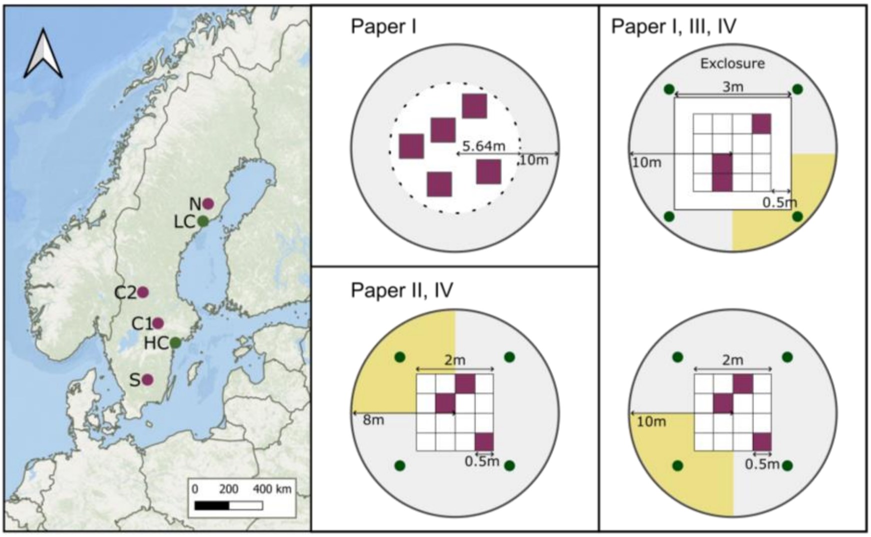


Figure 1. Map showing the location of the six study sites. Plot dimensions and design varied for each study. For all papers, the outer circle indicates the level at which data on the overstory layer were collected, within 8 m for paper II and IV and 10 m for the rest. Purple squares, of 0.25 m^2, represent the subplots, the unit for data collection of ericaceous shrubs. Green dots represent the approximate location where soil samples were collected. The central 2 x 2 m square was the sampling area for papers II and III, but note how in paper III we built an exclosure surrounding the square. Yellow shaded areas represent the quadrant where the sample collection for paper IV was carried out.

2.2 Paper I

To determine the relationship between the three ericaceous shrubs’ cover and their biomass, we collected data from 2-3 circular plots in each stand (36 stands in total, Figure 1), selected with the aim to capture as much variation as possible at the understory level within the stand. We carried out the data collection in July and beginning of August of 2019. We collected tree layer data within the plot, which had a 5.64 m (100 m^2) radius in the youngest stands (between 7 and 18 years since stand-replacing disturbance) and 10 m (314 m^2) radius in older stands. Within the central 5.64 m radius of each plot, we collected data on ericaceous shrubs in five 0.25 m^2 squared-shaped subplots (referred to as "quadrates" in Paper I). The measurements of the tree layer gave us data on basal area per tree species, mean stand age and site index (tree height in meters at 100 years' age, a proxy for stand fertility). In each subplot we visually estimated the percentage cover for each of the three shrub species. We also measured the top height (i.e. without stretching the ramet, from the top of the soil to the highest tip of the ramet) of the two tallest ramets per species. In clonal rhizomatous species, such as ericaceous shrubs, a ramet is the aerial shoot that branches from the horizontal below-ground rhizome. We then collected all above-ground biomass of the three species present in each of the five subplots. We recorded the total fresh wet weight per species in each subplot and collected a subsample to dry for 12h at 103^{o}C to assess relative water content per species.

To build forage biomass models, we selected ten representative ramets per species from the total biomass collected in each plot (i.e. material pooled from the five subplots). These ramets were used to estimate how the biomass was distributed along the stem. We separated leaves from stems, and measured all stems with an electronic calliper, cutting and splitting them into seven diameter fractions. Leaves were collated into an eighth fraction. We used a subset of ramets per sample to determine the leaves' distribution along the seven stem fractions. We calculated the proportion of each diameter fraction in relation to the total biomass of the ramet and used this as our dependent variable in the models. Additionally, we carried out a collection of ramets from the three shrub species browsed by cervids in sites HC and LC. We measured the diameter of the stem at the bite, which allowed us to determine which of the measured fractions could be considered as forage for the cervids.

2.3 Paper II

Data on the biomass of annual shoots produced by the three species of ericaceous shrubs were collected from a total of 47 forest stands. The data collection was carried out at the end of the growing season of 2020, prior to the plants entering dormancy. In each stand we selected three circular plots (Figure 1), where we carried out the same measurements for the overstory layer as described for Paper I. Additionally, we collected a total of four soil samples within each plot, consisting of the 10 cm top soil, including humus and mineral soil fractions. Samples were pooled per plot, dried, and the total carbon (C), nitrogen (N) and pH were measured. We calculated and used the C:N ratio in the analysis. We used the SLU moisture map (Ågren *et al.*, 2021) to extract the soil moisture value at the plot level.

In the centre of each plot, a 2 x 2 m square consisting of 16 0.25 m^2 subplots was used for the sampling of ericaceous shrubs. In each plot we randomly selected three subplots and collected three ramets per shrub species in each. For each ramet we measured the top height. After harvesting, we counted the number of terminal shoots per ramet (from here on referred to as the number of branches). We separated the new shoots' growth from the ramet, identifying them through observations on the coloration changes in stem and leaves between the new shoot biomass and the old biomass. We used the methods described in Tolvanen (1995) for bilberry, Shevtsova *et al.* (1997) and Tolvanen (1995) for cowberry, and Mohamed and Gimingham (1970) for heather, as reference material. New shoot biomass fraction and old biomass fraction were weighed after drying at 60°C until reaching a constant weight.

2.4 Paper III

In order to understand the effect of browsing on the growth and morphological traits of the ericaceous shrubs, we selected 10 pine-dominated stands in HC and LC respectively (Figure 1). In each stand, we selected two 10 m radius plots, targeting areas where, when available, both bilberry and cowberry were present. We conducted the same measurements of the overstory layer as described for Paper I. In the centre of each plot, we delimited a 2 x 2 m square divided into 16 0.25 m^2 subplots (same design as for Paper II). We randomly selected which of the two plots would serve as a control, and on the other we built an exclosure (2 m tall and 3 x 3 m wide) around the 16 subplots. Data were collected at the end of the growing season (August and September) for three consecutive years: 2020, 2021 and 2022.

In each plot and sampling occasion, we collected data from three randomly selected subplots. In each subplot we carried out the same plant measurements as we did for Paper II, measuring each ramet height, number of branches and separating the new shoot biomass from the old biomass.

We used camera traps to determine the effects of the cervids on the differences between control and exclosure treatments in the measured plant traits. Throughout each growing season (approximately between the months of April until September) we monitored each control plot using a camera trap (a total of 20). Images taken by the camera traps were classified using the software Trapper (Bubnicki *et al.*, 2016) and Wildlife Insights (Ahumada *et al.*, 2020). Pictures obtained from the cervid species moose, roe deer, red deer and fallow deer (Figure 2) allowed us to determine their passage rate (number of passages in each stand divided by the number of days the cameras were operable in each stand). Passage rates from camera traps are a consequence of cervid densities and the individuals' behaviour, and can thus be used to infer browsing pressure (Hofmeester *et al.*, 2019; Hofmeester *et al.*, 2017). We summed the passage rates of roe deer, red deer and fallow deer, creating a deer passage rate to determine the different effect of the smaller-bodied deer species compared to the moose on the shrubs' growth and morphological traits.

Figure 2. Pictures of the four cervid species considered in our study: moose (A), roe deer (B), red deer (C) and fallow deer (D), captured by the camera traps in our study sites.

