Global Ecology and Conservation 54 (2024) e03195

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Modelling and mapping the abundance of lingonberry (*Vaccinium vitis-idaea* L.) in Norway

Jari Miina [a,*], Marius Hauglin [b], Aksel Granhus [c], Anne Linn Hykkerud [d], Inger Martinussen [e]

[a] *Natural Resources Institute Finland (Luke), Natural resources, Yliopistokatu 6 B, Joensuu 80100, Finland*
[b] *Norwegian Institute of Bioeconomy Research (NIBIO), Department of National Forest Inventory, Høgskoleveien 8, Ås 1430, Norway*
[c] *Norwegian Institute of Bioeconomy Research (NIBIO), Department of Forest Management, Høgskoleveien 8, Ås 1430, Norway*
[d] *Norwegian Institute of Bioeconomy Research (NIBIO), Department of Horticulture, Holtvegen 66, Tromsø 9016, Norway*
[e] *Norwegian Institute of Bioeconomy Research (NIBIO), Department of Horticulture, Holtvegen 66, Tromsø 9016, Norway*

A R T I C L E I N F O

Keywords:
ALS
Generalized linear mixed model
Ground vegetation
National forest inventory data
Sentinel-2
Wild berries

A B S T R A C T

Lingonberry (*Vaccinium vitis-idaea* L.) grows in a range of nature types in the boreal zone, and understanding factors affecting the abundance of the plant, as well as mapping its spatial distribution, is important. The abundance of the species can be an indicator of ecosystem changes, and lingonberry can also be a source for commercial utilisation of berry resources. Using country-wide data from 6404 field plots of the Norwegian national forest inventory (NFI), we modelled the relationship between lingonberry cover and airborne laser scanning (ALS) and satellite metrics and bioclimatic variables describing the forest structure, terrain, soil properties and climate using a generalised mixed-effects model with a quasipoisson distribution. The validation carried out with an independent set of 2124 NFI plots indicated no obvious bias in predictions. The most important predictors were found to be interactions between dominant tree species, stand basal area and latitude, as well as the reflectance in the near-infrared band from Sentinel-2 satellite imagery, the dominant height based on the ALS variable and the long-term mean summer (June–August) temperature. The results provide an indicator of the effects of global warming, as well as the possibility of giving forest management prescriptions that favour lingonberry and locating the most abundant lingonberry sites in Norwegian forests.

1. Introduction

Lingonberry (*Vaccinium vitis-idaea* L.) is a circumpolar dwarf shrub species of the *Ericaceae* family that favours cool climates and produces high-value, healthy berries. The lingonberry plant grows in a range of habitats, including bogs, several forest types, open rocky slopes, and tundra, thriving low pH soil conditions (Nestby et al., 2019). Abundant populations of lingonberries are present across vast areas of Norway. Norway's unique topography is characterised by a blend of mountain plateaus, and coastlines, with the majority of its landmass comprised of elevated areas with a potential for commercial utilisation of wild growing lingonberries (Jonsson and Uddstål, 2002; Vaara et al., 2013). Despite the relatively diminutive biomass of shrub vegetation, including *Vaccinium*, compared

* Corresponding author.
E-mail addresses: jari.miina@luke.fi (J. Miina), marius.hauglin@nibio.no (M. Hauglin), aksel.granhus@nibio.no (A. Granhus), anne.linn.hykkerud@nibio.no (A.L. Hykkerud), inger.martinussen@nibio.no (I. Martinussen).

https://doi.org/10.1016/j.gecco.2024.e03195
Received 2 May 2024; Received in revised form 12 August 2024; Accepted 7 September 2024
Available online 8 September 2024
2351-9894/

to arboreal entities, these shrubs have a substantial influence on, for example, nutrient and carbon cycling and storage, and wildfire hazard in forest ecosystems (Nilsson and Wardle, 2005; Botequim et al., 2015). A decline in lingonberry abundance could therefore significantly disrupt both the functionality and services provided by boreal forest ecosystems.

Mapping abundance for wild berries, like lingonberry carries substantial significance due to its versatile adaptability across diverse terrains and its consequential ecological and economic relevance (Hjalmarsson and Ortiz, 2001; Nilsson and Wardle, 2005; Jones et al., 2014). Profound comprehension of lingonberry distribution is of ecological, botanical, and potentially economic importance, facilitating extensive investigations into ecosystems, biodiversity, and interrelationships within disparate geographic regions (Angelstam, 1998; Olsson et al., 2000).

In Finland, the decline in the abundance of lingonberry from 16 % to 6 % from the 1950s through the 1990s (Salemaa, 2000) has been linked to industrial forestry including clearcuttings combined with site preparation (Tolvanen, 1994). Additionally, increased forest density and a rise in the proportion of young forests have negatively impacted the abundance of *Vaccinium* shrubs (Salemaa, 2000; Hedwall et al., 2013).

High latitude areas experience amplified climate change, with is profound and often accelerated impacts on their ecosystems. According to Villén-Peréz et al. (2020), global warming may affect the abundance of boreal plant species and lingonberry showed significant negative response to temperature. A decline in lingonberry populations could significantly impact the ecosystem within boreal forests, emphasising the importance of understanding their distribution and the environmental conditions necessary for their growth (Kausrud, 2022). Studies further indicated that increased temperature could lead to domination of the allelopathic, evergreen shrub crowberry (*Empetrum nigrum* L.) which can have severe negative effects on the ecosystem (Bråthen et al., 2018). Understanding key factors important for lingonberry abundance is therefore crucial for the conservation and sustainable management of a key species like lingonberry to maintain the ecological functions they provide within ecosystems.

Mapping the abundance of lingonberry can have several approaches including field surveys and data collection. The current research utilised the Norwegian national forest inventory (NFI), a comprehensive dataset spanning the entire country, to investigate the association between lingonberry cover and stand characteristics. In prior studies conducted in Sweden (Hedwall et al., 2013) and Finland (Turtiainen et al., 2013), comparable nationwide forest inventory datasets were used to examine the correlations between lingonberry cover and various influencing factors, encompassing both biotic and abiotic elements. The primary predictors influencing lingonberry cover in Swedish and Finnish forests were identified as site fertility, stand basal area or volume and the dominant tree species.

Remote sensing has been used for mapping of forest attributes for decades, and orthophotos and airborne laser scanning (ALS) are routinely used in local forest inventories (Maltamo et al., 2014). At the national, and even global level, satellite data are used to create maps of forest resources (cf., (Hansen et al., 2013). In Norway, a national forest resource map is produced, with remote sensing data as a key input factor (Hauglin et al., 2021). The abundance of lingonberry cannot be directly observed using remote sensing data, but we assume that it can be predicted from remote sensing metrics describing canopy structure together with other forest and environmental variables. Majasalmi and Rautiainen (2020) found forest understory composition in boreal forests to be better correlated with remote sensing metrics describing canopy structure than with field-measured mean stand characteristics. Therefore, in addition to stand variables such as tree species dominance, stand density, development stage, etc., ALS-based metrics for the structure of tree canopy may also describe the understory growing conditions suitable for lingonberry. In addition, understory vegetation affects forest reflectance observed in optical satellite data (Majasalmi et al., 2015), and thus satellite images could also benefit the detection of the abundance of lingonberry in Norway.

The aim of this study was to fit and validate a model for lingonberry cover assessed in the Norwegian NFI data, and to apply the fitted model to map the abundance of lingonberry in Norwegian forests. We hypothesised that various forest and environmental variables, especially those describing tree species composition, stand density, topography and location in Norway, would be significant predictors in the cover model and thus control the distribution of the species. Moreover, it was expected that remotely sensed variables could provide additional information on stand structure compared to stand basal area alone. Increased understanding of the forests suitable for lingonberry in Norway and mapping their spatial distribution at local scales is of both ecological and economical importance. This knowledge will enable the development of forest management prescriptions favouring lingonberry populations and the commercial utilisation of the species.

2. Material and methods

Three categories of data were used in this study: data derived from registrations in the field (NFI), data derived from remote sensing (ALS, Sentinel-2 and SR16) and auxiliary full-coverage data (e.g., climate, topography and soil properties). By modelling the relationship between field-observed lingonberry cover and variables representing factors such as forest structure, topography and climate, we were able to first assess the response of lingonberry to different factors, and then create a national map of lingonberry cover using the fitted model. A requirement for being able to produce the map was to build a model that uses only predictors with a full national coverage.

