



Predicting bilberry and cowberry yields using airborne laser scanning and other auxiliary data combined with National Forest Inventory field plot data

Inka Bohlin^{a,*}, Matti Maltamo^b, Henrik Hedenås^a, Tomas Lämås^a, Jonas Dahlgren^a, Lauri Mehtätalo^c

^a Swedish University of Agricultural Sciences, Department of Forest Resource Management, Skogsmarksgränd, SE-901 83 Umeå, Sweden

^b University of Eastern Finland, School of Forest Sciences, P.O. Box 111, Joensuu, Finland

^c Natural Resources Institute Finland, Yliopistokatu 6, 80100 Joensuu, Finland

ARTICLE INFO

Keywords:

Lidar
Vaccinium myrtillus
Vaccinium vitis-idaea L.
 Berry yield
 Remote sensing
 Forest structure
 Mixed models
 NFI

ABSTRACT

The increasing availability of wall-to-wall remote sensing datasets in combination with accurate field data enables the mapping of different ecosystem services more accurately and over larger areas than before. The provision of wild berries is an essential ecosystem service, and berries are the most used non-wood forest products in Nordic countries. The aim of the study was to 1) develop general prediction models for bilberry and cowberry yield based on metrics derived from airborne laser scanning (ALS) data and other existing wall-to-wall data and 2) to identify laser-based structural features of forests that can be linked to locations of the highest berry yields. We used the indirect approach where the correlation between forest structure described by the ALS data and the berry yields are utilized. Berry data collected in the Swedish National Forest Inventory (NFI) 2007–2016 were used for training the models and ALS data from 2009 to 2014 from the national ALS campaign of Sweden. Berry yields were modelled using generalised linear mixed models (GLMMs), and forest structural differences were demonstrated in histograms of presence/absence data.

The ALS-based canopy cover was an important variable both in bilberry and cowberry models. Other significant variables were ALS-based height variance, shrub cover, height above sea level, slope, soil wetness and terrain ruggedness, satellite-based species-specific volume and percentage, seasonality of temperature and precipitation and annual precipitation, inventory year, soil type and land use class. In addition, the time difference between the inventory day and the Julian day when berries were expected to be ripe showed a 1.5% decrease for bilberry and a 1.1% decrease for cowberry yield per day during the season. The highest bilberry yield was identified in forests with a canopy cover of 50% and the highest cowberry yield in forests with a canopy cover close to zero. The canopy height of 15 m reflected the highest bilberry yield, whereas a canopy height close to 0 m resulted in the highest cowberry yield. The shrub cover was close to zero both with highest bilberry and cowberry yields.

This is the first study combining ALS metrics with other wall-to-wall variables and NFI field data to model bilberry and cowberry yields. Prediction models can be used to produce maps showing the most potential locations for berry picking. Further, the models may, in the future, be imported into forest planning systems to obtain stand-level prognoses of berry yield development under different forest management strategies.

1. Introduction

The Nordic landscape contains a variety of forest habitats that provide multiple benefits, natural resources and ecosystem services (e.g.,

Esseen et al., 1997, Snäll et al., 2014). The increased use of ecosystem services may lead to conflicts between different objectives. However, many forest owners appreciate the multiple benefits of the forest and want to integrate non-wood forest products and services in forest

* Corresponding author.

E-mail addresses: inka.bohlin@slu.se (I. Bohlin), matti.maltamo@uef.fi (M. Maltamo), henrik.hedenas@slu.se (H. Hedenås), tomas.lamas@slu.se (T. Lämås), jonas.dahlgren@slu.se (J. Dahlgren), lauri.mehtatalo@luke.fi (L. Mehtätalo).

<https://doi.org/10.1016/j.foreco.2021.119737>

Received 9 July 2021; Received in revised form 21 September 2021; Accepted 24 September 2021

Available online 30 September 2021

0378-1127/© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

management planning (Kangas, 1998, Eggers et al., 2014). Wild berries are the most utilized non-wood forest products by Nordic people (e.g., Kardell, 1979, Turtiainen, 2015), where bilberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea* L) are economically most important and provide the most abundant annual yields (e.g., Kardell, 1979, Turtiainen et al., 2011). The right of public access (Naturvårdsverket, 2021) makes it possible for everyone to pick berries for household consume and sale, and berry picking is also seen as an important recreational hobby (e.g., Hytönen, 2005). Further, the health effects of this “super-food” are widely recognised and even of international interest (e.g., Olas, 2018). Bilberries and cowberries are important species in understory vegetation and essential nutriment of various animals such as grouse, vole and bear (e.g., Lakka and Kouki 2009).

In northern Europe, bilberry and cowberry are adapted to different site types in conifer-dominated forests (e.g., Ritchie, 1955, 1956). Bilberry and cowberry are growing at the bottom of the shrub layer. Heights of the bilberry plants are about 10–50 cm and cowberry plants about 5–30 cm above the ground (Fig. 1). Plants reproduce both via vegetative means and form seeds and are pollinated by insects, in particular bumblebees. Bilberry typically grows in heath forests of medium site fertility and dominated by spruce (*Picea abies* (L.) Karst.) or pine (*Pinus sylvestris* L.), whereas cowberry prefers light pine-dominated dryish heath forests (e.g., Raatikainen et al., 1984, Salo, 1995). Both also occur and produce yields in many marginal forest types such as fell forests and on pristine and drained peatlands (e.g., Salo, 1995, Hotanen et al., 2000). The production of bilberry and cowberry has been subject of numerous studies because of the wide range of habitats occupied by the species and the large number of factor influencing berry yield, such as temperature, precipitation, frost, drought, pollination success, site type, forest structure (e.g., Eriksson et al., 1979, Raatikainen and Raatikainen, 1983, Rixen et al., 2010, Turtiainen, 2015, Kilpeläinen et al., 2016). However, in Swedish and Finnish forests, the coverage of bilberry has decreased, mainly due to forest management (Kardell, 1979, Salemaa, 2000, Dahlgren and Fridman, 2012). Climate change may also affect berry yields (growth, pollination and ripening) by changing the local climate and by the occurrence of more extreme weather conditions (e.g., Wallenius, 1999, Rixen et al., 2010, Bădescu et al., 2017).

Since 2003, worldwide unique berry yield data have been collected annually in the Swedish National Forest Inventory (NFI) (Fridman et al., 2014) at the Swedish University of Agricultural Sciences (SLU). For this, the number of bilberries and cowberries are counted in small vegetation

plots, here called “berry plots”, inside the NFI plots (see more detailed description below in “NFI field data”), and the annual berry yields of ripe berries kg/ha are estimated for each county with the help of local annual berry yield measurements from SLU’s research parks. In 2006–2016, this information was used together with local models of berry yield development over the season (flowers to raw berries and raw berries to ripe berries) from SLU’s research parks to forecast the yields of bilberry and cowberry for northern, middle and southern Sweden. These prognoses achieved also high interest among the public. The unique time series of bilberry and cowberry data also offers possibilities for spatial and temporal studies of berry yields in Sweden. Such data, combined with other datasets, such as wall-to-wall remote sensing data, offer possibilities to improve the forecasting of berry yields and maps at the landscape level, which is of high interest to many users.

Remote sensing data such as airborne laser scanning (ALS) data and satellite and aerial images are extensively used, especially in forest-related studies, because they enable 100% spatial coverage of study areas at lower costs compared to field inventories (e.g., Yichun et al., 2008). The usefulness of ALS data for forestry applications is based on the strong relationship between the height (above ground) distribution of the ALS data and the vertical structure of the vegetation (e.g., Maltamo et al., 2005). Due its cost efficiency, it has become the most efficient method in large-scale stand level forest inventories in many countries. Most of these studies have been focusing on forest attributes, such as the prediction of stem volume, biomass, tree species and canopy cover (Maltamo et al., 2014), which is understandable because of the economic value of wood and forestry, but also because of the ecological value of forests in national and international politics.

On the other hand, efficient forest planning requires knowledge about the supply and spatial distribution of all types of ecosystem values such as species habitats, ecosystem functioning and services within forest landscapes (e.g., Öhman et al., 2011). Predicting and mapping non-wood forest products has been challenging because of the characteristics of non-wood products such as small size, seasonality, rarity, difficult locations, among others. In addition, collecting field data for modelling is laborious and expensive. In the earlier studies, field measurements of bilberries and cowberries and accurate descriptions of tree stock and site type have been used to model berry yields. The main findings have been the relationship between berries and tree stock variables such as stand density, stand development, tree species and site type (Miina et al., 2009, Turtiainen, 2015). However, the general



Fig. 1. Bilberry (left) and cowberry (right) with ripen berries.

drawback of field measurement-based approaches is that accurate field data are typically not available for applications of the elaborated models. This information can be replaced with auxiliary remote sensing data (e.g., McRoberts et al., 2010), such as ALS data describing the forest structure and terrain variables as well as satellite and aerial images describing the forest types and tree species.

When predicting the dominant tree layer variables (e.g. tree height, stem volume, basal area) with ALS data the ALS metrics are directly measuring the structure of the forest, since laser points are reflecting from the forest canopy and the ground. However, when predicting variables under the dominant forest canopy, which are also usually small in size, such as many plant species, the use of ALS data is not as straightforward. This is because ALS data is usually too sparse in resolution to measure the structure of surface vegetation but also because large proportion of the laser hits reflects from the dominant tree canopy. In such cases indirect method can be used; that are based on the correlation between forest structure (such as tree height and density and canopy cover of trees described by ALS data) and the target variables (such as shrub cover or berry yield) instead of direct ALS measurements of the target variables. This type of method has been earlier applied e.g. in the prediction of plant species richness (e.g. Lopatin et al., 2016), downed dead wood (Pesonen et al., 2008), natural regeneration (e.g. Bollandsås et al., 2017) and forest beetle assemblages (Müller and Brandl, 2009).

Local studies have investigated the species richness of undergrowth plants using ALS data (e.g., Lucas et al., 2010, Nijland et al., 2014, Lopatin et al., 2016, Barber et al., 2016, Mao et al., 2018, Moeslund et al., 2019, Nielsen et al., 2020). Most of these studies have modelled species richness as a whole and not by individual plants. But for example, Barber et al. (2016) modelled the abundance and fruit production of buffaloberry, huckleberry and saskatoon shrubs using ALS data, concluding that models including stand structural variables improved, especially models of saskatoon and huckleberry. Similarly, Nielsen et al. (2020) used ALS based canopy cover and shrub abundance when predicting fruit production of velvet-leaf blueberry.

The first study where remote sensing-based forest and land use maps were used in bilberry and cowberry yield prediction was performed by Kilpeläinen et al. (2016). The authors used multisource national forest inventory (MS-NFI) data, combing field data, satellite images, terrain models and other mapped data sources. They concluded that both field- and MS-NFI-based input data were equally suitable for berry yield modelling. Recently, Vauhkonen (2018) modelled the suitability of picking bilberry and cowberry based on ALS data and MS-NFI data in a local study area. In his study, the training data of forest suitability for berry picking were based on expert models (Ihalainen et al., 2002) using forest stand characteristics, not empirical yield measurements. After field calibration, a better ability to explain the variation in ecosystem service proxies (including potential for berry picking) was observed for ALS-based models compared to MS-NFI-based ones (Vauhkonen, 2018).

Our current study is the first to combine berry yield data from Swedish NFI with nationwide ALS data to predict berry yields. The specific aims are 1) to develop general prediction models for bilberry and cowberry yields based on ALS data and other existing wall-to-wall data and 2) to identify laser-based structural features of forests that can be linked to locations of the highest bilberry and cowberry yields, highly interesting for berry pickers. This information can be used for multi-objective forest planning, developing the next-generation berry yield forecasting applications and mapping berry yields in forest landscapes.

2. Material and methods

Most of Sweden is covered by boreal forest dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.). The proportion of deciduous trees is higher towards the south and in the mountain areas. The Scandinavian Mountains in the west and northwest

create unique climate and soil conditions. Swedish forests are made up of 22.7 Mha productive forest land (site productivity $\geq 1 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$), largely well-managed for timber production, and consist of all kinds of development stages owned by private forest companies (24%), non-industrial private land forest owners (52%) and other owners (24%) (Skogsdata, 2019).