2.5 Paper IV

To understand if forest characteristics influence macro-nutritional composition of the browse from the *Vaccinium* species, samples of bilberry and cowberry were collected in the same stands used in paper II and III (65 forest stands in total, Figure 1). Due to the large importance of the *Vaccinium* species as a winter food resource for the cervids in Sweden (Spitzer, 2019), we carried out our sample collection after dormancy had set in, during the months of October and November of 2021, starting in the north and continuing southwards. We selected two plots per stand and collected samples within the plot area and outside the 2 x 2 m central square (used for the sampling collection in Papers II and III). Within the sampling area, called quadrant, we cut handfuls of twigs of approximately 3-4 cm in length from the top layer of the plants, mimicking the feeding behaviour of cervids (as per Spitzer *et al.* (2023), Felton *et al.* (2021), Figure 3, referred to as the "mouthful" method). We collected material until we reached 60-100g of wet weight per species in each plot.

Figure 3. Sample collection of cowberry (on the left) and bilberry (on the right) to analyse their nutritional composition. We followed the mouthful method, collecting the first 3-4 cm on the top of ramets.

Samples were stored at -20°C shortly after collection, dried to 60°C for 24 hours until reaching a constant weight and then ground using a cutting mill. Due to the high cost of laboratory assays, we used near-infrared spectroscopy (NIRS) to estimate the concentrations of the nutritional constituents and analysed a subset of representative samples using wet chemistry for calibration purposes (i.e. 35% of the whole population of samples). Samples were analysed for ash, total nitrogen, acid-detergent fiber (ADF), ADF-N (insoluble nitrogen within the ADF fraction), crude fat, amylase and sodium sulfite treated neutral-detergent fiber (aNDF), lignin, starch, and water-soluble carbohydrates (WSC). Results from the lab were used to build multivariate regression models, where NIRS spectra were used as explanatory variables and the above-mentioned laboratory-measured traits were used as response variables, obtaining models to predict the concentrations of macronutrients for the whole data set.

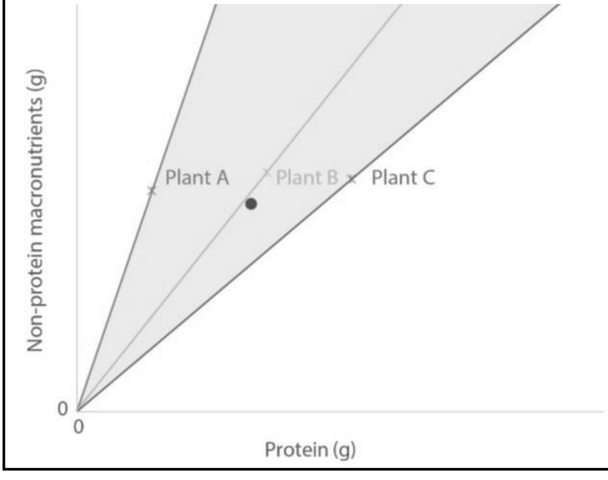
We calculated available protein (AP) and total carbohydrates (TCH, which is the sum of cellulose, hemicellulose and non-structural carbohydrates (TNC, the sum of starch and WSC)), and calculated the AP:TCH ratio, as we were interested in placing our findings in the context of cervid diet choice and nutritional balancing (text box 1). In this context, the AP:TCH ratio has been shown to be useful when relating nutritional composition of browse in relation to the moose' target balance (Spitzer *et al.*, 2023), which appears to coincide with the composition of browse from *Salix* spp. (Spitzer *et al.*, 2023; Felton *et al.*, 2016). The well-balanced nutritional composition of *Salix* twigs was first proposed by Felton *et al.* (2016), when carrying out a cafeteria experiment with captive moose, and has more recently been given support by Spitzer *et al.* (2023), with data on free-ranging moose.

We used the same plot and stand data collected for papers II and III to link the nutritional composition of the shrubs to the overstory and soil C:N, pH and moisture.

Text box 1. Background to nutritional balancing, with focus on macronutrients

It is becoming increasingly clear that foraging should be seen as a dynamic process which involves balancing the intake of many different nutrients and anti-nutrients to satisfy complex nutritional needs that change over multiple time scales (the Nutrient Balancing hypothesis, Simpson & Raubenheimer, 2012a). Here we focus on macro-nutrients, i.e. energy-providing compounds that occur in large amounts in plants. For ruminants, these include the protein available for digestion, non-structural carbohydrates (sugars and starches), digestible structural carbohydrates (cellulose and hemicellulose), and fats (also called lipids). The nutritional state of an individual can change with each meal. Thus, an ideal food choice at one moment may be less suited at another. Animals deal with this complexity by selecting foods to achieve a *target nutrient balance* over a given time period; a finding replicated both in controlled feeding experiments (e.g. Hewson-Hughes *et al.*, 2011; Raubenheimer & Jones, 2006), and in the wild (e.g. Raubenheimer *et al.*, 2015). As a result, animals continuously regulate the amounts they eat of different foods. While doing so, trade-offs are unavoidable, as different nutrients come as food packages, not individual units. Many studies of nutritional balancing use the Geometric Framework for nutrition (Simpson & Raubenheimer, 2012a), as illustrated in the figure below.

Figure TB1. Illustration of how the balance between protein (P) and non-protein macronutrients (NP) in forage items (plants A-C) can differ (P and NP can be expressed in energy or biomass units). The radials are called *food rails* and represent the nutritional balance of each item (x = laboratory value). The more an animal ingests (e.g. per meal or day), the further away from origin it ends up. When an animal is given uninhibited access to all food items, they can reach any point within the available *nutrient space* (shaded). The more items vary, the larger the nutrient space. Intake during uninhibited access indicates their *preferred target* (dot). While some forage items may provide a straight path to the target (Plant B), other items (A and C), may be combined to reach a similar composition. Such forage items are *complementary*.



2.6 Statistical analysis

All analyses in this thesis were performed in R (RCoreTeam, 2023), and considered a significance level of $\alpha = 0.05$. Prior to analysis, we carried out a collinearity test (Spearman correlation coefficient > 0.6) for the candidate explanatory variables in each model. All models were implemented in the glmmTMB function from the *glmmTMB* package (Brooks *et al.*, 2023). The random intercepts used in the presented mixed models depended on our study design. In Paper I, our data was analysed at subplot level, and the random intercept consisted of the plot nested into stand, site was also included in some models. In Papers II, III and IV, where data was analysed at the plot level, stand nested into site was used as random intercept. In Paper II and III, site was only included when it was not part of the fixed effects in a model. Coefficients of determination were calculated using the function r2 in the *performance* package (Lüdecke *et al.*, 2021) as developed by Nakagawa *et al.* (2017). We carried out a model evaluation for the presented models, which did not reveal any patterns when plotting the residuals against predicted values or against each predictor.

2.6.1 Paper I

The above-ground biomass per m^2 of the three shrub species were modelled using linear mixed models (LMMs). We included the following variables in our models: log percentage cover (of the specific plant species we built the model for), mean height of the shrub species, site, site index, mean stand age, pine, spruce and total basal area. We built a total of seven models, which included the same variables for the three plant species. The simplest model only included percentage cover, and we then tested the additional effect of adding other predictors listed above. The intercept was excluded from all models to force predictions through the origin.

We built generalized linear mixed models (GLMMs) with a beta error distribution and a logit link to model the relationship between the explanatory variables and the proportion of each fraction class per plant species. We included fraction ID (from 1 to 6) as an explanatory variable and also interacting with all other explanatory variables included in each model. This allowed us to determine the effect of the explanatory variables on each individual fraction ID from one single model. For each plant species, we first ran full models, and then explored all possible model combinations, selecting the model with the lowest AIC.