2.1. Forest inventory data

The permanent sample plots of the Norwegian national forest inventory (NFI) cover the entire mainland area of Norway and are surveyed according to a five-year rotation cycle, with one fifth of the plots being re-measured each year (Breidenbach et al., 2020). The plots that are located entirely or partly in forest (n = 11,726) are laid out systematically in four different strata, with grid spacings varying from 3 × 3 km in the main strata which cover most of the productive forest, to 9 × 9 km in the birch (*Betula pubescens* L.) dominated areas of the northernmost county Finnmark. Measurements on the individual trees are done within a circular plot sized 250 m^2 (r = 8.92 m). Here, measurements are taken to obtain information on species and diameter at breast height (DBH, 1.3 m above ground) of all trees with DBH ≥5 cm, whereas height measurements are done on a subset of sample trees from which plot-specific DBH-volume relationships can be derived. From the measured data, the growing stock in terms of standing volume (m^3 ha^{-1}) is calculated using standard procedures and functions as detailed by Breidenbach et al. (2020), together with other density metrics such as stand basal area (m^2 ha^{-1}) and stem density (n ha^{-1}). Stand-level variables such as stand age, main forest type (e.g., dominated by Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) or broadleaves) and site index (mean height of the 100 largest (by diameter) trees ha^{-1} at a reference age of 40 years at breast height, Tveite, 1977) are assessed for a larger plot area (0.1 ha, r = 17.84 m), together with data describing terrain conditions (e.g., slope, aspect). For further details on the tree-, site- and stand-level data recorded by the NFI, we refer to the extensive review presented by Breidenbach et al. (2020) and the NFI field protocol (Viken, 2021).

The assessment of percent cover of lingonberry was introduced in the NFI in 2019 and is estimated by the surveyor within four 0.5 × 0.5 m subplots, located 5 m from the plot centre in each cardinal direction. In the data analysis, species abundance was averaged across the four subplots for each NFI plot. Note that percent cover of bilberry (*Vaccinium myrtillus* L.) was also estimated within the same subplots (Eldegard et al., 2019). For the current study, we used data collected during 2019–2021 to derive the cover model, whereas data collected in 2022 were used for model validation. The data used to derive the model included 6404 plots or plot parts, whereas the corresponding figure for the validation data is 2124.

2.2. Remote sensing data

Remote sensing data were used as a basis for predictor variables describing the structure and composition of the vegetation and forest, and several remote sensing variables were considered as candidate variables in the modelling. The candidate variables derived from remote sensing data came from two sources: a national airborne laser scanning (ALS) campaign and Sentinel-2 satellite imagery. In addition to variables directly derived from these two remote sensing sources, we also used variables from the Norwegian forest resource map SR16 (Hauglin et al., 2021), which is partly based on data from the same two sources. The remote sensing-based

Table 1
Main characteristics of the Norwegian NFI plots included in the modelling (n = 6404) and validation (n = 2124) data sets.

	Modelling data (2019–2021)			Validating data (2022)		
Variable	Mean	SD	Range	Mean	SD	Range
Lingonberry cover (%)	3.1	4.9	0–59	3.7	5.5	0–53
Stand basal area (m^2 ha^{-1})	14.8	12.7	0.1–88.5	15.1	12.5	0.1–80.3
Spruce	6.1	10.8	0.0–88.5	5.9	10.3	0.0–66.8
Pine	4.5	7.8	0.0–57.8	4.8	8.3	0.0–56.1
Broadleaves	4.2	6.1	0.0–54.2	4.4	6.2	0.0–56.3
Latitude (degrees)	62.4	3.2	58.0–70.6	62.4	3.2	58.1–70.6
Longitude (degrees)	11.1	4.0	4.8–30.5	11.2	3.9	5.1–30.2
Altitude (m a.s.l)	394.0	257.1	0–1132	394.8	258.4	2–1130
Slope (%)	23.6	20.2	0–230	23.9	20.4	0–208
Aspect (degrees)	178.1	104.2	0–360	176.5	103.9	0–360
Distance to coast (km)	80.3	70.6	0–268	81.5	70.7	0–271
Temperature January (°C)	−4.6	3.0	−13.8–3.1	−4.6	2.9	−13.6–3.1
Temperature June–August (°C)	12.4	1.5	8.3–16.3	12.4	1.6	7.9–16.3
Precipitation June–August (mm)	300.3	81.9	90.3–733.8	295.3	76.6	110.6–712.7
Temperature sum (dd)	1737.8	408.8	655–2847	1742.1	414.3	760–2806
Sentinel−2 B8A (unitless)	2831	754	617–15562	2824	716	734–8085
ALS H10_first (m)	0.5	1.7	0.0–18.5	0.4	1.6	0.0–15.7
ALS H50_last (m)	0.9	2.5	0.0–20.4	0.8	2.3	0.0–19.5
ALS H50_all (m)	2.8	3.8	0.0–23.4	2.7	3.6	0.0–20.2
ALS H95_first (m)	10.3	5.8	0.0–32.2	10.3	5.5	0.1–29.7
		n	%		n	%
Soil parent material						
Class 1		3812	60 %		1317	62 %
Class 2		191	3 %		60	3 %
Class 3		400	6 %		128	6 %
Class 4		2001	31 %		619	29 %
Main tree species						
Spruce		1984	31 %		643	30 %
Pine		2227	35 %		734	35 %
Broadleaves		2193	34 %		747	35 %

Sentinel-2 B8A = reflectance value for Sentinel-2 band B8A; ALS H*i*_*j* = ALS derived above-ground heights of the *i*th percentile, *j* = first, last or all returns; Soil parent material classes: 1 = moraine deposits, glacial river sediments, riverine deposits, landslide material and weathering residues, 2 = marine and fjord sediments, 3 = peatland and marsh soils, 4 = thin peat overlay and exposed rocks.

variables can therefore be categorised into three groups, which will be described in the following.

ALS is widely used for modelling of forest attributes, and ALS data has been shown to capture well the vertical structure of the vegetation (Maltamo et al., 2014). The ALS data which were used in the current project were provided by the Norwegian Mapping Authorities as part of a national scanning and consisted of data with point density of ~ 2–10 points per m^2 acquired in the period 2012–2021. More details about this set of ALS data are given by Hauglin et al. (2021). We used area-based ALS metrics similar to the ones used in forest inventories, and typically calculated from the distribution of above-ground heights of the laser echoes within a specified area. In the present study this area was the 250 m^2 circular field plots (for modelling) and 16 m square pixels (for predictions in the final map). The area-based method used in forest inventories is further described by Næsset (2004) and in Maltamo et al. (2014). The ALS-based variables selected in the final models are described in Table 1, and all candidate variables in Appendix A.

In addition to the ALS metrics described above, altitude, slope and aspect were derived from a 10 m digital terrain model created using data from the national ALS campaign. Values for slope and aspect were calculated using default values in the raster package (Hijmans et al., 2020) with the R programming language (R Core Team, 2022).

Imagery from the Sentinel-2 satellites captures the colour of the forest and vegetation and can complement the structural information from ALS. In the current study, we used spectral values from the following Sentinel-2 bands as candidate variables: B2, B3, B4, B5, B6, B7, B8, B8A, B11 and B12. The values were derived from a level-2A cloud free mosaic acquired in July 2018. The data from individual images in the mosaic were not calibrated to each other. We used July data to ensure data from well within the growing season at all locations. The conditions and the length of the growing season vary with altitude and latitude, and using satellite imagery from early or late in the summer season increases the chance of conditions such as snow, vegetation with completely no leaves at all or autumn colours. In addition to the level-2A values on the bands, the following ecological indices derived from Sentinel-2 were used as candidate variables: ratio vegetation index = B8/B4, normalised difference vegetation index (NDVI) = (B8-B4)/(B8+B4), moisture index = B11/B8, normalised difference moisture index (NDMI) = (B8-B11)/(B8+B11), normalised difference red edge index (NDRE) = (B5-B4)/(B5+B4) and plant senescence reflectance index = (B4-B2)/B5.

The Norwegian national forest resource map SR16 is created using remote sensing data from ALS and Sentinel-2, with ground reference data from the NFI field plots. The forest resource map SR16 and the attributes in it are further described by Hauglin et al. (2021) and Antón-Fernández et al. (2023). From the forest resource map, the following candidate variables were considered: dominant tree species, site index, stand volume, stand basal area and the number of trees. Note that for the modelling dataset we used field-measured values for these attributes wherever these were available (2.1). The data from the forest resource map were mainly used for prediction (2.6).

We calculated values from each of the raster datasets described above for the field plots using a weighted mean. The area of the intersection between each raster cell and the circular field plot was used as the weight.