2.1. NFI field data

We used field data from the Swedish NFI 2007-2016 covering the entire country (Fridman et al., 2014). In the Swedish NFI, two independent field samples are carried out annually on permanent and temporary plots. During the period of this study, the NFI consisted of systematic (square grid) field samples randomly placed either on permanent (plot radius 10 m) or temporary plots (plot radius 7 m) located in square or rectangular clusters. Sampling intensity decreases and the side length of clusters (from 300 to 1,800 m) and the distance between plots within the clusters (from 300 to 600 m) increases towards the north. Since 2017, temporary plots have been established for balanced sampling, where auxiliary information is used (Grafström et al., 2017). Annually, about 9,500 plots are field-surveyed, of which 65% are permanent and re-measured every fifth year and 35% are temporary, i.e., measured only once. The coordinates of the plots are recorded using GPS (global positioning system) from the centre of the plots according to the instructions of the NFI. Several environmental variables, such as land use, soil, species richness, as well as habitat variables and forest variables such as tree species, stem volume, forest operations and forest damages, are measured or estimated in each plot (RIS, 2020).

2.1.1. Berry data and berry data processing

In the Swedish NFI, the unique bilberry and cowberry data collected from 2007 to 2010 from the permanent plots and from 2011 to 2016 both from permanent and temporary plots were used in this study. Only plots within a single forest stand or land use class were used (i.e., non-divided plots), and plots on mountains and in farmland, built areas, roads/railways, other land and water areas were excluded. A detailed bilberry and cowberry inventory was performed in two 0.25-m² circular berry plots inside the NFI plot. These two berry plots were located 2.5 m from the centre of the NFI plot, at 45 (right) and 225 (left) degrees from the original walking direction. In the berry plots, where at least one living bilberry or cowberry plant occurred, a development class (before flowering, flowering, raw berries, ripen berries, berries fallen of) was evaluated, and the numbers of flowers and berries (only in development classes flowers, raw berries and ripe berries) were counted by species. The development class was selected based on the stage of the majority of the bilberry and cowberry plants inside the berry plots and had to be same for both plots. If flowers or berries were missing from the berry plots, the development class was evaluated from the vegetation around the berry plots. All flowers and berries were counted despite different development classes, and afterwards, the sum of the counted flowers and berries of two berry plots was calculated.

We removed NFI plots with major changes in field and ALS data acquisition caused by management operations, natural disturbances and growth. This was done in three steps: first, only field plots inventoried maximum 3 years before or after ALS data acquisition were selected. Second, the NFI plots measured maximum 3 years after laser data acquisition, in which new clearcuts, thinnings and clearings were recorded, were removed. In the third step, Mahalanobis distance measurement was used to compare the laser-based grid-value (mean value of grid-cells inside the NFI plot) of stem volume ($\text{m}^3 \text{ ha}^{-1}$) and basal area weighted mean height (m) from the National attribute map of Sweden (Nilsson et al., 2017, based on the same ALS data as used in this study) with the field-measured stem volume and the mean height of each remaining NFI plot. In total, 15% of NFI plots selected after the second step were determined as outliers and removed from the dataset in the third step (the same percentage was used when the National Forest

attribute map of Sweden was created).

In the final phase, to be able to model the berry yield, only those bilberry and cowberry plots where flower and berry numbers had been counted (development stages flowering, raw berries and ripe berries from May to November) were used for modelling, together with plots which did not have any bilberry or cowberry vegetation. Berry plots with development stages before flowering and berries fallen off were removed since they contained no information on the potential berry production in the plot. The final plot numbers were 13,715 for modelling bilberries and 13,613 plots for modelling cowberries. In both datasets, approximately 29% of plots did not have any bilberry or cowberry plants. The proportion of plots in each berry yield class is presented in Fig. 2. Generally, the number of plots including bilberry and cowberry plants (Fig. 4, middle and right) and the amounts of berries were higher in the north of Sweden compared to the south of Sweden.

The numbers of flowers and berries are affected by the inventory day of the growing season. To make the model parameters easily interpretable, the middle of July (Julian Day 196) for bilberries and the middle of August (Julian Day 227) for cowberries were used as reference days in modelling, indicating the day when berries should be ready for picking (ripe berries) (Fig. 3). The time difference between field data collection and the reference day was used as predictor variable in the models (Mid_July/August), together with other variables (See Auxiliary data below). The coefficient of this variable indicates the change in berry amount (% per day) throughout the season.

The data showed a spatial hierarchical structure because sample plots were located inside NFI clusters inside laser blocks inside counties. The municipality level was excluded in this study because of large variations in municipality size and replaced with equal-size laser blocks covering the entire country. If plots in the same cluster were located in different laser blocks, they received a different cluster ID; laser blocks were treated similarly if they were divided by the county border. The final cluster numbers were 3,736 in 438 laser blocks in 21 counties for bilberry data and 3,688 in 440 blocks in 21 counties for cowberry data. This hierarchy was taken into account by mixed-effect modelling (see statistical modelling below).

The number of plots used for modelling from different years and different parts of Sweden varied because it depended on the year and location of laser scanning (only plots 3 years before and after scanning were included). As an example, Fig. 4 (left) presents the location of plots

used in bilberry modelling by scanning year on laser blocks.

2.2. Remote sensing and other auxiliary data

Airborne laser scanning data were derived from a campaign for a new national digital elevation model (DEM) by the Swedish National Land Survey (Lantmäteriet, 2014), which started in 2009. At the end of 2015, over 97% of the productive forest land in Sweden had been scanned. Flying height was between 1,700 and 2,300 m, point density 0.5–1 pulse/m², maximum scanning angle 20 degree and side overlap 20% between scanning strips. Scanning was organised in 397 blocks with a size of 25 × 50 km. Most blocks were scanned with Leica, but Optech, Riegl and Trimble were also used. Southern Sweden was scanned mainly in spring and autumn during the leaf-off period and northern Sweden in the summer with leaves. The new national DEM (pixel size of 2 × 2 m) was used as ground reference when calculating the above ground heights of ALS returns. In this study, data from 2009 to 2014 were used, including all different scanners and about 50% leaf-on and 50% leaf-off data. Examples of maps of laser blocks, scanners, scanning season and scanning years can be found in Nilsson et al. (2017).

Due to the small size and seasonality of the bilberry and cowberry species located under the forest canopy it was impossible to measure the berry yields directly using low resolution ALS data. This is the reason why we applied indirect method to model the berry yields based on the correlation between forest structure (described by ALS data) and the berry yields measured from NFI plots. All ALS-based and other wall-to-wall metrics calculated were extracted from the 7-m buffer around the centre of the NFI field plots (corresponding to the size of temporary NFI plots where trees were counted). The ALS point cloud data were extracted from each NFI plot, and point cloud metrics were calculated using the FUSION software (McGaughey, 2021). All measurements between 0 and 50 m above the ground were used to calculate height and density metrics. A list of variables and their formulas are presented in McGaughey (2021). Forest canopy cover metrics (percentage of echoes above a specific height limit, %) were calculated using height limits of 0.2, 0.5, 1, 2 and 5 m, of which the 2 m limit was selected for final canopy cover. We also separately calculated “shrub cover” ((percentage of echoes below 2 m – percentage of echoes below 0.5 m)/(percentage of echoes below 2 m), %) (see e.g., Melin et al., 2016) and percentage of first echo from all echoes. In addition, the metric CCleaf (leaf-on canopy cover) was created; it was zero if leaf-off data were used and had a

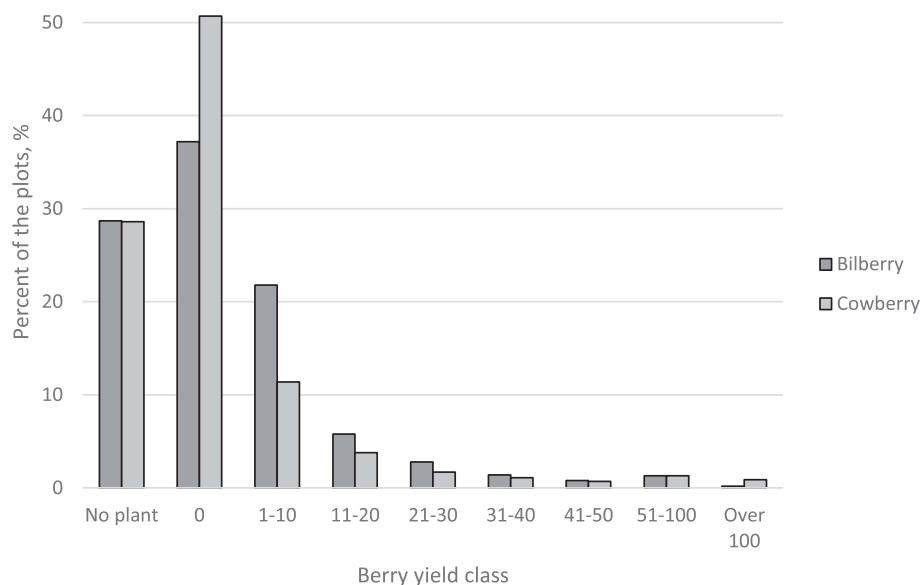


Fig. 2. Percentages of plots in berry yield classes (sum of number of flowers, raw berries and ripe berries) in the bilberry and cowberry data. No plant refers to data where no bilberry/cowberry plants were observed in the plots. Each plot represents sum of two 0.25 m² berry plots inside NFI plot.

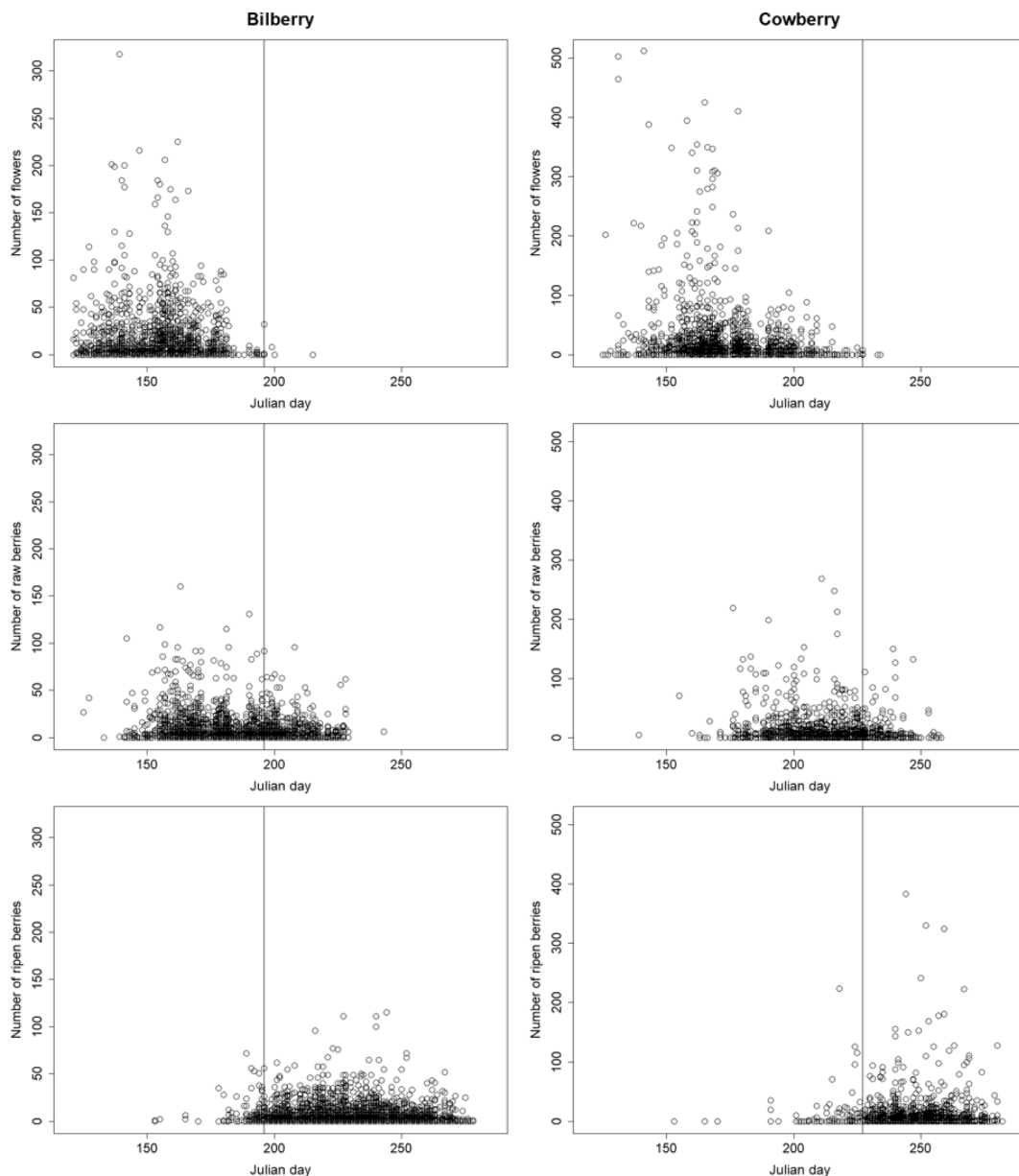


Fig. 3. Number of bilberries (left) and cowberries (right) by Julian day in different development classes (top = flowers, middle = raw berries, bottom = ripe berries). Horizontal line shows the middle of July/August, when berries are expected to be ripe. Each plot represents sum of two 0.25 m² berry plots inside NFI plot.