2.6.2 Paper II

To determine the effect of the stand and site characteristics (including basal area, spruce percentage, stand mean age, soil pH, C:N ratio and soil moisture) on the growth of the three shrub species, we calculated two parameters: absolute growth and relative growth. We define absolute growth as the average growth per ramet, obtained by dividing the total new biomass by the number of ramets sampled in each plot per species. This unit allows us to relate the plants' annual growth (g) to plot level differences in stand and site characteristics irrespective of the effects of these characteristics on the present biomass of the plants. The relative growth was calculated dividing the new shoot biomass by the old biomass from the harvested ramets per plot and species. Relative growth (%) provides a tool for predicting the yearly output of new biomass of these species relative to their existing biomass in forest stands given a certain canopy layer and soil conditions.

We built two different types of models using the absolute and relative growth of the shrubs as dependent variables. For bilberry and cowberry, we built GLMMs for the absolute growth (which followed a gamma distribution and log link) and LMMs for the relative growth (gaussian distribution with log link). For heather we built generalized linear models (GLMs) for the absolute growth and linear models (LMs) for the relative growth (absolute and relative growth of heather followed the same distribution and links as for bilberry and cowberry). We built two sets of models for each dependent variable, one included those independent variables associated with forest stand conditions (SM) and another set of models with predictors related to each shrub species (PM). We centred and standardized all independent variables, subtracting their mean and dividing by their standard deviation (SD). Starting with full models for SM, we carried out a backwards stepwise selection (removing the variable with the lowest explanatory effect on the dependent variable in each step) and obtained one final model per growth variable and plant species. The PM model set consisted of three models per growth variable and plant species: model 1 with percentage cover of the plant species, model 2 with cover and ramet height, and model 3 with these two variables plus the mean number of branches per ramet (only for bilberry and cowberry). From PM models we selected those with the lowest AIC per plant species and growth dependent variable (absolute and relative growth).

2.6.3 Paper III

To test the effect of the exclosure treatment on the ericaceous shrubs, we used the absolute growth (see statistical analysis from Paper II for definition), ramet height and number of branches as response variables. We run GLMMs with a gamma error distribution and log link for the dependent variables absolute growth and number of ramets, and we fitted LMMs with a gaussian distribution and identity link for ramet height. The fixed effects for both types of models were the treatment (control or exclosure), year, site, and their two-way and three-way interactions. We obtained the estimated marginal means to determine the contrasts between the exclosure and control plots within year and site.

To determine the effect of the cervids on the treatment effect we fitted a total of four models for each dependent variable and plant species, following the same distributions. Two models contained either deer passage rate or moose passage rate as a continuous fixed effect, and their two-way and three-way interaction with treatment and site. Additionally, we ran the same two models removing site from the fixed effects, to determine if there was a general effect of the cervid passages on the differences between treatments across sites.

2.6.4 Paper IV

Due to our *a priori* interest in macro-nutritional balancing by cervids, we assessed the effects of forest stand characteristics on the macro-nutritional composition of bilberry and cowberry by running a principal component analysis (PCA) per plant species. This allowed us to use a combined measure of the macronutrient mixture in each plant sample, rather than evaluating each nutritional variable in isolation. The PCA analysis included the measured variables AP, TNC, cellulose, hemicellulose, crude fat, ash (crude minerals) and lignin. We used the scores from PC1 and PC2 as dependent variables to test the relationships between the plants' nutritional mixture and stand characteristics using LMMs. The stand characteristics included in the models were: total plot basal area, the percentage of this basal area composed of spruce, site index, soil C:N, pH, and moisture. As explained for Paper II, the response variables were centred and standardized. To test how the ratio of AP:TCH in the *Vaccinium* species depends on the same above-mentioned forest stand characteristics, we ran GLMMs with a beta error distribution and logit link function. For all three types of models we first ran full models with all the stand characteristics as fixed effects in the model, then obtained all possible variable combinations and selected the model with the lowest AIC.

3. Results and discussion

3.1 Biometric functions of above-ground shrub biomass and the proportion providing forage for wild cervids (Paper I)

In this study we modelled above-ground biomass of the three ericaceous shrub species using data on their percentage cover ($R^2 = 0.51$ for bilberry, $R^2 = 0.47$ for cowberry and $R^2 = 0.71$ for heather). Ramet height had a positive significant effect on the biomass of the shrubs, and when adding it to the model together with percentage cover, the predictive ability of our models was further improved ($R^2 = 0.77$ for bilberry, $R^2 = 0.75$ for cowberry and $R^2 = 0.87$ for heather). Our results also showed how overstory tree data, although beneficial, was not crucial to estimate the biomass of the three shrubs. Inclusion of spruce basal area and site index to the cover models gave the highest R^2 (0.83 for bilberry, 0.81 for cowberry and 0.91 for heather). Site fertility had a positive influence on the above-ground biomass in our models. Site fertility is known to have a large influence on the ericaceous shrubs (Miina *et al.*, 2021; Hedwall *et al.*, 2013), where in larger ranges of site fertility their response can be unimodal, with a decrease in abundance at high fertility levels (Hedwall *et al.*, 2013). Most likely, we only observed the initial positive effect of site fertility on biomass, due to the limited range in fertility in our data.

We found spruce basal area to have a negative effect on the above-ground biomass of bilberry and cowberry. An increase in basal area is generally associated with a decrease in light availability (Eldegard *et al.*, 2019) but compared to pine dominated forests, this relationship is more pronounced in spruce dominated forests (Petersson *et al.*, 2019). The lack of light in the understory has been consistently found to be negative for the shrubs' cover (Hedwall *et al.*, 2013; Miina *et al.*, 2009) and biomass (Kuusipalo, 1983). Although the cover of heather has been reported to increase with light availability (Gaudio *et al.*, 2011), we did not find significant effects of spruce basal area on heather biomass. One possible cause for this lack of a relationship is that heather was only found in spruce stands at the lower ranges of basal area, where the lack of light availability is less pronounced. Including study location in the models did not substantially improve our models' prediction ability, which could indicate that the data on their percentage cover is already capturing much of the between-site variation, making it a strong variable for prediction of above-ground biomass regardless of location.

The true novelty of this study was to take the predictions beyond total above-ground biomass, and specifically estimate the part of this biomass that represents forage for cervids. As a first step, we identified which biomass fractions appear to be used by cervids in the wild. We found significant, although minor, between-site differences in the bite diameters in bilberry and cowberry, which were larger in the high cervid density site (HC). This indicates that the local population density of cervids influences the degree of biomass utilization, which needs to be considered when estimating forage biomass at local scales. Due to this, we included a dynamic aspect in our models, considering six biomass fractions that depended on the thickness of the ramets' stem, making the models applicable at varying cervid densities.

The models we used to estimate the forage biomass for the three species, showed that percentage cover did not play as important a role as it did in the predictions of above-ground biomass. Instead, shrub height was present in the best models for all three species (height had a positive effect on some of the thickest fractions of the plants). This likely illustrates how taller plants have a larger proportion of thick stems, and thus, a smaller proportion of what is considered browse for the cervids. The palatability of the shrubs likely decreases with increasing stem thickness, as observed for other foraged plant species edible by cervids (Shipley *et al.*, 1999; Palo *et al.*, 1992). In addition to shrub height, we found spruce basal area to be an important explanatory variable for all three species. Interestingly our results show that a larger proportion of the plants’ biomass is forage biomass in spruce dominated forests compared to pine dominated forests. Therefore, in forests with reduced light availability the plants of these species do not only have a lower above-ground biomass, but also a higher proportion of what can be considered edible for the cervids, which could make these plants potentially more vulnerable to browsing by cervids.