2.3. Other auxiliary data

The climate at a location is an important factor in determining the growing conditions. We included variables from a national dataset with climate data, provided by the Norwegian Meteorological Institute (Lussana et al., 2019). The dataset contains daily mean temperature and precipitation sums with a spatial resolution of 1 km. In the current study, we resampled the climate variables to 16 m resolution and applied a procedure for downscaling temperature in which the mean temperature is adjusted to the actual altitude of each 16 m pixel using a temperature lapse rate of 0.6 °C per 100 m of elevation (Skaugen et al., 2003). The climate variables considered as candidate predictors were the mean effective temperature sum (5 °C threshold) in degree days during the period of 1989–2018 as well as the averages of the mean monthly temperatures and the monthly precipitation sums during the same period.

The conditions for plants and vegetation vary along several gradients in Norway. Hence, altitude, latitude, longitude, and distance to coast were included as candidate variables describing the location of a particular plot or pixel in Norway. In addition, the country was divided into five regions: East, Central-South, West, North and North-East (Fig. 5).

Soil properties will affect conditions for plants, and we have included information from an existing national map of soil parent material (Geological Survey of Norway, 2021). From this soil parent material map with initially 60 classes, we used a division into four combined classes: 1) moraine deposits, glacial river sediments, riverine deposits, landslide material and weathering residues, 2) marine and fjord sediments, 3) peatland and marsh soils, and 4) thin peat overlay and exposed rocks. The grouping into the combined classes was done to reduce the number of classes, and it broadly corresponds to soil formation in the case of the three first classes (dynamic geological processes, marine environments, and organic processes). A complete list of the conversion from the initial 60 classes is given in Appendix B.

2.4. Modelling the lingonberry cover

A generalised linear mixed-effects model using a log-link function and a quasi-Poisson distribution assumption was used in modelling the lingonberry cover. The general multi-level quasi-Poisson model for lingonberry cover was as follows:

$$y_{ij} \sim \text{Poisson}(\pi_{ij})$$

$$\ln(\pi_{ij}) = f(X_{ij}, \beta) + u_i + u_{ij} \tag{1}$$

where y is the percent cover of lingonberry (i.e., the mean percent cover of four subplots) observed on the NFI plot; the conditional distribution of y, given the expected value π, is the Poisson distribution; $\ln(\pi)$ is a log-link function; $f(\cdot)$ is a linear function with fixed predictors X_{ij} and fixed parameters β; subscripts i and j refer to region ($i = 1, 2, \ldots, 5$) and NFI plot, respectively; and u_i and u_{ij} are respectively the normally distributed, between-region and between-plot effects with the means of 0 and constant variances. The expected value of variance was greater than the expected value of mean and thus, plot-level (observation-level) random effects were used to account for overdispersion (Browne et al. 2005).

The model was fitted by using the function glmmPQL in the R package MASS (Venables and Ripley, 2002) and the R package effects (Fox, 2003) was used in visualisation of the impacts of independent variables on dependent variable (R Core Team, 2022). Variables available in the NFI, remote sensing and auxiliary datasets as well as their interactions were considered as potential predictors in the model. Correlation analysis was performed as a preliminary exploratory analysis of the relationships among dependent and independent variables. The predictors included in the final model had to be logical and significant at the 0.001 level, and with no systematic errors observed in the residuals. The significance of the categorical variables was evaluated by the joined Wald χ^2 test (the function wald.test). A collinearity analysis with the predictors of the final model was performed by calculating the variance inflation factor (VIF) values using the R package usdm (Naimi et al., 2014).

The predictions in the arithmetic scale were computed based on the fixed part of the mixed-effects model by setting the random effects equal to zero. The bias of such marginal predictions was corrected by applying an empirical ratio estimator suggested by Snowdon (1991), so that the marginal predictions were multiplied by the ratio of the mean of the observations and the mean of the predicted values. The performance of the model was evaluated by examining the magnitude and distribution of the prediction errors (observation – prediction) as a function of the predictions as well as the predictors of the model. The aim was to detect any obvious dependencies or patterns that indicate systematic discrepancies. In Appendix C, residual plots were provided using the mywhiskers function of the lmfor package for adding vertical lines onto residual plots to show 95 % confidence intervals for individual observations in the classes of the variable on the x-axis (Mehtatalo and Kansanen, 2022). Pearsoń s correlation coefficient was calculated between the predicted and observed percent covers of lingonberry. To assess the accuracy of the predictions, the proportion of explained variance (R^2) and root mean square error (RMSE) were calculated. The relative RMSE was calculated by dividing the RMSE by the mean of the observed response.

2.5. Validation of the lingonberry cover model

The lingonberry cover model was validated with the data from the NFI plots resurveyed in 2022 (Table 1). In the model validation, the percent cover of lingonberry on plots surveyed in 2022 was predicted with the fixed part of the cover model (i.e., bias-corrected

Table 2
Parameter estimates of the multi-level quasi-Poisson model estimated for the percent cover of lingonberry on the Norwegian NFI plots (n = 6404).

Variable*	Estimate	Std. Error	t-value	p-value
Intercept	−5.476E+00	1.119E+00	−4.89	<0.001
Main tree species (ref. Spruce)			χ^2 (2) = 184.9	<0.001
Pine	−1.319E+00	9.782E−02	−13.49	<0.001
Broadleaves	−6.112E−01	9.124E−02	−6.70	<0.001
Soil parent material (ref. Class 1)			χ^2 (3) = 63.8	<0.001
Class 2	−3.574E−01	1.049E−01	−3.41	0.001
Class 3	−3.324E−01	7.306E−02	−4.55	<0.001
Class 4	1.769E−01	4.224E−02	4.19	<0.001
Mean temperature June–August	1.109E+00	1.759E−01	6.30	<0.001
(Mean temperature June–August)^2	−4.438E−02	7.049E−03	−6.30	<0.001
B8A	−4.217E−04	2.882E−05	−14.63	<0.001
H10_first	−9.806E−02	1.433E−02	−6.84	<0.001
H95_first	1.550E−01	1.423E−02	10.90	<0.001
(H95_first)^2	−6.356E−03	5.794E−04	−10.97	<0.001
H50_last	−6.127E−02	1.111E−02	−5.51	<0.001
H50_all	−4.740E−02	1.129E−02	−4.20	<0.001
Latitude: Distance to coast	2.980E−05	6.578E−06	4.53	<0.001
Latitude: Slope: cos(Aspect)	−6.634E−05	1.234E−05	−5.37	<0.001
Latitude: Slope: sin(Aspect)	−6.868E−05	1.231E−05	−5.58	<0.001
Latitude: Species: Stand basal area			χ^2 (3) = 344.1	<0.001
Latitude: Spruce: BA	−6.078E−04	1.153E−04	−5.27	<0.001
Latitude: Pine: BA	2.118E−03	1.500E−04	14.12	<0.001
Latitude: Broadleaves: BA	−6.966E−04	1.524E−04	−4.57	<0.001
Latitude: Species: (BA)^2			χ^2 (3) = 131.7	<0.001
Latitude: Spruce: (BA)^2	7.160E−07	1.893E−06	0.38	0.705
Latitude: Pine: (BA)^2	−3.676E−05	3.383E−06	−10.87	<0.001
Latitude: Broadleaves: (BA)^2	5.237E−06	3.846E−06	1.36	0.173
Variance components at				
Region level (n = 5)	0.2581			
Plot level (n = 6404)	1.8085			

* Units: Main tree species (0/1); Soil parent material (0/1); Mean temperature (°C); B2A = reflectance value for Sentinel-2 band B8A (unitless); Hi_j = ALS derived heights of the ith percentile, j = first, last or all returns (m); Latitude (degrees); Distance to coast (km); Slope (%); Aspect (radians); BA = stand basal area (m^2 ha^{-1}). Soil parent material classes are defined in Table 1.

marginal predictions), using the variables measured in 2022 as predictors. Pearsoń's correlation coefficient was calculated between predicted and observed percent covers in 2022. Prediction errors were evaluated to detect any obvious dependences or patterns that indicate systematic discrepancies (Appendix C). The accuracy of the predictions in the validation data was assessed by calculating the proportion of explained variance (R^2), root mean square error (RMSE) and the relative RMSE.

The lingonberry abundance and yield are linked, and the cover model is aimed to be utilised together with a berry yield model to locate the most productive berry habitats in Norwegian forests. Therefore, the cover model was evaluated based on the model's applicability in identifying the most abundant lingonberry sites. Ten percent of the NFI plots with the highest cover were selected to represent the high abundance (649 plots with lingonberry cover > 9 % in the modelling data and 230 plots with lingonberry cover > 10 % in the validation data). The numbers and frequencies of the plots with observed and predicted high abundance plots were calculated by regions, dominant tree species and soil parent material classes. The aim was to identify discrepancies between the most abundant lingonberry sites observed and predicted.