percentage of echoes above 2 m when leaf-on data were used (%). This metric was used to indicate the difference in canopy cover (especially in the case of deciduous trees) between leaf-on and leaf-off data. Metrics were calculated both from first echo data and all echo data. The intensity values were excluded because they varied among scanners. In addition, we also used categorical information about scanning time (leaf-on/off data), scanning year and scanner type (Leica, Optech, Riegl and Trimble) from each laser block as predictor variables.

Three common variables, namely percentage of first echoes above a height limit of 2 m, called “canopy cover” (CC), Elev.P95 (height, where 95% of the first echoes are accumulated), called “tree height”, and “shrub cover” from first echo data described above, were selected to identify the critical structural differences of forest in presence/absence data (high berry yield/no berries) to locate the forests with highest berry yields.

Other auxiliary data used in this study were divided into surface metrics, bioclimatic variables and other metrics (Appendix 1). Surface metrics consisted of variables calculated from the ALS-based digital

elevation model (DEM, expressing height above sea levels (m), pixel size of 2 × 2 m) created by the Swedish Lantmäteriet and ALS-based soil wetness (SW, pixel size of 2 × 2 m) from the SLU soil moisture map (SLU, 2021a). The DEM and SW were clipped using a 14-m buffer around each field plot. Different surface metrics (Appendix 1) were created from DEM, using 8 neighbour pixels. Mean and standard deviation of pixel values inside each plot (7-m radius) from each raster were calculated as final metrics. New rasters were created in R (<https://www.r-project.org/>) using raster-package. Bioclimatic variables derived from the monthly temperature and the rainfall values from 1970 to 2000 with a raster cell size of 1 × 1 km were retrieved from worldclim.com (Fick and Hijmans, 2017). They represent climatic conditions of the NFI plots as annual trends, (e.g., mean annual temperature and precipitation) seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperatures of the coldest and warmest months, and precipitations of the wet and dry quarters). The value of the raster cells was extracted for each plot and in the case where several raster cell were overlapping the plot the mean value was used as

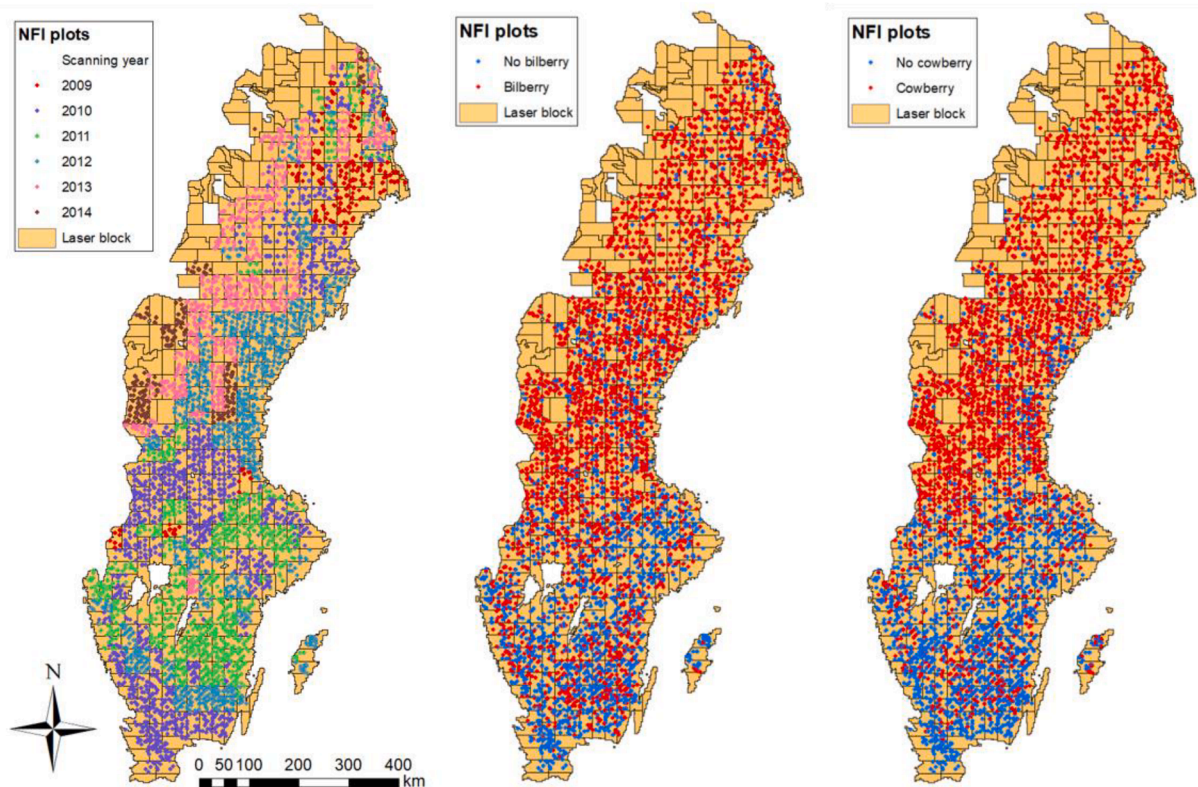


Fig. 4. Distribution of NFI plots used for modelling by scanning year (left) and by bilberry (middle) and cowberry (right) occurrence on laser blocks.

the final metrics. Detailed list of the variables is in [Appendix 1](#). Data sources for other metrics were the SLU forest map from 2010 (SLU, 2021b), soil type and soil depth maps from the Geological Survey of Sweden (SGU 2018, 2020) and the land cover map from the Swedish Environmental Protection Agency (Naturvårdsverket, 2014). Forest variables in the SLU forest map (pixel size of 25×25 m) were based on a combination of satellite images, Swedish NFI plots and kNN-imputation (Reese et al., 2003). In this study, only the stem volumes of pine, spruce and deciduous trees ($\text{m}^3 \text{ha}^{-1}$) and their calculated proportions (%) were used. The soil type map (vector data) includes a classification of common soil types. Both soil type and soil depth maps (pixel size of 10×10 m) were constituted from several different data sources (quaternary geological studies/drillings and existing map data). The land cover map (pixel size of 25×25 m) was based on classification from satellite data to EU land use classes (Corine Land Cover, reference year 2000). Classes with less than 100 observations were combined with closest class. The mean of the raster cells (continuous variables) or the maximum (categorical variables) was extracted from each plot to represent the predictor variables. A detailed list of variables and used classes can be found in [Appendix 1](#).

2.3. Statistical modelling

Models were created for bilberry and cowberry yields (number of berries) using generalised linear mixed-effect models (GLMMs). Berry counts were modelled using the Poisson distribution and expressed by the log-link function (McCullagh and Nelder, 1989). The hierarchy and unbalanced structure of the data were taken into account by random effects at different levels of grouping (county, laser-block, cluster). The year effect was included as dummy variable in the fixed part of the model. The models were defined as follows:

$$y_{ijk} \sim \text{Poisson}(\pi_{ijk}) \quad (1)$$

$$\ln(\pi_{ijk}) = \mathbf{x}'_{ijk}\beta + u_i + u_j + u_{ijk}$$

where y is the sum of flowers and berries in two 0.25-m^2 circular plots inside the NFI plot; Poisson distribution with mean π_{ijk} is the conditional distribution of y_{ijk} given the random effects u_i , u_j and u_{ijk} ; $\ln(\pi)$ is a log-link function and \mathbf{x}'_{ijk} are the fixed predictor variables with corresponding coefficient vector β . Subscripts i , j and k refer to nested cluster, laser block and county levels, respectively, and u_i , u_j and u_{ijk} are normally distributed random effects with mean of zero and constant variances.

For Poisson random variables, the variance equals the mean, but frequently, the data do not follow this due to the lack of independence. This means that it might show more or less variation than what would be expected based on the Poisson distribution (“over- and under-dispersion”). One way to allow over- or under-dispersion is to use Penalized Quasi likelihood (PQL) in model fitting, which allows the scaling factor of the variance function to deviate from 1, thus modelling the over-dispersion (see e.g., Mehtätalo and Lappi, 2020, Section 8.3.2). When using PQL with GLMM, the nonlinear function of the mixed-effect model is determined by applying the log-link function and the variance function where the above-mentioned variance of the Poisson distribution is multiplied by scaling factor r . If the estimate of $r > 1$, it indicates over-dispersion, and if $r < 1$, under-dispersion is given. If modelling over-dispersion is ignored, it would lead to an underestimation of standard errors of parameter estimates, and ignoring under-dispersion would lead to overestimation; therefore smaller (over-dispersion) or higher (under-dispersion) p-values are produced, leading to misinterpretation of the importance of the variables.

Mixed-effect models were fitted using the `glmmPQL` function of the R-software (<https://www.r-project.org/>). Because `glmmPQL` does not allow the crossed random effects, the effects of the years 2007–2016 were included as dummy variables in the fixed part of the model. All variables selected into the models had to be logical and statistically

significant (level 0.05), and no high correlation was allowed between variables. To rank and select the best variables into models, initial models were prepared by scaling continuous variables (comparison between variables possible). The final models were produced using these metrics without scaling to easier interpret the coefficient of the metrics, such as the variable Mid_July/August, showing the change (percentage, %) in flowers and berries per day during the season. Also, different transformations of the variables were tested.

When applying the model to the new area/dataset, the random effects are unknown and cannot be predicted. A naïve approach for prediction in such case is to use the fixed part of the model. However, because the random effects are inside the link-function, such predictions are downward biased. A bias-corrected prediction is as follows (e.g., Mehtätalo and Lappi, 2020):

$$\hat{y} = \exp\left(x\hat{\beta} + \frac{\hat{\sigma}_i^2 + \hat{\sigma}_j^2 + \hat{\sigma}_k^2}{2}\right) \quad (2)$$

where $\hat{\sigma}_i^2$, $\hat{\sigma}_j^2$ and $\hat{\sigma}_k^2$ are the variance estimates of each random level i , j , k (cluster, laser block and county level).

The structural differences of commonly used ALS-based variables are demonstrated in the histograms of presence/absence (high berry yield/no berries) data. Only bilberry and cowberry plots with ripe berries were included (Mid_July/August > 0). Five percent of the plots with the highest berry amount was selected to represent the high berry yield (452 plots with bilberry and 391 plots with cowberry). This corresponded to 15 berries or more in bilberry data and 9 berries and more in cowberry data in two 0.25-m² circular plots. Class “no berries” included bilberry/cowberry plots with zero berries (similarly Mid_July/August > 0) and all other plots without bilberry/cowberry plants.