Nowadays there is a growing pressure to enhance forest productivity in Sweden, where pine stands are continuously being replaced with spruce, especially in the south (Petersson, 2019; Lodin *et al.*, 2017). Other studies lend support to our results, suggesting that spruce dominated forests do not provide enough forage alternatives for the cervids (Jarnemo *et al.*, 2014). Extensive areas partly lacking ericaceous shrub biomass could drive cervids to continuously deplete the available food supply provided by these shrubs. Notably, in spruce stands, this resource was consistently found to be poorer in terms of biomass. This scarcity might potentially force cervids to seek alternative forage options, including shifting to forests characterized by a different overstory composition or switching to other forage sources, such as tree saplings.

The biomass models presented in this study can be used to predict forage biomass of ericaceous shrubs on a scale relevant for management and policy development. Data on cover of these shrub species are regularly collected in national forest inventories (NFI), and are therefore readily available for managers and policy makers. However, the methodology used to obtain cover data is not universal and observer bias can make the accuracy of the estimations vary, complicating comparisons among data from different sources (Alberdi *et al.*, 2010). Our cover estimates were carried out on 0.25 m^2 subplots, while for example, the NFI works with 100 m^2 plots. Due to the difference in scales, to be able to implement the biomass models we present at a larger spatial scale, the differing methodologies for data collection must first be compared and potential systematic differences corrected for.

3.2 Forest stand characteristics influence the growth of ericaceous shrubs (Paper II)

We found that the absolute growth (new shoot biomass per ramet) of the three ericaceous shrub species was significantly reduced with increasing levels of tree basal area. This effect was stronger in stands where the percentage of basal area of spruce was high, which indicates reduced understory light availability.

3.2.1 Absolute growth

Within the set of stand models (SM) for absolute growth for bilberry, the one with the lowest AIC (R^2=0.30) contained the variables total basal area, spruce percentage, their interaction, and the soil variables C:N ratio, pH and moisture, all with a significant negative effect. From these, pH, soil moisture and spruce percentage had the strongest effects, and total basal area showed a negative effect only in combination with spruce percentage when the latter was in high proportion (Figure 4). The selected model for cowberry (R^2=0.42) included the variables total basal area, spruce percentage, their interaction, and pH, all with a negative effect on the absolute growth. Spruce percentage had comparatively the highest effect on the dependent variable, followed by the basal area (Figure 4). The model with the lowest AIC for heather (R^2=0.39) included the variables total basal area, spruce percentage, soil C:N and pH. All had a negative effect on the absolute growth of heather, with the strongest effects from plot basal area followed by pH.

Overall, our results showed how an increase in basal area and the percentage of spruce had a consistent negative effect for the ericaceous shrubs. The basal area in a stand is negatively correlated with canopy openness (Díaz-Calafat *et al.*, 2023), and an increase in basal area is associated with a decrease in light availability, especially in spruce dominated stands (Petersson *et al.*, 2019). This means that ericaceous shrubs in areas with low light availability, apart from having a lower abundance and biomass (Paper I), also produce less new biomass per ramet. This pattern is confirmed by our second set of models (PM) which included plant cover and morphological traits instead of stand characteristics. These models showed for example that patches with higher abundance (cover) and/or taller ramets produce a comparatively higher amount of new growth. All three species showed a consistent decrease in absolute growth with increasing soil pH, which is consistent with the fact that these are adapted to grow in relatively acid soils with low fertility (Mäkipää, 1999).

While bilberry is more often found on sites of intermediate fertility and mesic heath forest, having lower abundance in the driest sites (Taulavuori *et al.*, 2013), cowberry and heather are tolerant to drought but can also be found in wet sites (Hedwall *et al.*, 2017). Our results show how bilberry was negatively affected by increasing soil moisture, which corresponds with them not growing as well on wet sites (Taulavuori *et al.*, 2013). In contrast, we found no such pattern for cowberry and heather, indicating that their growth might be less dependent on soil moisture. Although all three species are nutrient conservative (Ellenberg, 1974), bilberry is the most nutrient demanding of the three (Nielsen *et al.*, 2007) which coincides with our results, where the absolute growth of bilberry was negatively affected by increasing soil C:N.

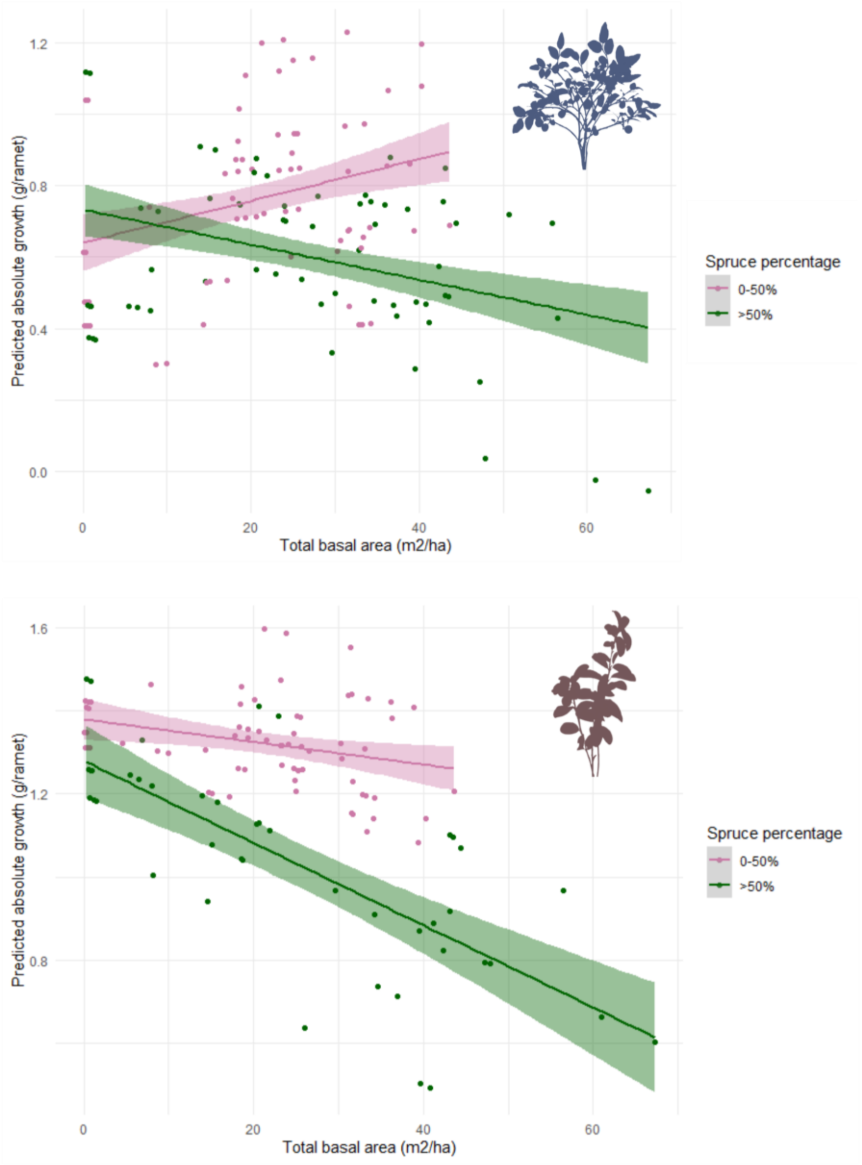


Figure 4. Predicted absolute growth (g ramet^{-1}) of bilberry (above) and cowberry (below) depending on total plot basal area and percentage of spruce. Predicted values are obtained from the best fitting stand models (those including variables associated with forest stand conditions, SM) for bilberry and cowberry. Other independent variables included in the same model were kept to their mean.