2.6. Mapping the abundance of lingonberry in Norway

The fitted model was used to predict lingonberry cover at the national level. The predictions were done for 16 × 16 m pixels, corresponding to the pixel resolution of the SR16 forest resources map, and approximately (256 vs 250 m^2) to the area of the NFI plots. Candidate predictor variables had been selected based on availability in the modelling stage and could therefore be used to produce a raster map at the national level.

3. Results

3.1. Validation of the fitted lingonberry cover model

The most important predictors of the percent cover of lingonberry were the interaction terms of tree species, stand basal area (BA) and latitude, as well as the reflectance in the narrow near-infrared band (Sentinel-2 B8A) from the satellite imagery (Table 2). In pine dominated forests, lingonberry cover increased with BA up to the stand density of about 30 m^2 ha^{-1}, after which cover gradually decreased (Fig. 1). In spruce and broadleaves dominated forests, only low BA values were able to promote the abundance of lingonberry. The optimal dominant height (based on the ALS variable H95_first) for lingonberry was found to be about 12 m (Fig. 2). The Sentinel-2-based variable B8A and the ALS-based variables H10_first, H50_last and H50_all were significant predictors of the abundance of lingonberry, describing the effects of stand characteristics, not captured solely by species-specific BA, especially those of understory and canopy vertical structure (Fig. 2). Describing the long-term average of the climatic conditions in each location, the mean summer (June–August) temperatures of 12–13 °C favoured the abundance of lingonberry (Fig. 3). Also, soil parent material was a significant predictor in the model; the highest cover was found on thin soil or bare rock and the lowest one on organic and marine sedimentary soils (Fig. 3). Lingonberry cover was higher at the more southern and continental locations (Fig. 3). Logically, south-, west- and especially southwest-facing slopes being dryer and warmer, better supported drought-resistant lingonberry compared with east- and north-facing slopes (Fig. 4).

The VIF values of the forest structural variables (BA, B8A, H10_first, H50_last, H50_all and H95_first) of the model were from 1.19 to 4.70, the highest correlation of 0.82 being between BA and h50_all. The VIF values less than 5 indicate that there is no serious collinearity problem in the model.

In the validation data (the NFI plots surveyed in 2022), the model for the percent cover of lingonberry gave positively biased predictions (0.6 %-units) (Table 3). However, the residuals did not show any obvious bias after the logarithmic predictions were back-transformed to arithmetic scale (Appendix C). In general, the cover model behaved rather similarly, showing positive Pearson's correlation coefficient of 0.38 ($p < 0.001$) between measurements and predictions in both the modelling and validation data sets. Due to asymmetric distribution and zero or close-to-zero values of the response variable, the model was not able to predict either very low

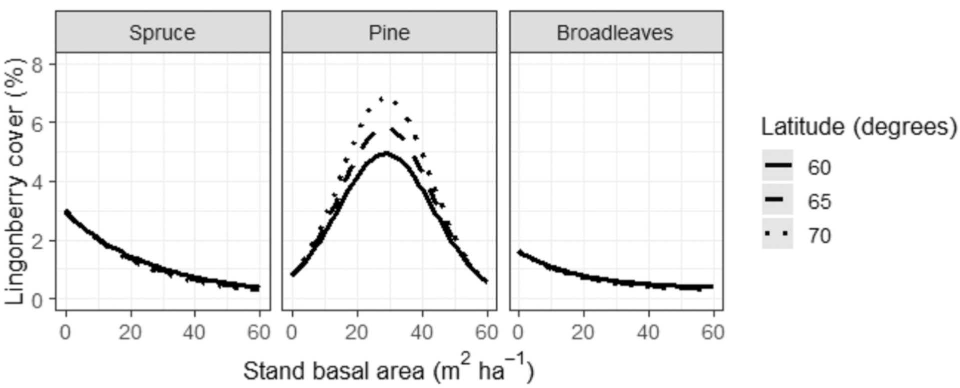

Fig. 1. Predicted responses of lingonberry cover to tree species, stand basal area and latitude.

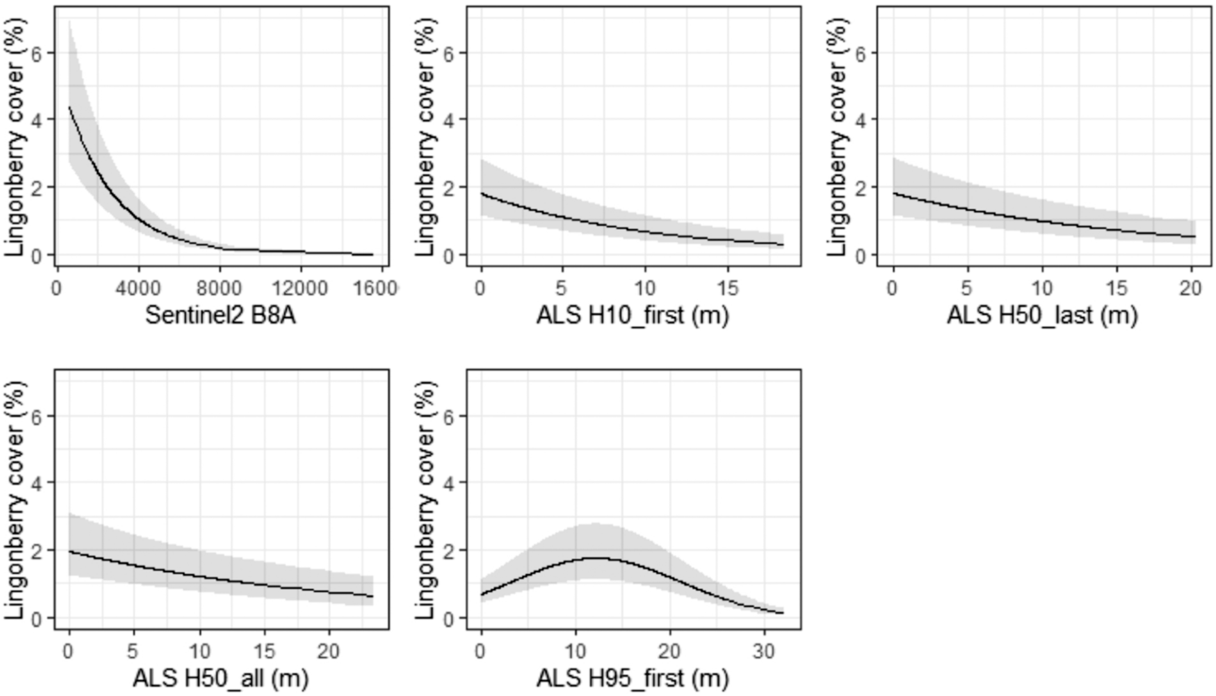

Fig. 2. Predicted responses and 95 % confidence intervals of lingonberry cover to the Sentinel-2-based variable B8A, and the ALS-based variables H10_first, H50_last, H50_all and H95_first.

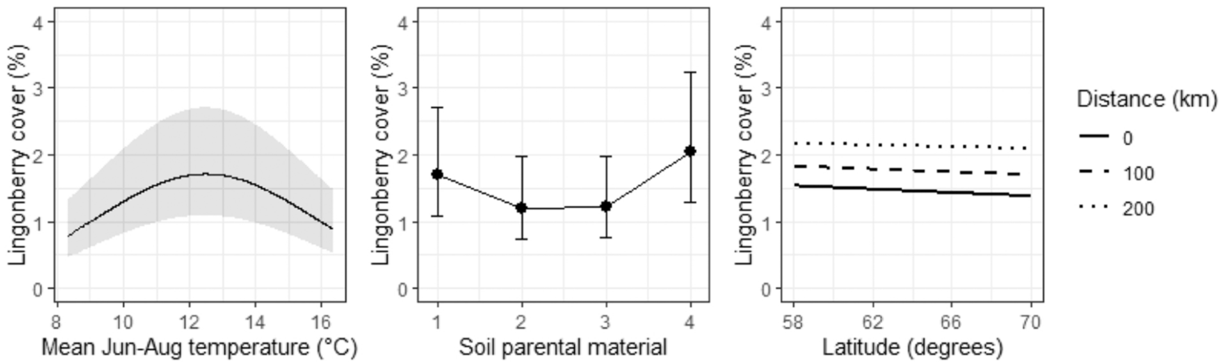

Fig. 3. Predicted responses and 95 % confidence intervals of the lingonberry cover to the mean temperature of June–August, soil parent material classes (defined in Table 1), as well as latitude and distance to coast.

or high values for lingonberry cover.