3. Results

3.1. Models for bilberry and cowberry yield

The bilberry model with significant fixed predictors is shown in Table 1. The continuous variables were ranked based on the weight they obtained when the models were prepared with standardised predictors (scaled using the scale function in R). The time difference between the inventory day and the middle of the July (Mid_July), when the berries were expected to ripen, showed a 1.5% decrease in bilberry yield per day during the season (the coefficient -0.0145 in the Table 1). The number of bilberries increased when temperature seasonality, Elev.variance (McGaughey, 2021), DEM, PineVolume, Slope, SW and canopy cover (up to 50%) increased. The number of bilberries decreased when CCLeaf, DecidPro, SpruceVolume, shrub cover and precipitation seasonality² increased. The optimal canopy cover of 48.8% was calculated using a quadratic equation ($ax^2 + bx$). Leaf-on/off and land use class (only class conifer forest > 15 m was significant) were significant categorical variables in the model. In addition, the variable Year showed significant variation among years, and the number of bilberries was highest in 2015 and in conifer forests at a height > 15 m and lowest in 2009 and in conifer forests on mire.

The cowberry model with significant fixed predictors is shown in Table 2. The time difference between the inventory day and the middle of the August (Mid_August) showed a 1.1% decrease for cowberry yield per day during the season (the coefficient -0.0107 in the Table 2). The number of cowberries increased when canopy cover, temperature seasonality, annual precipitation, Elev.variance (McGaughey, 2021) and TRI increased and decreased when DEM, CCLeaf, DecidPro, SprucePro and PineVolume and shrub cover increased. The calculated optimal canopy cover was 13.6%. Soil type (Clay, Moraine and mountain/rock were significant) and land use class (conifer forest in mire, clear cut and other mires were significant) were significant categorical variables in the cowberry model. In the cowberry data, the variable Year showed

Table 1

Bilberry model for the number of berries in two 0.25-m² plots. Scaled refers to model, where continuous predictors were scaled (standardised). Continuous variables are ordered by estimate of scaled variables (the weight the variables received when the models were prepared with standardised predictors). * = metric calculated from the first echo ALS data. Only fixed parameters are shown in the table.

| | Estimate | Std. Error | t-value | p-value | Scaled |
|---|----------|------------|---------|---------|---------|
| Intercept | -3.6588 | 0.3265 | -11.21 | <0.001 | 0.9969 |
| Mid_July | -0.0145 | 0.0006 | -22.29 | <0.001 | -0.5847 |
| Temperature seasonality | 0.0005 | 0 | 15.65 | <0.001 | 0.4306 |
| CCLeaf | -0.0106 | 0.0017 | -6.38 | <0.001 | -0.3876 |
| Canopy cover ^{2*} | -0.0004 | 0 | -16.22 | <0.001 | -0.3206 |
| Elev.variance | 0.0136 | 0.0012 | 11.55 | <0.001 | 0.2443 |
| DEM_mean | 0.0018 | 0.0002 | 9.12 | <0.001 | 0.2333 |
| DecidPro(%) | -0.0191 | 0.0027 | -6.98 | <0.001 | -0.222 |
| PineVolume (m ³ ha ⁻¹) | 0.0031 | 0.0004 | 7.59 | <0.001 | 0.1347 |
| SpruceVolume (m ³ ha ⁻¹) | -0.0025 | 0.0004 | -6.2 | <0.001 | -0.1294 |
| Slope_mean | 0.0192 | 0.0037 | 5.22 | <0.001 | 0.09 |
| Shrub cover | -0.8380 | 0.2242 | -3.74 | <0.001 | -0.0776 |
| Precipitation seasonality ² | -0.0007 | 0.0001 | -5.83 | <0.001 | -0.0681 |
| SW_mean | 0.0086 | 0.0023 | 3.72 | <0.001 | 0.0616 |
| Canopy cover* | 0.0409 | 0.0033 | 12.28 | <0.001 | -0.0573 |
| <i>Year (ref. 2007)</i> | | | | | |
| 2008 | 0.1473 | 0.1571 | 0.94 | 0.348 | 0.1336 |
| 2009 | 0.0750 | 0.1561 | 0.48 | 0.631 | 0.0727 |
| 2010 | 0.3379 | 0.1490 | 2.27 | 0.023 | 0.3398 |
| 2011 | -0.2977 | 0.1330 | -2.24 | 0.025 | -0.3045 |
| 2012 | 0.2066 | 0.1161 | 1.78 | 0.075 | 0.2072 |
| 2013 | 0.3402 | 0.1306 | 2.60 | 0.009 | 0.3289 |
| 2014 | -0.1358 | 0.1384 | -0.98 | 0.327 | -0.1326 |
| 2015 | 0.5667 | 0.1389 | 4.08 | 0.000 | 0.5862 |
| 2016 | 0.2987 | 0.1574 | 1.90 | 0.058 | 0.2911 |
| <i>Leaf-on/off (ref. leaf off)</i> | | | | | |
| Leaf-on | -0.2892 | 0.0839 | -3.45 | 0.001 | -0.3101 |
| <i>Land use (ref. others)</i> | | | | | |
| Deciduous forest | 0.1447 | 0.1992 | 0.73 | 0.468 | 0.1486 |
| Conifer forest with lichen | 0.2340 | 0.1918 | 1.22 | 0.223 | 0.2232 |
| Conifer forest 7–15 m | 0.3005 | 0.1871 | 1.61 | 0.108 | 0.2961 |
| Conifer forest > 15 m | 0.4138 | 0.1871 | 2.21 | 0.027 | 0.4142 |
| Conifer forest in mire | -0.2105 | 0.2218 | -0.95 | 0.343 | -0.2086 |
| Conifer forest in mountain | 0.1749 | 0.2155 | 0.81 | 0.417 | 0.1434 |
| Mixed forest | 0.1007 | 0.1909 | 0.53 | 0.598 | 0.0993 |
| Clear cut | 0.3111 | 0.1901 | 1.64 | 0.102 | 0.2981 |
| Young forest | 0.1825 | 0.1901 | 0.96 | 0.337 | 0.1756 |
| Other mires | 0.1103 | 0.2248 | 0.49 | 0.624 | 0.1036 |

significant variation among years, and the number of cowberries was highest in 2015 in forests on moraine-clay and in clear cuts and lowest in 2013 in water areas (misclassified) and in other mires.

Several ALS-based structural forest and surface metrics were significant predictors for the berry models, but they had a high correlation (± 0.7 – 0.95) with the best metrics and were thus excluded from the model. Similarly, we also tested the north and south coordinates of plots, but they were highly correlated with more significant bioclimatic metrics and were therefore not used. The year effect was significant in both models, but it cannot be directly used to evaluate the true yearly variation because plot number, inventory year and inventory day varied among different areas.

We also calculated the R² values (degree of determination) for the full model and for the fixed part of the model separately. The R² was 0.4 for the full bilberry model and 0.08 for the fixed part and 0.53 for the full cowberry model and 0.03 for the fixed part. Most of the unexplained (random) variation was found in the cluster level both in bilberry and cowberry models (83 and 56%). The laser block level accounted for

Table 2

Cowberry model for the number of berries in two 0.25-m² plots. Scaled refers to model, where continuous predictors were scaled (standardised). Continuous variables are ordered by estimate of scaled variables (the weight the variables received when models were prepared with standardised predictors). * = metric calculated from the first echo ALS data. Only fixed parameters are shown in the table.

| | Estimate | Std. Error | t-value | p-value | Scaled |
|---|----------|------------|---------|---------|---------|
| Intercept | -5.6022 | 1.2265 | -4.57 | <0.001 | 0.0704 |
| Canopy cover* | 0.0101 | 0.0033 | 3.05 | 0.002 | -0.7791 |
| Temperature seasonality | 0.0006 | 0.0001 | 5.77 | <0.001 | 0.671 |
| Mid_August | -0.0107 | 0.0008 | -14.07 | <0.001 | -0.4319 |
| DEM_mean | -0.0024 | 0.0004 | -6.14 | <0.001 | -0.3985 |
| CCLeaf | -0.0087 | 0.0016 | -5.35 | <0.001 | -0.3181 |
| Annual precipitation ² | 0.03 | 0.0086 | 3.47 | <0.001 | 0.2863 |
| Canopy cover ^{2*} | -0.0004 | 0 | -11.76 | <0.001 | -0.2833 |
| DecidPro(%) | -0.0189 | 0.0026 | -7.13 | <0.001 | -0.2254 |
| SprucePro(%) | -0.0078 | 0.0009 | -9.06 | <0.001 | -0.2162 |
| PineVolume (m ³ ha ⁻¹) | -0.0032 | 0.0005 | -6.07 | <0.001 | -0.1458 |
| Elev.variance | 0.0078 | 0.0014 | 5.76 | <0.001 | 0.143 |
| TRI_mean | 7.2822 | 0.895 | 8.14 | <0.001 | 0.1369 |
| Shrub cover | -1.2526 | 0.2229 | -5.62 | <0.001 | -0.1163 |
| <i>Year (ref. 2007)</i> | | | | | |
| 2008 | -0.5022 | 0.1834 | -2.74 | 0.006 | -0.5022 |
| 2009 | 0.2717 | 0.1680 | 1.62 | 0.106 | 0.2717 |
| 2010 | -0.2970 | 0.1771 | -1.68 | 0.094 | -0.2970 |
| 2011 | -0.2268 | 0.1453 | -1.56 | 0.119 | -0.2268 |
| 2012 | 0.0386 | 0.1204 | 0.32 | 0.748 | 0.0386 |
| 2013 | -0.5305 | 0.1475 | -3.60 | 0.000 | -0.5305 |
| 2014 | -0.2725 | 0.1551 | -1.76 | 0.079 | -0.2725 |
| 2015 | 0.2822 | 0.1614 | 1.75 | 0.080 | 0.2822 |
| 2016 | -0.4076 | 0.1928 | -2.11 | 0.035 | -0.4076 |
| <i>Soiltype (ref.sediment)</i> | | | | | |
| Peatland | 0.2258 | 0.1218 | 1.85 | 0.064 | 0.2258 |
| Sand-gravel | -0.2132 | 0.1533 | -1.39 | 0.165 | -0.2132 |
| Clay | -0.3687 | 0.1794 | -2.06 | 0.040 | -0.3687 |
| Water (misclassified) | -0.6815 | 0.5467 | -1.25 | 0.212 | -0.6815 |
| Moraine | 0.2473 | 0.0964 | 2.57 | 0.010 | 0.2473 |
| Mountain/Rock (berg) | 0.2971 | 0.1113 | 2.67 | 0.007 | 0.2971 |
| Moraine-Clay | 0.4353 | 0.2379 | 1.83 | 0.0673 | 0.4353 |
| <i>Land use (ref. others)</i> | | | | | |
| Deciduous forest | 0.1042 | 0.2572 | 0.41 | 0.6854 | 0.1042 |
| Conifer forest in lichen | 0.4397 | 0.2417 | 1.82 | 0.0689 | 0.4397 |
| Conifer forest 7–15 m | 0.2981 | 0.2349 | 1.27 | 0.2043 | 0.2981 |
| Conifer forest > 15 m | 0.2814 | 0.2339 | 1.20 | 0.2289 | 0.2814 |
| Conifer forest in mire | -0.7316 | 0.2934 | -2.49 | 0.0127 | -0.7316 |
| Conifer forest in mountain | 0.0007 | 0.2849 | 0.00 | 0.9980 | 0.0007 |
| Mixed forest | -0.1651 | 0.2452 | -0.67 | 0.5007 | -0.1651 |
| Clear cut | 0.7850 | 0.2346 | 3.35 | 0.0008 | 0.7850 |
| Young forest | 0.4542 | 0.2369 | 1.92 | 0.0552 | 0.4542 |
| Other mires | -0.7745 | 0.2984 | -2.60 | 0.0094 | -0.7745 |

about 15–17% of the variation in both models. In the cowberry model, the county level accounted for over 28% and in the bilberry model for less than 1%. The dispersion parameter was greater than 1 both in bilberry and cowberry models, indicating over-dispersion of the data (more variation than expected). The variances of random effects and

Table 3

Variances of random effects and dispersion parameters of bilberry and cowberry models.

| Random effects, grouping | Bilberry | | Cowberry | |
|---------------------------------------|----------|-------|----------|-------|
| | Std.Dev | n.obs | Std.Dev | n.obs |
| County | 0.0003 | 21 | 0.5654 | 21 |
| Laserblock | 0.1804 | 438 | 0.3249 | 440 |
| Cluster | 0.8965 | 3736 | 1.1384 | 3688 |
| Under-/over-dispersion (σ^2) | 3.17 | | 3.63 | |

dispersion parameters of bilberry and cowberry models are presented in Table 3.