3.2.2 Relative growth

The SM model with the lowest AIC for the relative growth of bilberry ($R^2=0.35$) included the fixed effects total basal area and spruce percentage. Basal area had a significant negative effect, while spruce percentage had a positive effect but explained less of the variation. For cowberry, the selected model ($R^2=0.29$) included only total basal area, which had a negative effect on the relative growth. The model for heather (marginal $R^2=0.14$) included C:N, pH and soil moisture. The relative growth of heather was negatively affected by C:N and pH, and soil moisture had a positive effect, stronger than the other two variables.

We found that in predicting the relative growth of bilberry and cowberry, the total basal area and the percentage of spruce were the most influential factors. The positive effect of spruce percentage (for bilberry) indicates that shrubs in darker stands, with a higher percentage of spruce, have a smaller size, but a larger proportion of their biomass consists of new biomass (similarly observed in Paper I). This coincides with the negative effect of ramet height on the relative growth of bilberry and cowberry (results from our PM models), indicating that taller shrubs – which are most likely older – produce less new biomass relative to their old biomass (Tolvanen, 1995). Tolvanen (1995) describes how younger, and usually shorter bilberry ramets produce a larger amount of vegetative shoots, which are longer and heavier than reproductive shoots (produced in larger numbers in older ramets, these shoots are finer and produce flowers and fruit). This is consistent with the negative effect found of the number of branches on the relative growth of bilberry in our study, which is also supported by Atlegrim and Sjöberg (1996). Similar patterns were found for cowberry, where ramet size and age are most likely behind the patterns observed in the relative growth of this shrub. Additionally, we observed a negative effect of basal area on the relative growth of bilberry and cowberry. Increased forest density does not exclusively result in reduced light availability for the understory, but can also involve other factors, including increased competition for soil resources (Coomes & Grubb, 2000) or changes in the understory microclimate (Díaz-Calafat *et al.*, 2023). These factors may influence the competitive interactions with the overstory and contribute to the observed relative growth decline. For heather, we found that soil stand variables explained more of the variation than the tree related data, although the performance of these models is not as good as the comparative models for the other two species. We did not find any significant effects of the cover and plant traits on the relative growth of heather.

It is interesting to see the similarity in patterns found between this study and Paper I in terms of the importance of the explanatory variables percentage cover and ramet height. In Paper I we found that these two variables successfully predicted the above-ground biomass of the three plant species. Here we also determined how these variables can contribute to the prediction of the relative growth of bilberry and cowberry. This implies that, when data on shrub biomass or cover of the shrubs are available (e.g. by using the functions presented in Paper I), the models presented in this study can in-turn be used to introduce a dynamic aspect to the above-ground biomass predictions, and predict the annual output of relative growth of the shrub species in forest stands.

3.3 Growth and morphology of ericaceous shrubs in areas with different cervid densities (Paper III)

Despite conducting three years of repeated surveys across 20 exclosure and control plots spanning a large range in cervid densities, we did not find any evidence that the absolute growth, ramet height and number of branches of bilberry and cowberry were significantly different between treatments. Furthermore, we detected no differences between treatments with varying cervid passage rates (proxy for local browsing pressure), even when separating the effects of the large-bodied moose from the three smaller-bodied cervids (roe deer, red deer and fallow deer).

Absolute growth, ramet height and number of branches of bilberry and cowberry were not found to be significantly different between control and exclosure plots within sampling year and site. Although, it’s important to note that in 2022, the absolute growth of cowberry in LC was near to significantly higher in control plots (P=0.058), and cowberry ramet height in the same year was almost significantly lower in control plots than in the exclosures (P=0.064). Our camera trap data allowed us to determine passage rates, and thus browsing pressure. The average moose passage rate was the same in HC and LC, but deer passage rates were five times higher in HC than in LC. Despite this difference, we did not find any evidence that the treatment effect varied within site or across sites.

The lack of significant differences observed can have several potential explanations. First, the recovery of the shrubs post-browsing might be substantial enough that morphological differences become indistinguishable from the absence of cervids. Ericaceous shrubs are highly adapted to browsing, and their growth has been found to be promoted by some level of browsing (Tolvanen, 1994). Angelstam *et al.* (2017), similarly showed a lack of response in the volume of bilberry and heather between plots where cervids were absent and plots with high cervid densities. A possible explanation developed in this previous study (Angelstam *et al.*, 2017) is that these shrubs are primarily consumed during winter, making them vulnerable to browsing for a short period, allowing them to recover and to have no long-term effects on their volume. Although more research is needed, the effects caused by changes in the overstory might have more profound effects on the growth and morphology of these species than the level of browsing to which they were subjected.

However, there is a possibility that our study design may have failed to capture the treatment effects. While we did observe that some of the sampled ramets in our plots had indeed been browsed, their differences in terms of annual growth, height and number of branches, might have been diluted compared to the larger amount of sampled ramets lacking signs of recent browsing. Future studies should integrate plant measurements that take less time and can allow for a larger sample size (e.g. by measuring only ramet height), and thereby increase the chances of monitoring browsing events. Additionally, this study may have been benefited by a longer exclusion time, similarly as in Hegland and Rydgren (2016), where a significant negative response in abundance of bilberry was found along a herbivore gradient involving a 10-year long exclosure. The almost significant differences found for the absolute growth and ramet height of cowberry between treatments in 2022 (last year of treatment), may be an indication of the potential benefit of increasing the exclosure time.

3.4 The nutritional composition of bilberry and cowberry is influenced by forest structure (Paper IV)

Changes in the overstory conditions were found to influence the nutritional composition of bilberry and cowberry. These responses by the plants may in-turn have repercussions for the cervids' nutritional space and their foraging decisions.

3.4.1 Relationship between stand characteristics and the macro-nutritional balance of bilberry and cowberry

We found that bilberry and cowberry browse exhibited a large within-species variation in the relative proportions of macronutrients (Figure 5). From the total variation for bilberry, 65% was explained by the first two PCs, while a total of 60% was explained for cowberry. For both species, PC1 was most strongly correlated with TNC (sugar and starches) in one direction, and lignin and AP in the opposite direction (though more closely for cowberry than for bilberry). In PC2, both plant species displayed crude fat and cellulose having a negative correlation with each other, while hemicellulose and cellulose only co-varied in cowberry samples.

For bilberry, the best LMM for PC1 according to AIC (R^2=0.39) included the variables total basal area, spruce percentage and their interaction, as well as soil C:N. Both basal area and spruce percentage had a positive significant effect on the scores on PC1 for bilberry, while their interaction had no significant effects. Soil C:N was negatively related to PC1. The model for PC1 scores for cowberry (R^2=0.43) showed similar results, with a significant positive effect of plot basal area, spruce percentage and their interaction. We were not able to predict the values of bilberry along PC2 (R^2=0.02). The PC2 model for cowberry (R^2=0.19) indicated a significant positive relationship between the scores and spruce percentage, while showing a negative association to site index.