The predictions of the cover model were evaluated by identifying NFI plots with lingonberry cover higher than the 90th percentile of the modelling and validation data sets. Comparison of the observed and predicted numbers and frequencies of the NFI plots with a high abundance of lingonberry are presented in Table 4. In the southern regions (1–3), predictions agreed better with observations than in the north. Surprisingly, the accuracy of the regional predictions using both the fixed and random region effects was not better than those obtained using only the fixed effects. The model over-estimated the number of pine-dominated plots with high abundance and under-estimated the number of spruce- and broadleaves-dominated plots. There were only slight discrepancies between observations and predictions in the most common soil parent material classes (i.e., classes 1 and 4). The NFI plots with a high abundance of lingonberry were identified similarly with both the modelling and validation data.

3.2. Map of the predicted abundance of lingonberry plant in Norway

A raster map with spatial resolution of 16 m was produced for all of Norway (Fig. 5). The map shows the predicted cover of lingonberry plant, given the values of the predictor variables at a particular location (pixel). At the national level, the map indicates a

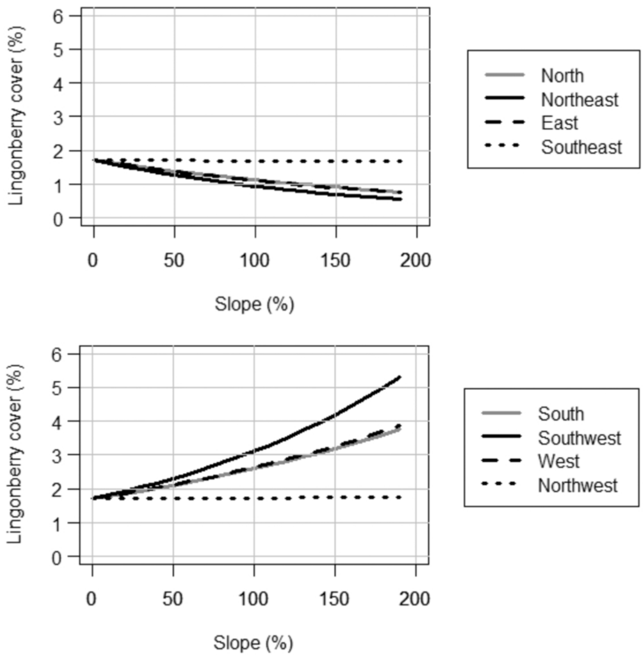

Fig. 4. Predicted responses of lingonberry cover to the steepness and direction of the slope.

Table 3
Main statistics, bias and precision of predictions of the fixed part of the model for the percent cover of lingonberry (Eq. (1)), Table 2), as well as Pearson's correlation coefficients between observations and predictions. The modelling (n = 6404) and validation (n = 2124) data included the Norwegian NFI plots surveyed in 2019–2021 and 2022, respectively. The relative error statistics are in parentheses. Note that in the modelling data, predictions are unbiased due to bias correction.

Variable	Predicted cover (%) in the modelling data	Predicted cover (%) in the validation data
Snowdon's bias correction ratio	1.6983	1.6983
Mean	3.14	3.19
Standard deviation	3.02	2.94
Range	0.0–24.6	0.0–18.0
Pearson correlation	0.38	0.38
Proportion of explained variance R^2	8.7 %	11.8 %
Bias (relative bias)	0 (0 %)	0.6 (14.7 %)
RMSE (relative RMSE)	4.7 (151 %)	5.1 (137 %)

high abundance of lingonberry in the south-eastern part of Norway and along the west coast of the Oslo fjord. More scattered occurrences of lingonberry are shown at the west coast and in Trøndelag and Nordland counties. High abundance sites are also found in Finnmark, the northernmost county of Norway. At the local level, the map shows how the predicted cover of lingonberry varies in the landscape, and one example of a local map is given in Fig. 6.

4. Discussion

The aim of the current study was to map lingonberry cover and assess its response to forest structure and environmental variables in Norway. Lingonberry cover was surveyed on the sample plots of the Norwegian national forest inventory (NFI) covering a wide range of forest structures and environmental conditions across the entire country. The cover model was fitted and validated by using NFI data collected during 2019–2021 and 2022, respectively. Using an extensive nationwide sampling, we were able to provide new quantitative information on factors influencing lingonberry cover and to map the distribution of the species within the country.

The results obtained from the modelling indicate several key predictors influencing the percent cover of lingonberry across different forest types and environmental conditions. Pine forests had generally the highest lingonberry cover (Salemaa, 2000). *Vaccinium* shrubs prefer well-drained acidic soils, which pine forests often provide. In pine-dominated forests, the cover initially increased with stand basal area (BA) up to a density of around 30 m^2 ha^{-1}. However, beyond this threshold, lingonberry cover gradually decreased. This suggests that while moderate BAs can promote lingonberry, excessively dense pine stands inhibit growth (cf. Miina et al., 2021). Conversely, in spruce and broadleaved dominated forests, lingonberry cover was favoured by lower BA values which are most probably indicating low site fertility. The emphasis on optimal light conditions has also been seen for bilberry (Eldegard et al.,

Table 4
The observed and predicted number and frequency of the NFI plots with lingonberry cover higher than the 90th percentile of the modelling and validation data by region, tree species and soil parent material.

	Modelling data					
	Observed		Predicted (fixed part)		Predicted (fixed + random)	
Region	n	%	n	%	n	%
1	256	13.6 %	250	13.3 %	287	15.2 %
2	153	10.6 %	218	15.1 %	237	16.4 %
3	48	5.5 %	75	8.6 %	18	2.1 %
4	171	8.3 %	87	4.2 %	66	3.2 %
5	21	15.2 %	11	8.0 %	33	23.9 %
Total	649	10.1 %	641	10.0 %	641	10.0 %
	Validation data					
	Observed		Predicted (fixed part)		Predicted (fixed + random)	
Region	n	%	n	%	n	%
1	90	13.3 %	90	13.3 %	103	15.2 %
2	50	10.9 %	67	14.7 %	72	15.8 %
3	8	3.0 %	15	5.6 %	2	0.7 %
4	75	11.0 %	40	5.9 %	30	4.4 %
5	7	17.1 %	1	2.4 %	6	14.6 %
Total	230	10.8 %	213	10.0 %	213	10.0 %
	Modelling data					
	Observed		Predicted (fixed part)		Predicted (fixed + random)	
Tree species	n	%	n	%	n	%
Spruce	182	9.2 %	21	1.1 %	29	1.5 %
Pine	368	16.5 %	620	27.8 %	609	27.3 %
Broadleaves	99	4.5 %	0	0.0 %	3	0.1 %
Total	649	10.1 %	641	10.0 %	641	10.0 %
	Validation data					
	Observed		Predicted (fixed part)		Predicted (fixed + random)	
Tree species	n	%	n	%	n	%
Spruce	57	8.9 %	5	0.8 %	8	1.2 %
Pine	135	18.4 %	208	28.3 %	203	27.7 %
Broadleaves	38	5.1 %	0	0.0 %	2	0.3 %
Total	230	10.8 %	213	10.0 %	213	10.0 %
	Modelling data					
	Observed		Predicted (fixed part)		Predicted (fixed + random)	
Soil parent material	n	%	n	%	n	%
Class 1	395	10.4 %	389	10.2 %	414	10.9 %
Class 2	12	6.3 %	0	0.0 %	0	0.0 %
Class 3	27	6.8 %	7	1.8 %	10	2.5 %
Class 4	215	10.7 %	245	12.2 %	217	10.8 %
Total	649	10.1 %	641	10.0 %	641	10.0 %
	Validation data					
	Observed		Predicted (fixed part)		Predicted (fixed + random)	
Soil parent material	n	%	n	%	n	%
Class 1	152	11.5 %	121	9.2 %	128	9.7 %
Class 2	4	6.7 %	0	0.0 %	0	0.0 %
Class 3	8	6.2 %	6	4.7 %	6	4.7 %
Class 4	66	10.7 %	86	13.9 %	79	12.8 %
Total	230	10.8 %	213	10.0 %	213	10.0 %

Soil parent material classes are defined in Table 1.