We studied the model estimates based on only the fixed part of models, as done when applying new datasets. Although bias-correction improved the estimates, the mean values were still low in the highest berry yield classes (Table 4.). The reason for this was found when observing the distribution of random effects; with GLMM, the random effects are expected to be normally distributed, but in our models, the distributions were slightly positively skewed (Fig. 5), which caused the underestimation of the high berry yields and the smaller effect of the bias-correction. The true and estimated mean values of flowers and berries in each prediction class with bias-correction, are presented in Table 4. Although our model could not provide highly accurate estimates for berry yields, underestimating especially high yields, the model can be used as an effective tool for predicting the most potential locations for berry yields in forest landscapes.

3.2. Laser-based structural differences and the berry map

The histograms in Fig. 6 show the commonly used structural ALS-based features: canopy cover (%), canopy height (m) and shrub cover (%) in presence/absence data (high berry yield/no berries). Histograms highlight the critical structural features, indicating the locations for the highest bilberry and cowberry yields. Clear differences between the distributions of high berry yield data and no berry data are shown, which follows the findings from the modelling.

Bilberry yield peaked in forests with a canopy cover (CC) of 50%, but even a CC close to zero showed good bilberry yield. Cowberry yield peaked drastically in forests with no canopy cover, but it was also high in sites with a canopy cover up to 80%. Highest bilberry yields were most commonly found in sites with a canopy height from 10 to 16 m, and highest cowberry yields were observed when the canopy height was close to zero. High bilberry and cowberry yields were identified for all stand heights. The shrub cover was most often close to zero, both with highest bilberry and cowberry yield, and the number of high-berry-yield plots decreased clearly when the scrub cover increased from 0 to 10%.

To demonstrate the use of the model in the forest landscape, we predicted the most potential locations of bilberry yields in a small study area and compared it to ALS-based canopy cover and stem volume values obtained from the National Forest attribute map (Fig. 7). Fig. 7 highlights the effects of canopy cover and stem volume on berry yields; too low or too high cover/volume values did not result in high berry yields.

4. Discussion

This is the first study using ALS and other wall-to-wall variables to model bilberry and cowberry yields, but also the first berry yield model developed for Sweden. Here, we also obtained valuable information about suitable remote sensing-based variables for predicting berry yields

Table 4

Means of the true and estimated values of flower and berry numbers in prediction classes with bias-correction. Prediction was done using only the fixed part of the model.

| | Predicted flower and berry numbers | | | | |
|-----------------|------------------------------------|-------|-------|-------|-------|
| | 0–10 | 10–20 | 20–30 | 30–40 | 40+ |
| <i>Bilberry</i> | | | | | |
| n. obs. | 11,916 | 1478 | 222 | 68 | 31 |
| Mean true | 3.22 | 12.53 | 18.54 | 17.51 | 18.10 |
| Mean est. | 3.63 | 13.50 | 23.45 | 33.56 | 48.19 |
| <i>Cowberry</i> | | | | | |
| n. obs. | 11,135 | 1642 | 502 | 169 | 165 |
| Mean true | 2.88 | 11.76 | 12.70 | 23.81 | 21.94 |
| Mean est. | 2.93 | 13.85 | 24.12 | 34.24 | 53.56 |

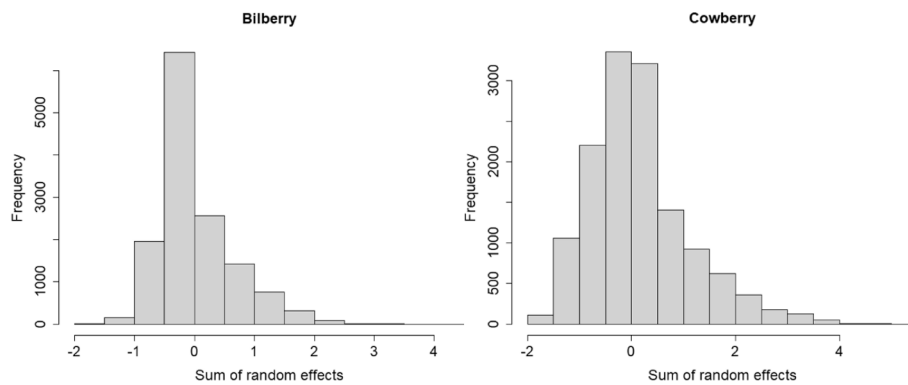


Fig. 5. Distribution of the sum of random effects ($u_i + u_{ij} + u_{ijk}$) in bilberry and cowberry models.

and about the ALS-based structural features that reflect the locations of the highest berry yields. Earlier studies modelling bilberry and cowberry yields for forest planning, mainly produced in Finland, have used field-measured stand attributes (such as site type, tree height, mean diameter, volume, basal area and age, tree species, soil type) and some geographical data (mean temperature and height above sea) as predictor variables (e.g., Muhonen, 1995, Miina et al., 2009, Turtiainen, 2015). These models can be used for forest planning purposes but not for accurate and cost-effective wall-to-wall prediction because of the lack of accurate field data. In our study, we used only remote sensing-based and other wall-to-wall variables in modelling to cost-effectively produce spatial information about potential berry yields.

The importance of mapping ecosystem services, such as berry yield, has been recognised by the European Commission (2013) in Action 5 of the EU Biodiversity Strategy to 2020, where they request the Member States to map ecosystem services, resulting in a number of initiatives (e.g., Burkhard and Maes, 2017). Our maps of potential berry yield are much needed as input for, e.g., land-use planning at landscape level (e.g., European Commission, 2016). These maps may support forest management, enabling multiple uses of the forest landscape. Further, such maps can aid in communication and knowledge transfer and increase our understanding among and between different stakeholders with different interests (Sandström et al., 2003). For local berry pickers, the berry yield maps make it easier to find the berries in the forest landscape.

4.1. Modelling berry yields

Both ALS-based structural forest and terrain variables were significant in the prediction of bilberry and cowberry berry yields, similar to species-specific volumes or percentiles and land use class. In our study, canopy cover of about 50% indicated the locations for the highest bilberry yields, along with high pine volume/conifer dominance and greater tree height. This supports earlier studies showing that the highest bilberry yields can be obtained in mature, not too dense stands with conifer dominance (e.g., Eriksson et al., 1979, Raatikainen et al., 1984, Miina et al., 2009, Turtiainen, 2015). In addition, more important than e.g. tree species is the light reaching the bilberry stand; it has been found that a crown density of 10–50% allows bilberry to flower and produce berries (Raatikainen and Raatikainen, 1983, Raatikainen et al., 1984). This supports the usability of ALS-based canopy cover measurement, especially in the prediction of bilberry yields (see also Figs. 6 and 7). Similarly, canopy cover and tree height close to zero indicated locations for the highest cowberry yields, but also denser canopy cover, greater tree height and conifer dominance resulted in good yields. These findings are also supported by earlier studies. High cowberry yields can be found in pine-dominated stands which are not too dense, in recently clear-felled open areas, small seedling stands and seed tree stands, but also in mature stands (e.g., Jaakkola, 1983, Belonogova, 1993,

Turtiainen, 2015).

The other ALS based metrics used in the models which were linked to the berry production were Shrub cover, Elev.variance, SW_mean and TR_mean. Shrub cover was close to zero both in plots of bilberry and cowberry, supporting the assumption that these berry species demand light. Berry yields of both species increased when height variance (Elev. variance) of laser pulses increased. In this study the large height variance means that heights of the laser point are reflecting both from the dominant trees and from the ground, thus, indicating gaps in the tree canopy. Also supporting the earlier finds about light demand of the considered berry species. Correspondingly, when soil wetness (SW_mean) increased the bilberry yield increased, which can be understood by the fact that bilberry produces berries also in peatlands. When terrain roughness (TR_mean) increased the cowberry yield increased, which is related to the fact that cowberry is growing in sunny slopes. In this study, the Height above sea (DEM_mean) were used in both models and had opposite effect to the different species; when DEM_mean increased the bilberry yield increased and cowberry yield decreased. The use of forest structural measures from ALS data, especially canopy cover have been applied also in other studies where occurrence and fruit production of other berry species have been studied (e.g. Barber et al., 2016, Nielsen et al., 2020).

Our results are also in agreement with the recent findings of Vauhkonen (2018), predicting the provisional potential of ecosystem services (including suitability for the picking of bilberries and cowberries) based on ALS data in the Evo study area in Finland. Provisional potentials were constructed based on expert models, and regression analyses were used to model the priority values for ecosystem services. The authors bilberry and cowberry models included structural ALS measures for relatively low vegetation and metrics separating and combining different echo categories in the models. Vauhkonen points out that the performance of his models should be tested by re-fitting or validating models against indicators which are not based on models but on direct observations in the field.

The site- and vegetation-related variables did not as such describe the berry yields optimally and, therefore, also bioclimatic variables describing the climate conditions of NFI plots, were included to the models. Seasonality of the temperature and the precipitation described the annual range/variation in the temperature and in the precipitation. The increasing variation in the temperature increased the yields of both berry species. This is logical since higher berry yields are found in the northern part of Sweden where the variation of monthly temperatures is larger than in the south. In addition, the higher variation in the precipitation decreased the bilberry yields and the increasing annual precipitation increased the cowberry yields. Earlier, Turtiainen et al. (2013) used the temperature sum in their cowberry models, whereas Barber et al. (2016), in addition to temperature and precipitation, used even variables such as mean annual solar radiation, beginning and ending of the frost-free period, reference atmospheric evaporation demand and