These results show that, for both plant species, the denser and more spruce dominated a forest stand is, the lower the concentration of sugar and starches (TNC), and the higher the concentration of available protein (AP). This pattern corresponds to expectations based on the carbon-nitrogen balance hypothesis (Bryant *et al.*, 1983). In environments with low light availability (such as dense forests dominated by spruce (Petersson *et al.*, 2019)) the carbohydrate concentrations in plants should decline due to the reduction of photosynthesis, creating a lack of carbon source, while nitrogen is expected to accumulate in the plants' tissues, if there is no lack of nutrients in the soil (Bryant *et al.*, 1983). This observed positive relationship between shade and nitrogen concentration in plant tissue has also been found in studies of other ericaceous shrubs (Michelsen *et al.*, 1996; van Horne *et al.*, 1988). Additionally, C:N had a negative effect on PC1, and consequently, on AP. This relationship aligns with what would be expected, as a higher C:N ratio in the soil indicates reduced nitrogen availability for the plants. While we did not find strong relationships between forest structure variables and the remaining macronutrients (cellulose, hemicellulose and crude fat), the concentration of lignin in both *Vaccinium* species was clearly positively correlated with basal area and spruce percentage. Lignin serves as an efficient digestion inhibitor for ruminants, which makes them avoid consuming large amounts of lignin-rich biomass (Van Soest, 2018; Shipley *et al.*, 1999). As the shrubs growing in dense and spruce dominated forests were richer in protein, and likely more palatable to cervids (see below), their higher lignin concentration may be an indication of an increased need for protection.

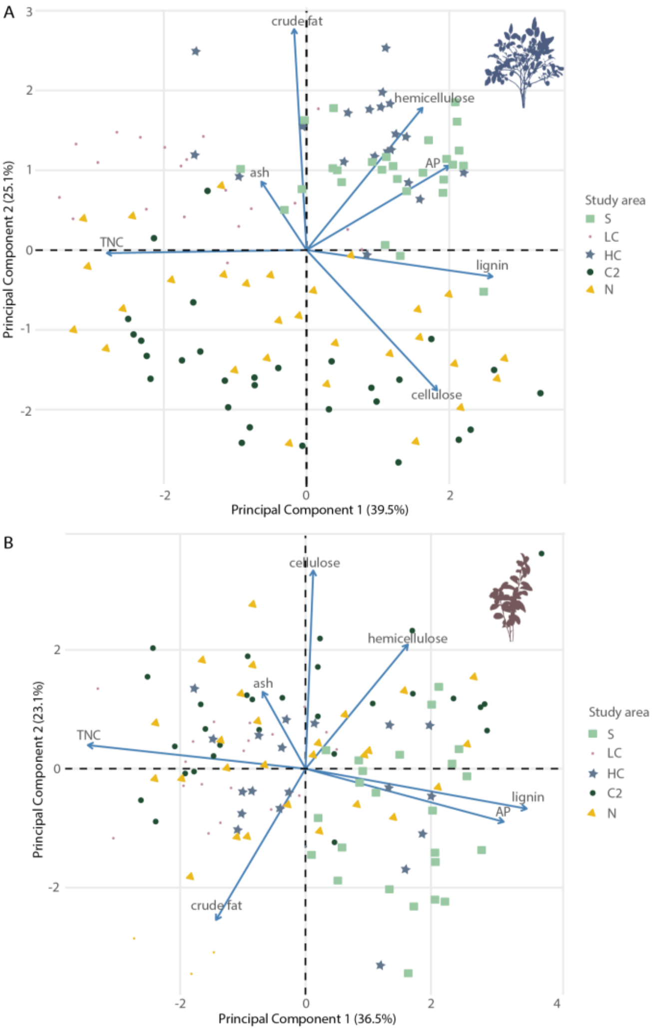


Figure 5. Loadings and scores from Principal Component Analysis (PCA) of the macro-nutritional composition of bilberry (A) and cowberry (B) samples collected. For each plant sample the concentrations (g 100g^{-1} dry weight) of available protein (AP), ash, crude fat, total non-structural carbohydrates (TNC), cellulose, hemicellulose and lignin are included in the model. Arrows indicate the correlation between macro-nutrient parameters, and between these and the principal components (x and y axes; percentages refer to the variation explained by each principal component). Dots indicate positions of individual plant samples along the principal components, with the symbol and colour specifying each of the five study areas (Figure 1).

3.4.2 Stand basal area and percentage of spruce are the main stand characteristics influencing how close *Vaccinium* browse is to the moose' macro-nutritional target

The best GLMM models for bilberry (R^2=0.24) and cowberry (R^2=0.24), according to AIC, showed that total basal area and spruce percentage have a positive significant effect on the AP:TCH (ratio of available protein to total carbohydrates). This indicated how bilberry and cowberry shrubs in dense and spruce dominated stands in general produced browse that is closer to the balance found in *Salix* twigs, and to the presumed nutritional target balance for moose (Spitzer *et al.*, 2023; Felton *et al.*, 2016). Specifically, our results illustrate that bilberry browse found in highly spruce dominated forests (70-100% spruce of total basal area) even overlapped in composition with *Salix* spp., regardless of whether the total basal area was within our lower or higher selected values (Figure 6). In addition, the nutritional space created by bilberry and cowberry together was larger in spruce dominated stands compared to stands that were more open and pine dominated (E and F in Figure 6).

These results indicate that dense and spruce dominated forests may actually hide some highly attractive parcels of browse under their canopies. If this browse really is attractive for the browsers, it may also imply that there may be indirect effects of decreasing light availability on the browsing of these plants that can have further contributed to their decline during the last decades. Consuming such browse should efficiently lead moose on a straight path to their winter macro-nutritional target. This could, in turn, impact the palatability of these shrubs. Previous research has shown that insect herbivory on bilberry leaves tends to increase with increasing shade (Schrijvers-Gonlag *et al.*, 2020).

Although spruce forests may harbour nicely balanced parcels of ericaceous browse, these parcels are likely too sparsely distributed to make it worthwhile for the large bodied moose to spend energy seeking them out, particularly if they need to share these resources with many other cervids. However, a food item does not need to be perfectly on-target to be of value to the consumer, and the conventional way of labelling food items as of “low” or “high” quality is rather simplistic and does not reflect the complexities of nutritional choices (Felton *et al.*, 2018). The value of a particular food to a feeding animal is not fixed, it changes with time and circumstance, as the food constituents sought-after by the animal can be altered in response to each meal consumed (Felton *et al.*, 2018; Raubenheimer *et al.*, 2014; Simpson & Raubenheimer, 2012b; Felton *et al.*, 2009). Bilberry and cowberry have been conventionally classified as low-quality food items, but due to the particular combination of constituents they contain, they might be of high quality at certain times. In general, the larger the variety of food items available to an animal, the wider the nutritional space for them to manoeuvre within (Felton *et al.*, 2021), increasing their ability to reach their macro-nutritional target (text box 1). The results from this study shows that the nutritional space available for local cervids can be made significantly larger, even considering only two species of forage plants, by just varying the composition of the dominant tree species.