2019) where stand density, solar irradiation and tree species composition were significant predictors. In the case of pine dominated forest, they found the cover of bilberry to peak at a basal area of around 40 m^2 ha^{-1}, which is somewhat higher than the optimal basal area for lingonberry detected in our study. It is noteworthy however, that the predictors derived from ALS and satellite imagery provided additional predictive power in our study. This shows that the remotely sensed variables captured additional information about the stand height and canopy structure, thus being able to describe, for example, the understory light conditions better than if using basal area alone. Forest structural measures derived from ALS data have been used also in earlier studies where understory shrub species have been studied (Barber et al., 2016; Majasalmi and Rautiainen, 2020; Nielsen et al., 2020; Bohlin et al., 2021). Interestingly, the values of narrow near-infrared band (B8A) outperformed the ecological indices derived from the band values of Sentinel-2. Choosing July as the single time point for the Sentinel-2 data ensured that the satellite imagery was within the growing season at all locations. The use of multi-temporal Sentinel-2 data (including leaf-off data) would have been possible, but not without complicating factors.

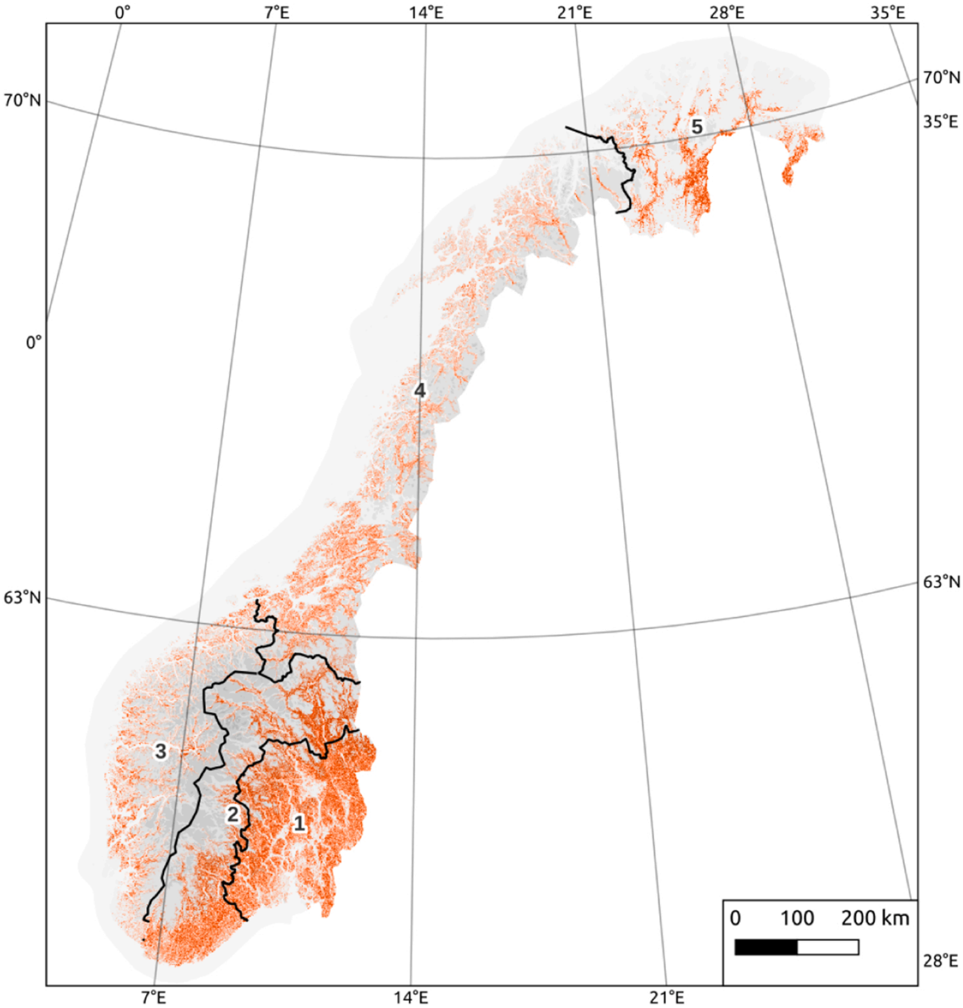

Fig. 5. National map of predicted lingonberry cover. Darker shades of red indicate a higher predicted value (the reader is referred to the online version of this paper for the colour information). The division of the country into five regions are shown on the map: East (1), Central-South (2), West (3), North (4) and North-East (5).

Based on our model, lingonberry was more abundant on south-facing slopes compared with north-facing slopes. South-facing slopes receive more sunlight and become drier and warmer, supporting drought-resistant lingonberry. Several studies have indicated that lingonberry is highly affected by the light environment beneath the forest canopy (Oldemeyer and Seemel, 1976; Holloway et al., 1982; Hjalmarsson and Ortiz, 1998; Tonteri et al., 2016). A study from Alaska found a strong correlation between lingonberry biomass and canopy coverage, suggesting that more shade leads to better plant growth (Oldemeyer and Seemel, 1976). Additionally, experiments manipulating light exposure found that leafy rhizome branches were longer under 73 % shade, while the rhizomes were longer without shade than under lower light intensities (Holloway et al., 1982). These findings suggest that lingonberry exhibits the highest growth rate under full sun exposure. In boreal forests in Sweden, the abundance of lingonberry varied only slightly across stand age. The lingonberry cover was around 5 % on clearcuts and in young stands, and around 7 % in old forests (Kardell, 1980). While, in a study from Finland, lingonberry cover decreased strongly after regeneration cutting but recovered relatively quickly and increased after thinning (Tonteri et al., 2016). Cuttings reduce the canopy coverage and thus modify the environmental conditions for understory vegetation by increasing light availability, causing the fluctuation of air and soil temperatures and hydrological conditions, and consequently influencing plant succession and the competitive interactions among plants. After regeneration cutting, lingonberry cover may decrease due to sudden changes in abiotic growth conditions, however mechanical damage caused by logging machinery, harvest residues and site preparation can cause large alterations.

Based on both controlled experiments and field observations, the conditions enabling optimal vegetative growth and berry yields differ. In a study by Smith (1962) in Alberta, Canada, abundance, and flowering of lingonberry was investigated. In that study, the highest abundance was found in moderate to heavy shade while plants in the most shaded habitats did not form flower buds. A similar pattern was observed in the study of Miina et al. (2021), detecting the highest berry yields in forest stands aged younger than 10 years, despite lingonberry cover increased with increasing stand age. Despite the seemingly contradictory patterns of lingonberry cover and

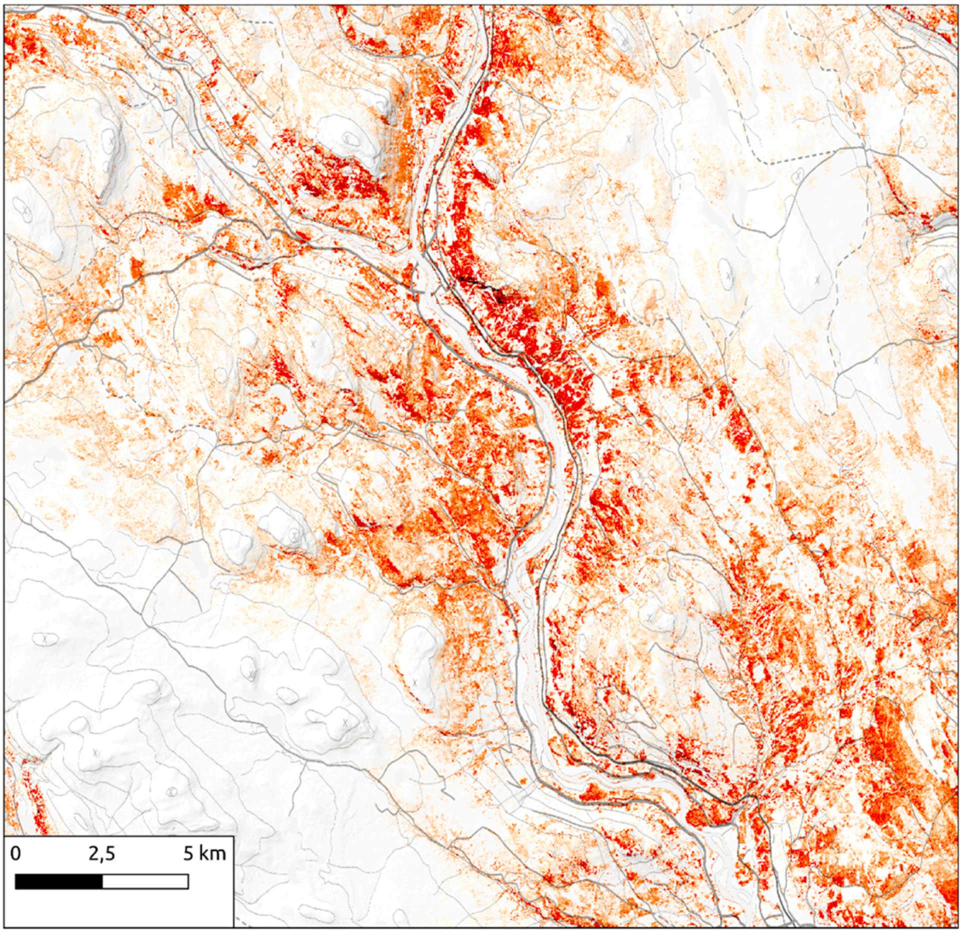

Fig. 6. Example of local view of the map with predicted lingonberry cover, from the middle of region 1 (see Fig. 5). Darker shades of red indicate a higher predicted value (the reader is referred to the online version of this paper for the colour information).

yield, along the gradients of light conditions and stand age that may appear, we can hypothesise that maintaining a cover of lingonberry throughout the rotation through stand density management could promote high yields after the next regeneration cut.