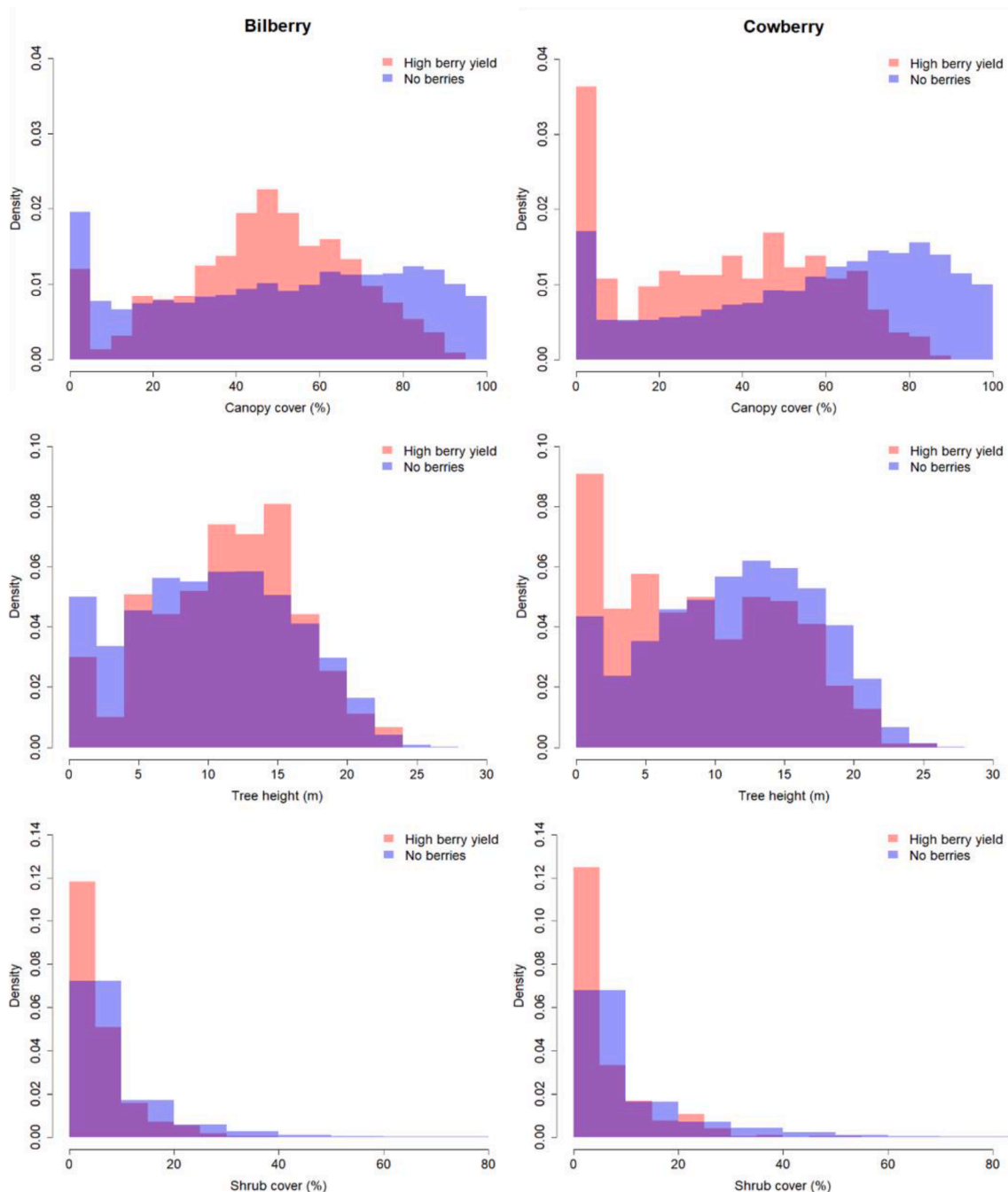


Fig. 6. Density distribution of ALS-based structural forest variables (first echo data) in plots with high bilberry (left) and cowberry (right) yields and no berries. Only plots with ripe berries were included in the berry data (Mid_July/August > 0). Five percent of the plots with the highest berry amount represent the high berry yield. Class “no berries” included bilberry/cowberry plots with zero berries (similarly Mid_July/August > 0) and other plots without bilberry/cowberry plants.

continentality in their wall-to-wall models for saskatoon, huckleberry and buffaloberry.

In our study, the numbers of flowers, raw berries and ripe berries at different times of the growing season we used. Therefore, we could use the inventory day (Mid_July/August) as predictor variable in the model and take into account the changes in berry yield throughout the season. In the case of bilberry, this was the most important variable in the model. By measuring field data during the entire season, the model can be updated continuously, and seasonal prognoses of berry yields are possible.

Our study supports the findings that accurate prediction of berry yields is difficult because of the complexity of berry yield production.

This was observed, for example, by obtaining high variations in estimation accuracies among plots and by small R^2 values for the fixed part of the model. This indicates that variables used in the models cannot catch the spatial and temporal variation of berry yields for accurate berry yield modelling. In addition, the model underestimated especially the high berry yields, which was caused by the non-normal distribution of the random effects. Similar results have been found in all earlier studies. For example, [Turtiainen \(2015\)](#) obtained an R^2 of 0.06–0.4 for the fixed part of their bilberry models and 0.03–0.62 for cowberry models. [Kilpeläinen et al. \(2016\)](#) tested the existing Finnish berry models in North Karelia, Finland, and obtained an RMSE percentage (kg ha^{-1}) between 154 and 179% for bilberry and between 238 and 322%

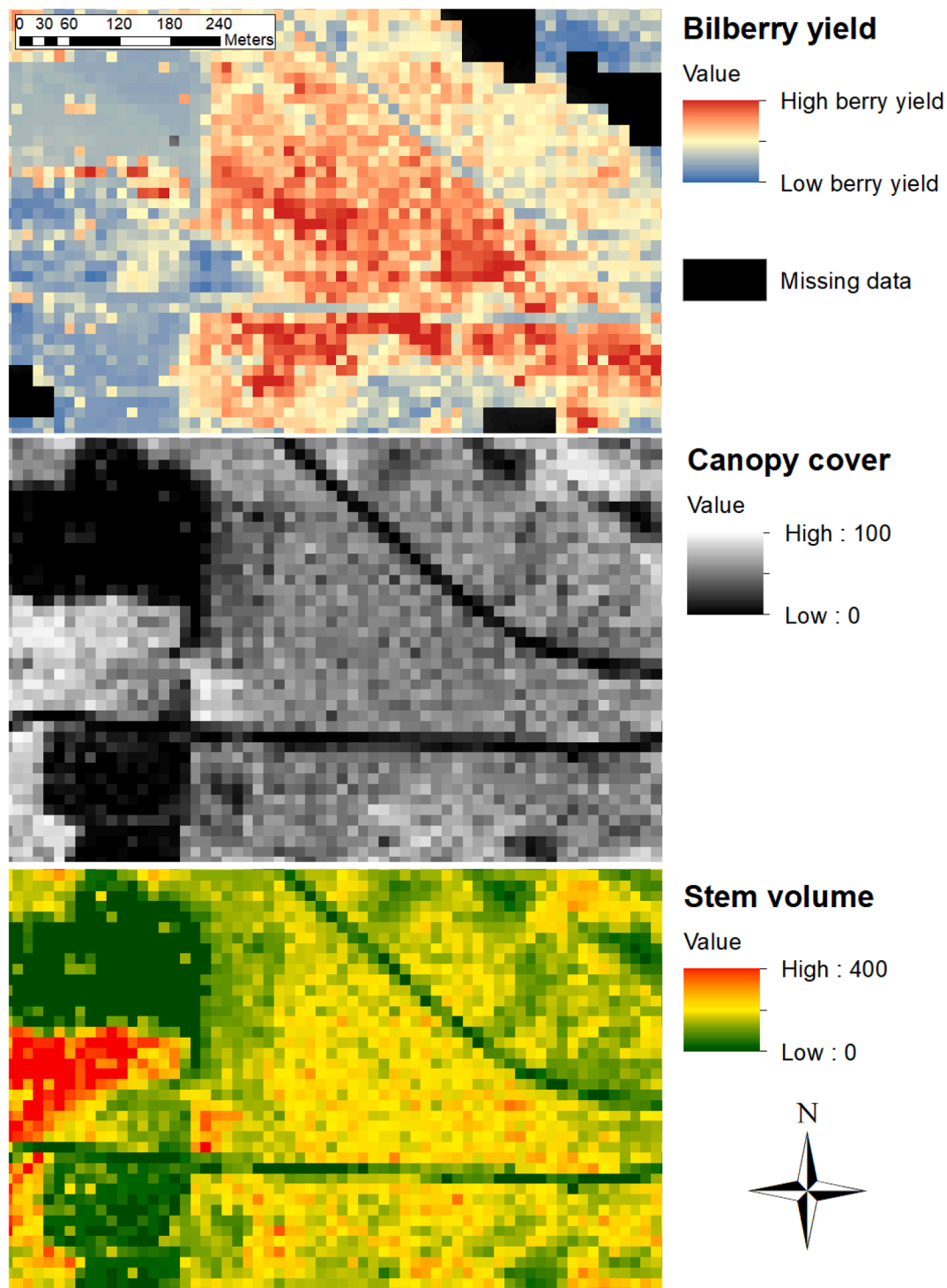


Fig. 7. Predicted potential locations of bilberry yields in a forest landscape (top) compared with canopy cover percentage (middle) and stem volume (m^3ha^{-1}), obtained from the National Forest attribute map.

for cowberry. Correspondingly, the ALS-based models by [Vauhkonen \(2018\)](#) resulted in RMSE values of 20–30% for the suitability for bilberry and cowberry picking. Both expert and empirical models as well as mixed-effects models have been used in earlier studies. However, our models cannot be totally compared to those developed in earlier studies due the different variables used (field-measured forest variables vs. wall-to-wall remote sensing variables), different environmental conditions, size of the study area (nationwide Sweden vs. local study area), different inventory set-ups, different modelling methods, among others.

Modelling spatiotemporal data could be done by using special spatiotemporal models (e.g., [Vanhatalo et al., 2017](#), [Hefley et al., 2017](#)), but we decided to use generalised linear mixed-effect models, which also have been used successfully in earlier berry yield studies (e.g., [Miina et al., 2009](#), [Turtiainen, 2015](#)). By using mixed-effect models, we could take into account the hierarchy of the data (here county, laser block, cluster) and calibrate the model based on that hierarchy. We only used the nested random effects because glmmPQL cannot take into account the crossed effects. Therefore, the year effect was included as fixed

dummy variable in the model. Modelling berry yields is challenging also because the response variable is seldom systematically or normally distributed (and many values are around zero (Kilpeläinen, et al., 2016)). We selected PQL estimation because it can apply non-normal distribution (here, Poisson distribution for count data) and can deal with overdispersion, which was present in our data, enabling us to trust the significance of the variables (p-values).

4.2. Further development

In this study, we predicted plot-level berry yields. Another option would have been to make the modelling in two phases; first, predicting the presence/absence of bilberry/cowberry vegetation and second, predicting the plot-level yields of bilberry and cowberry. Some earlier studies have shown a high correlation between berry vegetation cover and berry yield (Miina et al., 2009, Turtiainen et al., 2013). In the Swedish NFI, bilberry and cowberry cover are measured on approximately half of the permanent plots, and therefore, this approach would be possible, first predicting bilberry/cowberry cover and using this as a predictor variable in yield models.

Here, we used the structural forest variables from ALS data directly in the prediction; tree species variables were taken from the SLU forest map and are based on predictions of spectral values of satellite images and NFI field data. Direct spectral values could have been used instead of predicted tree species information, but that would have demanded calibration between images from different areas, years and sensors over the entire country. Earlier, Kilpeläinen et al. (2016) showed that the use of Finnish multi-source national forest inventory data (combining NFI data, satellite remote sensing data and other mapped data for forest attribute prediction) is suitable for berry models. Surely, it would be possible to test the suitability of the ALS-based wall-to-wall attributes from the Swedish National Forest attribute map (e.g., stem volume, basal area, tree height and diameter) (Nilsson et al., 2017) for berry yield prediction. By using predicted forest variables instead of direct laser or satellite variables, it might be easier to implement the models into forest planning systems, which not yet include direct remote sensing variables.

Natural and manmade changes in forest structure between field inventory and remote sensing data collection can affect model accuracy. For example, tree species information from the SLU forest map and the map of land cover classification was relatively old (2010 and 2000), and the accuracy of the used satellite data was not high at the plot or stand level (pixel size of 25×25 m). In particular, many of the classes in the land cover map might have changed, such as clear-cuts to young forest and young forest to mature forest, among others. In this sense, class information should be used with caution. Despite the possible old land use classes, land cover data can contain valuable information about site quality and fertility, which was the reason to keep this variable in the modelling. More accurate tree species and land cover data are developed constantly. For example, SLU has recently published a new species-specific forest map based on new Sentinel 2 satellite data (pixel size of 10×10 m) and height information from aerial images and NFI field plots. In addition, research using multitemporal satellite and ALS data for tree species classification is ongoing, and a more accurate Swedish land cover classification (Nationella marktäckedata, Naturvårdsverket, 2020), also based on Sentinel 2 and ALS height information, has been published in summer 2019. In the next-generation berry yield models, these more accurate datasets should be used.

In addition to demanding improvements in tree species detection and land use classification, one improvement in wall-to-wall berry prediction would be accurate information about site fertility. In most Finnish berry yield models, site type is a critical variable (e.g., Muhonen, 1995, Miina et al., 2009, Turtiainen, 2015), or models were developed only for a particular site type. On the other hand, according to Raatikainen et al. (1984), bilberry yield depends primarily on the canopy cover and only secondarily on the site fertility. For ALS based applications this

observation is positive, since the prediction of the site fertility by ALS data is not a straightforward task. In Swedish forestry, forest productivity is not usually expressed in terms of site type classes, and instead, the site index is used. Neither accurate site type classes nor site index values are currently available in wall-to-wall prediction in Sweden, but studies predicting the site index (based on tree height development) using multi-temporal laser data have been published, for example for Norway (Noordermeer et al., 2018). In addition, further development of sensor technologies, such as the use of more dense ALS data together with different wavelengths (multispectral), might provide more detailed information about the ground floor vegetation and its spatial distribution.