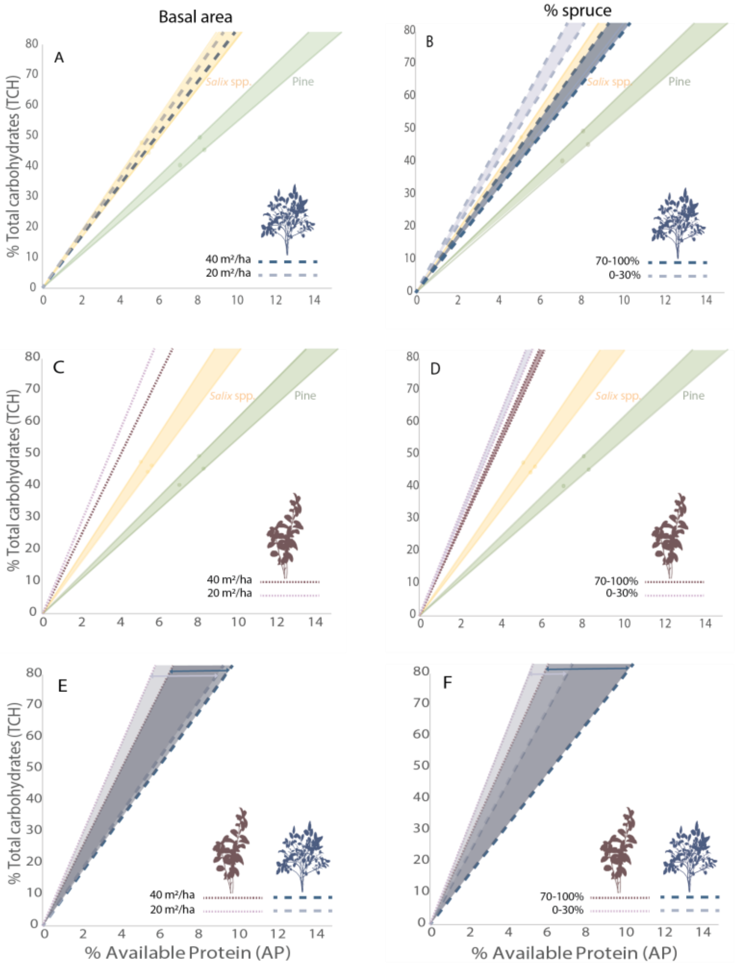


Figure 6. Macro-nutritional composition in the dimensions of available protein (AP) and total carbohydrates (TCH) in bilberry (twigs, blue dashed lines, panels A-B) and cowberry (twigs + leaves, purple dotted lines, panels C-D), in response to total plot basal area (A, C) and percentage of spruce (B, D). Lighter colors indicate our lower values of basal area (20 m^2/ha) and percentage of spruce (0-30%); darker colors represent higher basal area (40 m^2/ha) and percentage of spruce (70-100%). The values are presented in comparison with the average composition of Scots pine (green) and *Salix* spp. (yellow), as published in (Spitzer *et al.*, 2023) and (Felton *et al.*, 2021). **E-F**: Values of panels A-D combined to indicate the differences between bilberry and cowberry (and the resulting nutritional space the two species create together (text box 1), the width of which is indicated by arrows) in response to variation in basal area and percentage of spruce; light grey shade represents lower basal area and percentage of spruce (as defined above) and dark grey shade indicates higher basal area and percentage of spruce.

3.5 General limitations

It is important to note that not all factors that potentially influenced the response variables in our studies were quantified or accounted for. For example, the growth of a given ericaceous shrub is likely to be influenced by competition with other understory plant species (Hedwall & Brunet, 2016; Shevtsova *et al.*, 1995). Furthermore, in our studies we focused solely on the above-ground biomass of the ericaceous shrubs, due to our a priori focus on the shrubs' functionality as cervid forage. However, the shrubs are also subject to competition with trees and other plants below ground (Balandier *et al.*, 2022; Mielke *et al.*, 2022), and may adapt to canopy layer influences by altering the allocation of resources below ground (Nielsen *et al.*, 2007; Jäderlund *et al.*, 1997; Tolvanen, 1994). Such processes and responses were not addressed by our design. Since ericaceous shrubs are clonal species, we were limited to using the ramet as a unit in our studies. This limitation brings challenges in terms of tracing whether the effects we observed operate at the individual level (genet) or influence the population as a whole. The age of the ramet could also potentially influence the response variables in our studies, as discussed above. In our study we have no estimate of ramet age and are therefore limited in our ability to identify its role in explaining the patterns observed.

4. Connections among the four studies and relevant management recommendations

The key finding of my work is that the forest structure of conifer production stands in Sweden has a significant influence on both the quality and quantity of ericaceous plants, and the forage they provide to wild herbivores. In particular, our results provide novel information about the state of shrubs that grow on the floor of dense and spruce dominated production stands – a common forest type in Sweden. In Paper I we saw how these stands had comparatively less above-ground biomass of the three shrub species and their ramets were of a smaller stature than in pine forests. In addition, we found that a larger proportion of the total biomass of these smaller and light-suppressed shrubs consisted of forage biomass. Accordingly, Paper II showed how these shorter shrubs had a higher proportion of new shoot biomass, which roughly corresponds to the parts that cervids normally use as forage. The results from Paper IV add another important piece of information: bilberry and cowberry shrubs in stands with higher basal area and percentage spruce had more protein and a better balanced nutritional composition of their browse in relation to moose diet choice. These combined results suggest that ericaceous shrubs growing in spruce dominated forests may not only struggle with unfavourable conditions for growth but may also be disproportionately vulnerable to browsing; while those inhabiting relatively open pine forests appear to not be heavily impacted by the presence of browsers, at least under the population densities and circumstances assessed here (Paper III).

In addition to providing novel insights about the ecology of these foundation plant species, much of our work is in the form of predictive models that can be applied by practitioners. For example, we provide models that predict the above-ground biomass of the three ericaceous shrub species in response to their cover and varying production forest conditions in Sweden (Paper I). These can be used in a wide variety of forest ecosystems, as the biomass of the three shrub species in Sweden's boreal forests can be successfully predicted just using percentage cover data. Additionally, we provide dynamic models that can be adjusted to determine the proportion of this above-ground biomass that serves as forage for the wild cervids (adjustable depending on the bite diameters measured at local scales). As we used predictive variables which are readily available in large-scale inventories, the models presented can potentially be included in forestry decision support systems to i) determine the current availability of this resource in conifer forests, ii) model the potential effect of the overstory on forage availability in conifer forests, and iii) ultimately improve the future development of these foundation plant species. For even better refinement, models presented in Paper II can be incorporated to predict the annual output of new growth of the shrubs relative to their existing biomass in forest stands given a certain canopy layer and soil conditions. Relatedly, the predictive models I present in this thesis could potentially be used to refine estimations of the carrying capacity of cervids in Sweden. For example, in today's moose management system, the only guidance regarding carrying capacity provided to game managers is the number of hectares of young production stands (mean tree height 1 – 4 m (SFA, 2023)) that are present. This index only reflects the tree browse available in regenerating stands, leaving other forage types and stand phases unaccounted for. More encompassing estimates of forage availability should create a better basis for managers trying to improve game fitness and mitigate browsing damage.

I wish to highlight that the two factors that most strongly explained variation in biomass, growth and nutritional composition of the ericaceous shrubs in my studies – basal area and tree species composition – are the result of choices made by land owners during different phases of stand management. My results indicate that if forest management decisions are adopted which better allow for higher light levels to reach the understory, this would benefit both shrub abundance and the provision of forage resources for cervids. At the stand level, this can be achieved by reducing stand density, or by limiting the proportion of spruce in the overstory.

Cervids however are influenced by forest management decisions at both stand and landscape scales. Our results indicate that if people create a landscape matrix where forests are highly variable in terms of tree species composition and basal area, this should increase the likelihood that cervids can access both sufficient quantities and nutritional qualities of ericaceous shrubs. Working towards an increase in the quality and quantity of understory forage at landscape scales could help reduce competition over the ericaceous shrubs, and the problems that may result from their decreased availability, such as increased browsing damage to production trees (e.g. Jarnemo *et al.* (2014)). I suggest that, although the shrubs in low light environments might have a more desirable nutritional quality for cervids, actions which increase their quantity in the landscape are likely to be of greater overall benefit to cervid populations. Nevertheless, by providing a large variation of overstory structures on a landscape scale, the cervids will be given a larger nutritional space to navigate, and the overall forage availability might provide enough options to combine different forages and obtain a well-balanced diet. If we assume that the density of cervid populations will continue to be maintained at similar densities, such forest management decisions would ideally lead to reduced damage on commercially important trees. Simultaneously, measures should not threaten the provision of ericaceous shrubs, essential for the maintenance of the diverse range of ecosystem services they provide.