In the current study, the soil grouping aimed to combine soils with comparable nutrient and water availability characteristics. This approach reflects the composition of the plant community, which in turn determines the intensity of competition for below-ground resources and light. We found that thin soil or bare rock and more southern, continental locations had the highest lingonberry cover, while organic and marine sedimentary soils were less suitable for lingonberry. Earlier, (Coudun and Gégout, 2007) modelled the distribution of *V. myrtillus* in France, finding that soil conditions were a key predicting factor influencing the regional range of the species. Also, Smith (1962) has studied the abundance of three *Vaccinium* species in relation to the density of tree cover and soil characteristics, emphasising that lack of competition favours lingonberry. Additionally, the dominant tree species can partly determine soil properties like the nutrient status, pH, carbon-to-nitrogen ratio, and soil texture. Hansson et al. (2011) compared soil properties between adjacent forests of Norway spruce, Scots pine and silver birch (*Betula pendula* Roth), in southern Sweden. They found differences in soil parameters among the forest types in the organic layer, but decreased with soil depth, and were not significant at 20–30 cm depth.

As a climatic variable, the mean summer (June–August) temperatures of 12–13 °C favoured a high cover of lingonberry. In Norway, the mean summer temperature depends on e.g., longitude, latitude, altitude and distance to coast. Increased knowledge on optimal climatic conditions for lingonberry adapted to Norwegian conditions can be applied in predicting potential future changes in the abundance of lingonberry due to global warming. Studies like Villén-Peréz et al. (2020) indicated that in Finland lingonberry is a temperature sensitive species which will migrate northwards as the temperature increase. They also found that the abundance of lingonberry decreased with increasing precipitation, however precipitation was a non-significant predictor in our model. Due to the sensitivity of lingonberry, monitoring of the current and future abundance could provide as an indicator of the effects of global warming on Norwegian forest ecosystems.

Unbiased predictions of high-abundance sites are key for locating optimal sites for berry harvesting. Considering the interaction of all factors that affect lingonberry plant, the lingonberry cover model enables us to identify sites suitable for the species and quantify the species' responses to disturbances (e.g., forest management) and natural factors. Although the cover model struggled to predict very high lingonberry cover values, the model predicted reasonably the high-abundance sites by region and soil parent material.

Bohlin et al. (2021) have combined ALS metrics with other wall-to-wall variables and NFI field data to model bilberry and lingonberry yields in Sweden. They further demonstrated the use of these models to map the most promising sites for berry harvesting. We used the lingonberry cover model to map the abundance of lingonberry in Norway. Overall, the pattern emerging at the national level when assessing the lingonberry cover map corresponds with established knowledge of where lingonberry is typically abundant. The validation of the model provides a strong initial indication of the accuracy of the map since the data used in this study is a systematic sample of the entire forest area in Norway. However, a potential limitation could be due to using field measured values for some of the variables, whereas in the predictions for the map these variables were derived from remote sensing data. Consequently, the validation of the model does not directly reflect the accuracy of the predictions in the map. Since the remote-sensing derived variables will have an additional uncertainty, one can expect that the prediction in the map will have slightly lower accuracy than what was observed in the validation of the model. This difference was not quantified in the current study, i.e., no separate validation of the map predictions was carried out. Furthermore, the model was built using data from forested areas only (i.e., the NFI field plots) so the map is limited to forest areas in Norway. Hence, some area categories where lingonberry occur, such as mires and mountain areas, are not covered by the map. For lingonberry harvesting, the excluded areas are not so important as the highest berry yields are typically found in forested areas.

In conclusion, we were able to: 1) derive a model predicting the cover of lingonberry in forests across Norway, and 2) map lingonberry abundance at local scales, using the derived model. The model provides new information on species-environment relationship for lingonberry and could be used to identify site conditions suitable for the conservation and sustainable management of a key species and to forecast the impact of global warming on the abundance of the species within Norway. Moreover, in the future the cover model could also be linked to forest simulators to identify stand management regimes that favour lingonberry (cf., Miina et al., 2021). Since lingonberry yield is linked to the plant cover, the derived map can also aid berry picking for both household and commercial use.

CRediT authorship contribution statement

Miina: Conceptualization, Methodology, Formal analysis, Validation, Visualization, Writing – original draft. **Hauglin**: Conceptualization, Methodology, Data curation, Formal analysis, Data interpretation, Visualization, Writing – original draft. **Granhus**: Conceptualization, Methodology, Data interpretation, Writing – original draft. **Hykkerud**: Conceptualization, Methodology, Data interpretation, Writing – original draft. **Martinussen**: Conceptualization, Data interpretation, Funding acquisition, Project administration, Writing – original draft.

Ethical Statement

Not applicable

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

The authors do not have permission to share data.

Acknowledgements

This study was supported by The Research Council of Norway, Norway (grant number 294797), project "Norwegian wild berries – increased predictability and value creation – WILDBERRIES".

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03195.

References

Angelstam, P.K., 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. J. Veg. Sci. 9 (4), 593–602. https://doi.org/10.2307/3237275.

Antón-Fernández, C., Hauglin, M., Breidenbach, J., Astrup, R., 2023. Building a high-resolution site index map using boosted regression trees: the Norwegian case. Can. J. For. Res. 53 (6), 416–429. https://doi.org/10.1139/cjfr-2022-0198.

Barber, Q.E., Bater, C.W., Braid, A.C.R., Coops, N.C., Tompalski, P., Nielsen, S.E., 2016. Airborne laser scanning for modelling understory shrub abundance and productivity. For. Ecol. Manag. 377, 46–54. https://doi.org/10.1016/j.foreco.2016.06.037.

Bohlin, I., Maltamo, M., Hedenås, H., Lämås, T., Dahlgren, J., Mehtätalo, L., 2021. Predicting bilberry and cowberry yields using airborne laser scanning and other auxiliary data combined with National Forest Inventory field plot data. For. Ecol. Manag. 502, 119737 https://doi.org/10.1016/j.foreco.2021.119737.

Botequim, B., Zubizarreta-Gerendiain, A., Garcia-Gonzalo, J., Silva, A., Marque, S., Fernandes, P.M., Pereira, J.M.C., Tome, M., 2015. A model of shrub biomass accumulation as a tool to support management of Portuguese forests. iForest – Biogeosciences For. 8 (2), 114. https://doi.org/10.3832/ifor0931-008.

Bråthen, K.A., Gonzalez, V.T., Yoccoz, N.G., 2018. Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature gradient. Perspect. Plant Ecol. Evol. Syst. 30, 71–81. https://doi.org/10.1016/j.ppees.2017.06.005.

Breidenbach, J., Granhus, A., Hylen, G., Eriksen, R., Astrup, R., 2020. A century of National Forest Inventory in Norway – informing past, present, and future decisions. For. Ecosyst. 7, 46. https://doi.org/10.1186/s40663-020-00261-0.

Browne, W.J., Subramanian, S.V., Jones, K., Goldstein, H., 2005. Variance partitioning in multilevel logistic models that exhibit overdispersion. J. R. Stat. Soc. A 168, 599–613. https://doi.org/10.1111/j.1467-985X.2004.00365.x.

R. Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 〈https://www.R-project.org/〉.

Coudun, C., Gégout, J.-C., 2007. Quantitative prediction of the distribution and abundance of Vaccinium myrtillus with climatic and edaphic factors. J. Veg. Sci. 18 (4), 517–524. https://doi.org/10.1111/j.1654-1103.2007.tb02566.x.

Eldegard, K., Scholten, J., Stokland, J.N., Granhus, A., Lie, M., 2019. The influence of stand density on bilberry (*Vaccinium myrtillus* L.) cover depends on stand age, solar irradiation, and tree species composition. For. Ecol. Manag. 432, 582–590. https://doi.org/10.1016/j.foreco.2018.09.054.