It is also worth mentioning that the different size of the berry plots and the plots where auxiliary variables were extracted might affect the modelling accuracy, since berry plots covered only 0.3% of the area of the auxiliary data plot. On the other hand, auxiliary variables cannot accurately describe the forest and terrain structure if they are extracted from the size of the berry plots or, alternatively, the amount of time used for counting the berries/flowers is not realistic. The effect of plots size is thus interesting and worth exploring in the future.

In this study, the general berry yield models were produced for the entire country, but more accurate predictions may be possible by creating models locally. Here, models were calibrated at the county, laser block and even cluster level, and bioclimatic metrics and height above sea level, for example, were also used to indicate variations in berry yield in different parts of Sweden. It should be kept in mind that the number of plots as well as the inventory year and inventory day varied among different areas, making the model more reliable in some areas than in others. Local models could better take into account the local forest, terrain and weather conditions, but they would also require a larger number of field plots in the target area.

Our models are based on the available wall-to-wall variables and can therefore be used to create wall-to-wall prediction maps covering the entire landscape (Fig. 7). Wall-to-wall prediction makes it also possible to evaluate the variation in berry yields at the landscape and stand level all the way to the cell level inside stands. It is noteworthy that our models lack critical variables, such as site fertility and variables describing the temporal variation between and within years and the local spatial variation of berry yields (not available or unknown), which means that these models/maps can only be used for identifying the most potential locations for bilberry and cowberry in wall-to-wall prediction, not for measuring the exact yields.

To improve the yearly prognoses of berry yields, more accurate temporal and spatial data, such as weather, pollination, site type and operational history data from continuous measurements of berry yield development, together with localised observations of berry yield, are needed. Unfortunately, because of the lack of resources, only ripe berries have been counted in the Swedish NFI since 2018, excluding the possibility to calibrate models during the season by NFI plots. Because of the complexity of berry yield production and the impossibility to measure all factors, currently, only part of the variation can be explained by the existing variables.

Despite the difficulties in modelling berry yields, our models could be imported to the forest planning system, such as Heureka in Sweden (Wikström et al., 2011), and stand-level prognoses of berry yield development under different forest management strategies could be produced (e.g., Turtiainen, 2015). Integrating berry yields as non-wood forest services into forest planning system makes it possible to evaluate the trade-offs in different decision making situations and therefore supports the forest owners' growing interest in integrating multiple aspects of forests in management planning. So far, no berry yield models have been integrated in forest planning systems in Sweden.

CRediT authorship contribution statement

Inka Bohlin: Conceptualization, Methodology, Software, Formal

analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Matti Maltamo**: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition. **Henrik Hedenås**: Conceptualization, Methodology, Writing – original draft, Funding acquisition. **Tomas Lämås**: Conceptualization, Writing – original draft, Funding acquisition. **Jonas Dahlgren**: Resources, Data curation, Writing – original draft. **Lauri Mehtätalo**: Conceptualization, Methodology, Software, Formal analysis, Supervision, Writing – original draft, Writing – review & editing.

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.

Acknowledgements

This study is part of the project “Adding non-wood forest products as part of ecosystem services: Improving berry yield mapping prediction and mapping”, funded by FORMAS (2016-20056). In addition, we are grateful for Academy of Finland Flagship Programme “Human-Machine Interplay - Building Resilience, Redefining Value Networks and Enabling Meaningful Experiences (UNITE)” for financial support (decision number 337655). We also acknowledge Dr. Sven Adler from the Department of Forest Resource Management at SLU for his constructive comments on this study.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119737>.

References

- Bădescu, A., Asănică, A., Stănică, F., Bădescu, C., Ungurenuș, M., 2017. Climate change affects blueberry production in Romania. *Acta Hort.* 1180, 299–304. <https://doi.org/10.17660/ActaHortic.2017.1180.40>.
- 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. Manage.* 377, 46–54. <https://doi.org/10.1016/j.foreco.2016.06.037>.
- Belonogova, T., 1993. Changes in bilberry and cowberry yields under influence of forest measures. *Aquilo Series Botanica* 31, 17–20.
- Bollandsås, O.M., Hanssen, K.H., Marthinsen, S., Næsset, E., 2017. Measures of spatial forest structure derived from airborne laser data are associated with natural regeneration patterns in an uneven-aged spruce forest. *For. Ecol. Manage.* 255 (3–4), 953–961. <https://doi.org/10.1016/j.rse.2015.11.029>.
- Burkhard, B., Maes, J. (Eds.), 2017. Mapping ecosystem services. Pensoft Publishers, Sofia. 374 p. <https://ab.pensoft.net/article/12837/download/pdf/>.
- Dahlgren, J., Fridman, J., 2012. Här trivs blåbär och lingon bäst. [Here thrive bilberry and lingonberry best]. In: Skog & Mark 2012 – Om tillståndet i svensk landmiljö. Naturvårdsverket, p. 24–26. [In Swedish]. <https://www.naturvardsverket.se/Documents/publikationer6400/978-91-620-1293-9.pdf?pid=2694>.
- Eggers, J., Lämås, T., Lind, T., Öhman, K., 2014. Factors influencing choice of forest management strategy among small-scale private forest owners in Sweden. *Forests* 5 (7), 1695–1716. <https://doi.org/10.3390/f5071695>.
- Eriksson, L., Ingelög, T., Kardell, L., 1979. Blåbär, lingon, hallon. Förekomst och bärproduktion i Sverige 1974-1977. [Bilberry, lingonberry, raspberry. Occurrence and berry production in Sweden 1974-1977]. Report 16, Section of Environmental Forestry, The Swedish University of Agricultural Sciences. pp. 1–124. [In Swedish].
- Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. *Ecol. Bull.* 46, 16–47.
- European Commission, 2013. Mapping and assessment of ecosystems and their services. An analytical framework for ecosystem assessments under Action 5 of the EU Biodiversity Strategy to 2020. Discussion paper – Final, April 2013, European Union, 57 p. http://ec.europa.eu/environment/nature/knowledge/ecosystem_assessment/pdf/MAESWorkingPaper2013.pdf.
- European Commission, 2016. Mapping and assessment of ecosystems and their services. Mapping and assessing the condition of Europe's ecosystems: Progress and challenges. 3rd Report – Final, March 2016, European Union, 178 p. http://catalogue.biodiversity.europa.eu/uploads/document/file/1328/3rdMAESReport_Condition.pdf.
- Fick, Stephen E., Hijmans, Robert J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37 (12), 4302–4315. <https://doi.org/10.1002/joc.2017.37.issue-12.1002.joc.5086>.
- Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A. H., Ståhl, G., 2014. Adapting National Forest Inventories to changing requirements – the case of the Swedish National Forest Inventory at the turn of the 20th century. *Silva Fennica* 48(3), article id 1095. <https://doi.org/10.14214/sf.1095>.
- Grafström, A., Zhao, X., Nylander, M., Petersson, Hans, 2017. A new sampling strategy for forest inventories applied to the temporary clusters of the Swedish NFI. *Can. J. For. Res.* 47 (9), 1161–1167. <https://doi.org/10.1139/cjfr-2017-0095>.
- Hefley, T.J., Hooten, M.B., Hanks, E.M., Russel, R.E., Walsh, D.P., 2017. Dynamic spatio-temporal models for spatial data. *Spatial Statistic* 20, 206–220. <https://doi.org/10.1016/j.spa.2017.02.005>.
- Hotanen, J.-P., Korpela, L., Mikkola, K., Mäkipää, R., Nousiainen, H., Reinikainen, A., Salemaa, M., Silfverberg, K., Tamminen, M., Tonteri, T., Vanha-Majamaa, I., 2000. Metsä- ja suokasvien yleisyys ja runsaus 1951–95. [Frequency and abundance of forest and mire plants in Finland 1951–95]. In Reinikainen A., Mäkipää, R., Vanha-Majamaa, I., Hotanen, J.-P. (Eds.), *Kasvit muuttuvassa luonnossa. [Effects on the changes in land use and forest management on vegetation]*. Tammi, Helsinki, pp. 84–301. [In Finnish].
- Hytönen, M. (Eds.), 2005. Multiple-use of forestry in Nordic countries. Metla, Finnish Forest Research Institute, Helsinki Research Centre, 460 p.
- Ihalainen, Marjut, Alho, Juha, Kolehmainen, Osmo, Pukkala, Timo, 2002. Expert models for bilberry and cowberry yields in Finnish forests. *For. Ecol. Manage.* 157 (1–3), 15–22. [https://doi.org/10.1016/S0378-1127\(00\)00653-8](https://doi.org/10.1016/S0378-1127(00)00653-8).
- Jaakkola, I., 1983. Rovaniemen maalaiskunnan marjainventointi. [Berry inventory of Rovaniemi municipality]. *Metsäntutkimuslaitoksen tiedonantoja* 105, 134–143 [In Finnish].
- Kangas, J., 1998. Non-Wood forest goods and benefits and the choice of forest management practices. In: Lund, H.G., Pajari, B., Korhonen, M. (Eds.), *Sustainable development of non-wood goods and benefits from boreal and cold temperature forests*. EFI Proceedings 23, pp. 202–210.
- Kardell, Lars, 1979. Occurrence and production of bilberry, lingonberry and raspberry in Sweden's forests. *For. Ecol. Manage.* 2, 285–298.
- Kilpeläinen, H., Miina, J., Store, R., Salo, K., Kurttila, M., 2016. Evaluation of bilberry and cowberry yield models by comparing model predictions with field measurements from North Karelia, Finland. *For. Ecol. Manage.* 363, 120–129. <https://doi.org/10.1016/j.foreco.2015.12.034>.
- Lakka, Johanna, Kouki, Jari, 2009. Patterns of field layer invertebrates in successional stages of managed boreal forest: implications for the declining Capercaillie Tetrao urogallus L. population. *For. Ecol. Manage.* 257 (2), 600–607. <https://doi.org/10.1016/j.foreco.2008.09.042>.
- Lantmäteriet, 2014. Produktbeskrivning LASERDATA. Landmäteriet, 17 p. [In Swedish].
- Lopatin, J., Dolos, K., Hernández, H.J., Galleguillos, M., Fassnacht, F.E., 2016. Comparing Generalized Linear Models and random forest to model vascular plant species richness using LiDAR data in a natural forest in central Chile. *Remote Sens. Environ.* 173, 200–210. <https://doi.org/10.1016/j.rse.2015.11.029>.
- Lucas, K.L., Raber, G.T., Carter, G.A., 2010. Estimating vascular plant species richness of Horn Island, Mississippi using small-footprint airborne LiDAR. *J. Appl. Rem. S.* 4 (1), 043545. <https://doi.org/10.1117/1.3501119>.
- Maltamo, M., Packalén, P., Yu, X., Eerikäinen, K., Hyypä, J., Pitkänen, J., 2005. Identifying and quantifying structural characteristics of heterogeneous boreal forests using laser scanner data. *For. Ecol. Manage.* 216 (1–3), 41–50. <https://doi.org/10.1016/j.foreco.2005.05.034>.
- Maltamo, M., Næsset, E., Vauhkonen, J. (Eds.), 2014. *Forestry Applications of Airborne Laser Scanning, Concept and case studies. Managing Forest Ecosystems*, vol 27. Springer, Dordrecht.
- Mao, L., Dennett, J., Bater, C.W., Tompalski, P., Coops, N.C., Farr, D., Kohler, M., White, B., Stadt, J.J., Nielsen, S.E., 2018. Using airborne laser scanning to predict plant species richness and assess conservation threats in the oil sands region of Alberta's boreal forest. *For. Ecol. Manage.* 409, 29–37. <https://doi.org/10.1016/j.foreco.2017.11.017>.
- McCullagh, P., Nelder, J.A., 1989. *Generalized linear models*. 2nd edition. Chapman and Hall, University Press, Cambridge.
- McGaughey, R.J., 2021. FUSION/LDV: Software for LIDAR data Analysis and Visualization, January 2021 – FUSION Version 4.20. United States Department of Agriculture, Washington DC, 212 p. http://forsys.cfr.washington.edu/software/fusion/FUSION_manual.pdf (accessed 16.6.2021).
- McRoberts, R.E., Cohen, W.B., Næsset, E., Stehman, S.V., Tomppo, E.O., 2010. Using Remote sensing data to construct and assess forest attribute maps and related spatial products. *Scan. J. Forest. Res.* 25 (4), 340–367. <https://doi.org/10.1080/02827581.2010.497496>.
- Mehtätalo, L., Lappi, J., 2020. *Biometry for Forestry and Environmental Data. With Examples in R*. Chapman and Hall/CRC, New York, 426 p.
- Melin, M., Mehtätalo, L., Miettinen, J., Tossavainen, S., Packalén, P., 2016. Forest structure as a determinant of grouse brood occurrence – An analysis linking LiDAR data with presence/absence field data. *For. Ecol. Manage.* 380, 202–211. <https://doi.org/10.1016/j.foreco.2016.09.007>.
- Miina, J., Hotanen, J.-P., Salo, K., 2009. Modelling the abundance and temporal variation in the production of bilberry (*Vaccinium myrtillus* L.) in Finnish mineral soil forests. *Silva Fennica* 43 (4), 577–593. <https://doi.org/10.14214/sf.181>.
- Moeslund, J.E., Zlinszky, A., Ejrnæs, R., Brunbjerg, A.K., Bøcher, P.K., Svenning, J.-C., Normand, S., 2019. Light detection and ranging explains diversity of plants, fungi, lichens, and bryophytes across multiple habitats and large geographic extent. *Ecol. Appl.* 29 (5), e01907 <https://doi.org/10.1002/eap.1907>.