5. Conclusions

My thesis provides an additional piece to the evidentiary puzzle regarding how forest management decisions can have profound impacts on ericaceous shrub species and the services they provide. Throughout my studies, we have focused on the ecology and physiology of bilberry, cowberry and heather, studying them in the most prevalent forest types in Sweden, stands dominated by pine and spruce. We have managed to shed light on how variation in stand density and tree species composition influence their quantity, quality and productivity. Future research should focus on further investigating the observed trends, including more variation in tree species composition and their gradients, as well as other competitive paths between the understory and the overstory, or competition within the understory layer. We want to also emphasize the need to disentangle the combined effects of the tree overstory and the pressure from cervids on the ericaceous shrubs, and how landscape level approaches could be a solution to tackle forest damage and the loss of alternative forage sources. Lastly, further research could investigate the seasonal changes in the effects of the overstory on the nutritional composition of these shrubs. Similarly, more knowledge is needed about how the overstory influences the defence chemistry of these plants, and how this affects their net palatability and use as forage for cervids and other herbivores. If the remaining knowledge gaps outlined here are addressed in future research, even more explanatory pieces will be added to this complex puzzle of forest and cervid interactions.

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

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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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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

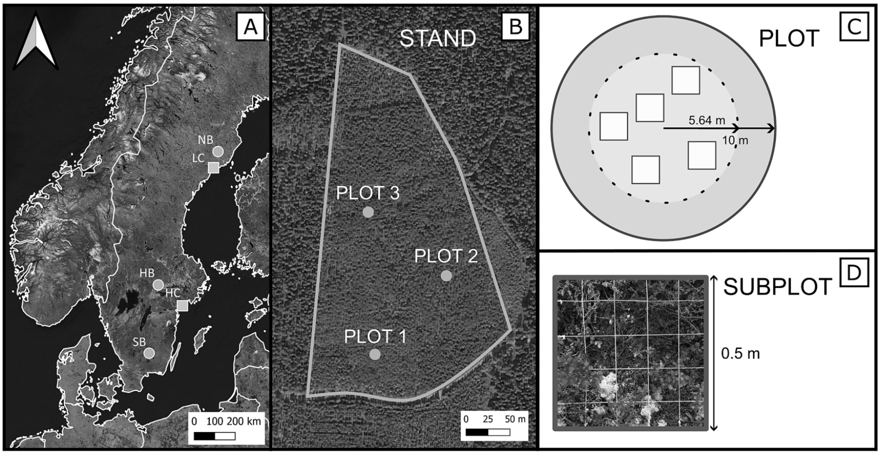

Fig. 1. Locations of the five study sites in Sweden in panel A. Dots (blue) indicate the location of sites where data on cover and above-ground biomass of bilberry, cowberry and heather was taken in the northern boreal region (NB), hemiboreal region (HB) and the southern hemiboreal region (SB). Squares (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

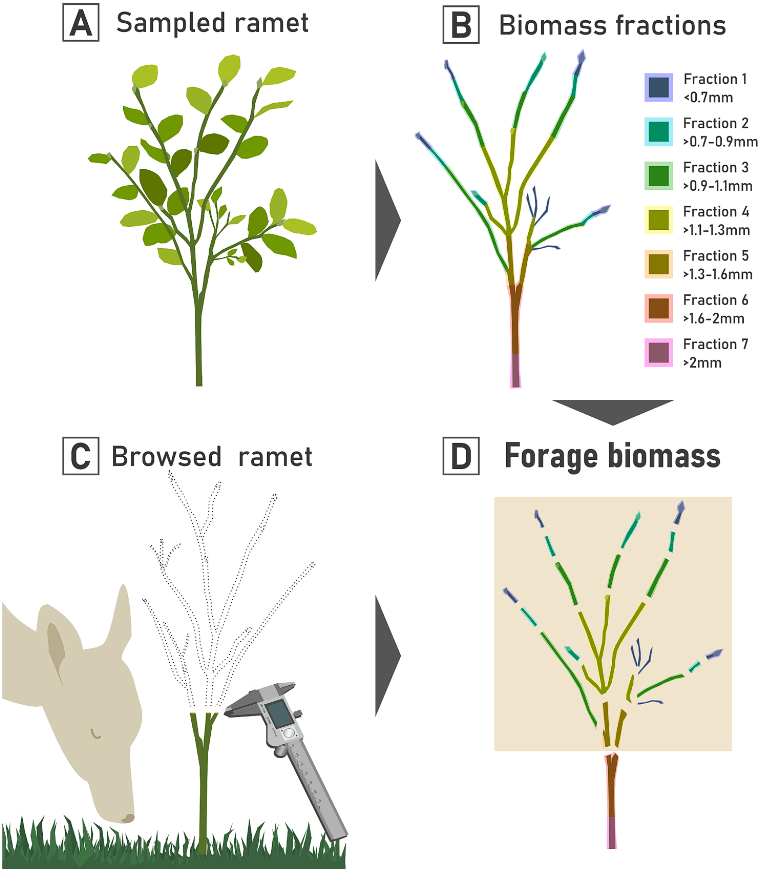

Fig. 2. We selected a subset of representative sampled ramets (A) per plot and species from our above-ground biomass collection, measured their stem diameter and split them into 7 diameter fractions (B) and calculated the biomass proportion of each fraction to the total sample biomass. To determine how 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.

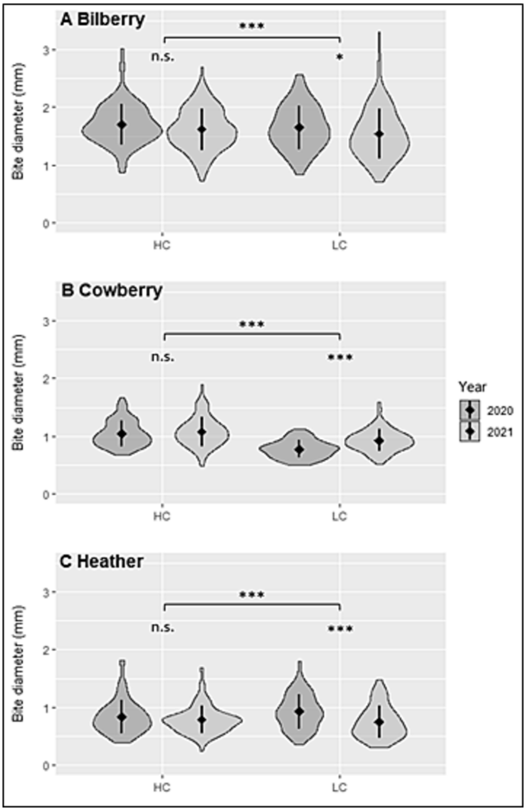

Fig. 3. Violin graphs showing the means and distributions of the measured diameter bites on stems of bilberry (A), cowberry (B) and heather (C), in the high cervid density (HC) and low cervid density (LC) locations, carried out in 2020 and 2021. "***" is $P < 0.001$, "*" is $P \leq 0.05$ and "n.s." is $P > 0.05$ 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: Δ0.103 for bilberry, Δ0.00 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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121120.

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In this thesis I provide new findings regarding the influence of the forest canopy on ericaceous shrubs (bilberry, cowberry and heather) growing in boreal and temperate forests, along a large latitudinal gradient in Sweden. My studies highlight the importance of stand density and tree species composition in shaping the shrubs' biomass, growth, macronutrient composition and forage provision for cervids. My findings have implications for the continued maintenance of these shrub species and the range of ecosystem services they provide.

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