Fox, J., 2003. Effect displays in R for generalised linear models. J. Stat. Softw. 8 (15), 1–27. 〈https://www.jstatsoft.org/article/view/v008i15〉.

Geological Survey of Norway (2021) Superficial deposits. Available from 〈https://kartkatalog.geonorge.no/metadata/loesmasser/3de4ddf6-d6b8-4398-8222-f5c47791a757〉.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 342 (6160), 850–853. https://doi.org/10.1126/science.1244693.

Hansson K., Olsson B.A., Olsson M., Johansson U., Kleja D.B. (2011) Differences in soil properties in adjacent stands of Scots pine, Norway spruce and silver birch in SW Sweden. Forest Ecology and Management 262: 522–530. https://doi.org/10.1016/j.foreco.2013.01.022.

Hauglin, M., Rahlf, J., Schumacher, J., Astrup, R., Breidenbach, J., 2021. Large scale mapping of forest attributes using heterogeneous sets of airborne laser scanning and National Forest Inventory data. For. Ecosyst. 8 (1)), 65 https://doi.org/10.1186/s40663-021-00338-4.

Hedwall, P.-O., Brunet, J., Nordin, A., Bergh, J., 2013. Changes in the abundance of keystone forest floor species in response to changes of forest structure. J. Veg. Sci. 24, 296–306. https://doi.org/10.1111/j.1654-1103.2012.01457.x.

Hijmans R.J., van Etten J., Sumner M., Cheng J., Baston D., Bevan A., Bivand R., et al. (2020) Raster: Geographic Data Analysis and Modeling. 〈https://CRAN.R-project.org/package=raster〉.

Hjalmarsson, I., Ortiz, R., 1998. Effect of genotype and environment on vegetative and reproductive characteristics of lingonberry (*Vaccinium vitis-idaea* L.). Acta Agric. Scand., Sect. B - Soil Plant Sci. 48, 255–262. https://doi.org/10.1080/09064719809362506.

Hjalmarsson, I., Ortiz, R., 2001. Lingonberry: Botany and horticulture. Hortic. Rev. 27 79–123. https://doi.org/10.1002/9780470650813.ch3.

Holloway, P.S., van Veldhuizen, R.M., Stushnoff, C., Wildung, D.K., 1982. Effects of light intensity on vegetative growth of lingonberries. Can. J. Plant Sci. 62, 965–968. https://doi.org/10.4141/cjps82-142.

Jones, M.S., Vanhanen, H., Peltola, R., Drummond, F., 2014. A global review of arthropod-mediated ecosystem-services in *Vaccinium* berry agroecosystems. Terr. Arthropod Rev. 7 (1), 41–78. https://doi.org/10.1163/18749836-06041074.

Jonsson, L., Uddstål, R., 2002. En beskrivning av den svenska skogsbärbranschen. Skog Og. Tr. ä 25 p..

Kardell, L., 1980. Occurrence and production of bilberry, lingonberry and raspberry in Sweden's forests. For. Ecol. Manag. 2, 285–298. https://doi.org/10.1016/0378-1127(79)90055-0.

Kausrud, K., 2022. Impacts of climate change on the boreal forest ecosystem. VKM Rep. 2022, 15.

Lussana, C., Tveito, O.E., Dobler, A., Tunheim, K., 2019. seNorge_2018, daily precipitation, and temperature datasets over Norway. Earth Syst. Sci. Data 11 (4), 1531–1551. https://doi.org/10.5194/essd-11-1531-2019.

Majasalmi, T., Rautiainen, M., Stenberg, P., Manninen, T., 2015. Validation of MODIS and GEOV1 fPAR products in a boreal forest site in Finland. Remote Sens. 7 (2), 1359–1379. https://doi.org/10.3390/rs70201359.

Majasalmi, T., Rautiainen, M., 2020. The impact of tree canopy structure on understory variation in a boreal forest. For. Ecol. Manag. 466, 118100 https://doi.org/10.1016/j.foreco.2020.118100.

Maltamo M., Næsset E., Vauhkonen J. (eds) (2014) Forestry applications of airborne laser scanning. Managing Forest Ecosystems 27. Springer, Dordrecht. 〈http://link.springer.com/10.1007/978-94-017-8663-8〉.

Mehtatalo L., Kansanen K. (2022) lmfor: functions for forest biometrics. R package version 1.6. 〈https://CRAN.R-project.org/package=lmfor〉.

Miina, J., Bohlin, I., Lind, T., Dahlgren, J., Härkönen, K., Packalen, T., Tolvanen, A., 2021. Lessons learnt from assessing the cover and yield of bilberry and lingonberry using the national forest inventories in Finland and Sweden. Silva Fenn. 55, 10573. https://doi.org/10.14214/sf.10573.

Næsset, E., 2004. Practical large-scale forest stand inventory using a small-footprint airborne scanning laser. Scand. J. For. Res. 19 (2), 164–179. https://doi.org/10.1080/02827580310019257.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37 (2), 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x.

Nestby, R., Hykkerud, A.L., Martinussen, I., 2019. Review of botanical characterization, growth preferences, climatic adaptation and human health effects of Ericaceae and Empetraceae wild dwarf shrub berries in boreal, alpine and arctic areas. J. Berry Res. 9 (3), 515–547. https://doi.org/10.3233/JBR-190390.

Nielsen, S.E., Dennett, J.M., Bater, C.W., 2020. Predicting occurrence, abundance, and fruiting of a cultural keystone species to inform landscape values and priority sites for habitat enhancements. Forests 11 (7), 783. https://doi.org/10.3390/f11070783.

Nilsson M.C., Wardle D.A. (2005) Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Frontiers in Ecology and the Environment 3(8): 421–428. https://doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2.

Oldemeyer, J.L., Seemel, R.K., 1976. Occurrence and nutritive quality of lowbush cranberry on the Kenai Peninsula, Alaska. Can. J. Bot. 54, 966–970. https://doi.org/10.1139/b76-101.

Olsson, E.G.A., Austrheim, G., Grenne, S.N., 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. Landsc. Ecol. 15 (2), 155–170. https://doi.org/10.1023/A:1008173628016.

Salemaa, M., 2000. *Vaccinium vitis-idaea*. Puolukka. In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I., Hotanen, J.-P. (Eds.), Kasvit muuttuvassa metsäluonnossa. [Effects of the changes in land use and forest management on vegetation]. Tammi, Helsinki., pp. 136–138.

Skaugen T., Hanssen-Bauer I., Førland E.J. (2003) Adjustment of dynamically downscaled temperature and precipitation data in Norway. Technical Report 20/02 KLIMA, Norwegian Meteorological Institute, Oslo, Norway.

Smith, D.W., 1962. Ecological studies of *Vaccinium* species in Alberta. Can. J. Plant Sci. 42, 82–90. https://doi.org/10.4141/cjps62-011.

Snowdon, P., 1991. A ratio estimator for bias correction in logarithmic regressions. Can. J. For. Res. 21, 720–724. https://doi.org/10.1139/x91-101.

Tolvanen, A., 1994. Differences in recovery between a deciduous and an evergreen ericaceous clonal dwarf shrub after simulated aboveground herbivory and belowground damage. Can. J. Bot. 72, 853–859. https://doi.org/10.1139/b94-110.

Tonteri, T., Salemaa, M., Rautio, P., Hallikainen, V., Korpela, L., Merilä, P., 2016. Forest management regulates temporal change in the cover of boreal plant species. For. Ecol. Manag. 381, 115–124. https://doi.org/10.1016/j.foreco.2016.09.015.

Turtiainen, M., Miina, J., Salo, K., Hotanen, J.-P., 2013. Empirical prediction models for the coverage and yields of cowberry in Finland. Silva Fenn. 47, 1005. https://doi.org/10.14214/sf.1005.
Tveite, B., 1977. Bonitetskurver for gran. [Site-index curves for Norway spruce (*Picea abies* (L.) Karst)]. Medd. fra Nor. Inst. Skogforsk. 33, 1–84.
Vaara, M., Saastamoinen, O., Turtiainen, M., 2013. Changes in wild berry picking in Finland between 1997 and 2011. Scand. J. For. Res. 28, 586–595. https://doi.org/10.1080/02827581.2013.786123.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th ed. Springer, New York. https://doi.org/10.1007/978-0-387-21706-2.
Viken, K.O., 2021. Landsskogtakseringens feltinstruks – 2021. NIBIO Bok 7 (5), 1–245. https://hdl.handle.net/11250/2826859.
Villén-Peréz, S., Heikkinen, J., Salemaa, M., Mäkipää, R., 2020. Global warming will affect the maximum potential abundance of boreal plant species. Ecography 43, 1–11. https://doi.org/10.1111/ecog.04720.