- Muhonen T., 1995. Mustikka- ja puolukkasatojen ennustaminen kasvupaikka- ja puustotunnusten avulla – asiantuntemukseen perustuva lähestymistapa. Master's thesis of forest planning and economics. University of Joensuu, Faculty of Forestry. 37 p. [In Finnish].
- Müller, J., Brandl, R., 2009. Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *J. Appl. Ecol.* 46, 897–905. <https://doi.org/10.1111/j.1365-2664.2009.01677.x>.
- Naturvårdsverket, 2014. Svenska marktäckedata, Produktbeskrivning. Naturvårdsverket, p49 p. https://gpt.vic-metria.nu/data/land/SMD_produktdeskription_20140627.pdf (accessed 16.6.2021). [In Swedish].
- Naturvårdsverket, 2020. Nationella marktäckedata 2018 basskikt. Produktbeskrivning. [National land cover data 2018. Product description]. Naturvårdsverket, 56 p. <https://www.naturvardsverket.se/upload/sa-mar-miljon/kartor/NMD-Produktdeskri-NM-D2018Basskikt-v2-2.pdf> (accessed 16.6.2021). [In Swedish].
- Naturvårdsverket, 2021. Right of public access. Naturvårdsverket. <http://www.swedishepa.se/Enjoying-nature/The-Right-of-Public-Access/>. (accessed 16.6.2021).
- 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* 2020, 11(7), 783. <https://doi.org/10.3390/f11070783>.
- Nijland, W., Nielsen, S. E., Coops, N. C., Wulder, M. A., Stenhouse, G. B., 2014. Fine-spatial scale predictions of understory species using climate- and LiDAR-derived terrain and canopy metrics. *J. Appl. Remote Sens.* 8(1), 083572. <https://doi.org/10.1117/1.JRS.8.083572>.
- Nilsson, M., Nordkvist, K., Jonzén, J., Lindgren, N., Axensten, P., Wallerman, J., Egberth, M., Larsson, S., Nilsson, L., Eriksson, J., Olsson, H., 2017. A nationwide forest attribute map of Sweden predicted using airborne laser scanning data and field data from the National Forest Inventory. *Remote Sens. Environ.* 194, 447–454. <https://doi.org/10.1016/j.rse.2016.10.022>.
- Noordermeer, L., Bollandsås, O.M., Gobakken, T., Næsset, E., 2018. Direct and indirect site index determination for Norway spruce and Scots pine using bitemporal airborne laser scanner data. *For. Ecol. Manage.* 428, 104–114. <https://doi.org/10.1016/j.foreco.2018.06.041>.
- Olas, B., 2018. Berry Phenolic Antioxidants – Implications for Human Health? *Front. Pharmacol.* 9, 78 p. <https://doi.org/10.3389/fphar.2018.00078>.
- Öhman, Karin, Edenius, Lars, Mikusiński, Grzegorz, 2011. Optimizing spatial habitat suitability and timber revenue in long-term forest planning. *Can. J. For. Res.* 41 (3), 543–551. <https://doi.org/10.1139/X10-232>.
- Pesonen, A., Maltamo, M., Eerikäinen, K., Packalén, P., 2008. Airborne laser scanning-based prediction of coarse woody debris volumes in a conservation area. *For. Ecol. Manage.* 255 (8-9), 3288–3296. <https://doi.org/10.1016/j.foreco.2008.02.017>.
- Raatikainen, M., Raatikainen, T., 1983. The berry yield, picking and marketing of *Vaccinium myrtillus* in the commune of Pihtipudas, northern central Finland. *Silva Fennica* 17(2), 113-123. [In Finnish with English summary].
- Raatikainen, M., Rossi, E., Huovinen, J., Koskela, M.-L., Niemelä, M., Raatikainen, T., 1984. The yields of the edible wild berries in central Finland. *Silva Fennica* 18, 199-219. [In Finnish with English summary].
- RIS, 2020. Riksinventering av skog. Fältinstruktion 2020. [National forest inventory. Field instructions]. SLU, Institutionen för skoglig resurshushållning, Institutionen för mark och miljö, 503 p. [In Swedish]. https://www.slu.se/globalassets/ew/org/centrb/rt/dokument/faltinst/20_ris_fin.pdf.
- Ritchie, J.C., 1955. Biological flora of the British Isles. *Vaccinium vitis-idaea* L. *J. Ecol.* 43, 701–708.
- Ritchie, J.C., 1956. *Vaccinium myrtillus* L. *J. Ecol.* 44, 291–299.
- Rixen, C., Schwoerer, C., Wipf, S., 2010. Winter climate change at different temporal scales in *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub. *Polar. Res.* 29, 85–94. <https://doi.org/10.3402/polar.v29i1.6056>.
- Reese, H., Nilsson, M., Pahné, T.G., Hagner, O., Joyce, S., Tingelöf, U., Egberth, M., Olsson, H., 2003. Countrywide estimates of forest variables using satellite data and field data from National Forest Inventory. *Ambio* 32 (8), 542–548. <https://doi.org/10.1579/0044-7447-32.8.542>.
- Salemaa, M., 2000. *Vaccinium Myrtillus*. Mustikka. In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I., Hotanen, J.-P. (Eds.). *Kasvit muuttavassa metsäluonnossa. [Effects of the changes in the land use and forest management on vegetation]*. Tammi, Helsinki, pp. 128–130. [In Finnish].
- Salo, K., 1995. Non-Timber forest products and their utilization. In: Hytönen, M. (Ed.), *Multiuse forestry in Nordic countries*. Gummerus Printing, Jyväskylä, pp. 117–155.
- Sandström, P., Pahlén, T.G., Edenius, L., Tømmervik, H., Hagner, O., Hemberg, L., Olsson, H., Baer, K., Stenlund, T., Brandt, L.G., Egberth, M., 2003. Conflict Resolution by Participatory Management: Remote Sensing and GIS as Tools for Communicating Land-Use Needs for Reindeer Herding in Northern Sweden. *Ambio* 32 (8), 557–567. <https://doi.org/10.1579/0044-7447-32.8.557>.
- SGU, 2020. Jorddjupsmodell, Produktbeskrivning. [Soil depth model, Product description]. Sveriges geologiska undersökning, 5 p. <http://resource.sgu.se/dokument/produkter/jorddjupsmodell-beskrivning.pdf> (accessed 16.6.2021). [In Swedish].
- SGU, 2018. Jordarter 1:25 000 - 1:100 000, Produktbeskrivning. [Soil types, Product description]. Sveriges geologiska undersökning, 13 p. <https://resource.sgu.se/dokument/produkter/jordarter-25-100000-beskrivning.pdf> (accessed 16.6.2021). [In Swedish].
- Skogsdata 2019, 2019. Sveriges officiella statistik. [Forest data. Swedish official statistic]. Institutionen för skoglig resurshushållning, SLU, Umeå, Sweden, 135 p. [In Swedish with english summary]. https://www.slu.se/globalassets/ew/org/centrb/rt/dokument/skogsdata/skogsdata_2019_webb.pdf.
- SLU, 2021a. SLU Soil moisture map, Dept. of Forest Ecology and Management, Swedish University of Agricultural Sciences. <https://www.slu.se/institutioner/skogens-ekologi-skotsel/forskning2/markfuktighetskartor/> (accessed 16.6.2021) [In Swedish].
- SLU, 2021b. SLU forest map, Dept. of Forest Resource Management, Swedish University of Agricultural Sciences. <https://www.slu.se/centrumbildningar-och-projekt/riksskogstaxeringen/statistik-om-skog/slu-skogskarta/> (accessed 16.6.2021) [In Swedish].
- Snäll, T., Moen, J., Berglund, H., 2014. Mapping and assessment of ecosystems and their services. The Swedish Forest Pilot. Report 6626. Swedish Environmental Protection Agency. <https://www.naturvardsverket.se/Documents/publikationer6400/978-91-620-6626-0.pdf?pid=13822>.
- Turtiainen, M., Salo, K., Saastamoinen, O., 2011. Variations of yield and utilisation of bilberries (*Vaccinium myrtillus* L.) and cowberries (*V. vitis-idaea* L.) in Finland. *Silva Fennica* 45(2), article id 115. <https://doi.org/10.14214/sf.115>.
- Turtiainen, M., Miina, J., Salo, K., Hotanen, J.-P., 2013. Empirical prediction models for the coverage and yield of cowberry in Finland. *Silva Fennica* 47 (3). <https://doi.org/10.14214/sf.1005> article id 1005.
- Turtiainen, M., 2015. Modelling bilberry and cowberry yields in Finland: different approaches to develop models for forest planning calculations. *Dissertations Forestales* 185, 56 p. <https://doi.org/10.14214/df.185>.
- Vanhatalo, Jarno, Hosack, Geoffrey R., Sweatman, Hugh, Bode, Michael, 2017. Spatiotemporal modelling of crown-of-thorns starfish outbreaks on the Great Barrier Reef to inform control strategies. *J. Appl. Ecol.* 54 (1), 188–197. <https://doi.org/10.1111/1365-2664.12710>.
- Vauhkonen, J., 2018. Predicting the provisioning potential of forest ecosystem services using airborne laser scanning data and forest resource maps. *For. Ecosyst.* 5, 24. <https://doi.org/10.1186/s40663-018-0143-1>.
- Wallenius, T.H., 1999. Yield variation of some common wild berries in Finland in 1956–1996. *Annales Botanici Fennici* 36, 299–314.
- Wikström, P., Edenius, L., Elfving, B., Eriksson, L.O., Lämäs, T., Sonesson, J., Öhman, K., Wallerman, J., Waller, C., Klinteback, F., 2011. The Heureka forestry decision support system: An overview. *Math. Computat. Forestry Nat.-Resource Sci.* 3(2): 87–94. <https://mcfns.net/index.php/Journal/article/view/MCFNS.3-87>.
- Yichun, Xie, Zongyao, Sh.a., Mei, Yu., 2008. Remote sensing imagery in vegetation mapping: a review. *J. Plant Ecol.* 1 (1), 9–23. <https://doi.org/10.1093/jpe/rtm005>.