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Modeling the Abundance of Boreal Foundation Species: The Impact of Forest Structure, Soils, and Legacy Effects on Ericaceous Shrubs

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ABSTRACT

Aims: The dwarf shrubs *Calluna vulgaris*, *Vaccinium myrtillus*, and *V. vitis-idaea* are functionally important species in boreal forest, driving ecosystem processes and delivering multiple ecosystem services. Their dependency on previous and present land-use calls for tools to estimate the outcomes of different forest management strategies on their abundance. Here we built models for estimating their cover as a response to forest structure, soils, and legacy effects, with the ultimate target to be used in decision support systems to be able to adapt future management.

Location: Sweden.

Methods: We fitted Generalized Linear Mixed Models with beta error distribution, and accounting for zero-inflation, based on data ($n > 2800$) on plant cover, forest structure, and soils from the Swedish National Forest Inventory.

Results: The resulting best models include forest density and tree species composition, and their interaction effects, likely governing the light availability in the forest understory for all three species. These models also included soil fertility indicated by the C:N ratio, the age of the forest as an indicator of time since disturbance, and the cover of the focal species 10 years earlier to account for legacy and time-lag effects. Although these variables were important for the model predictions of all three species, there were interspecific differences in the response due to the stress tolerance of the species and their placement in the leaf economics spectrum.

Conclusions: We show that it is possible to predict the cover of these species with higher accuracy ($R^2 = 0.44$–0.60) than previously has been achieved, using predictors available from for example, national forest inventories. Hence, our models will improve the estimations of the outcomes of different forest management strategies on the cover of these species. This will be important when weighing pros and cons for ecosystem functions and services, and thus imperative for sustainable forest management.

1 | Introduction

Ericaceous dwarf shrubs are foundation species in the boreal biome due to their high abundance and importance for ecosystem processes and functions. In northern Europe, the three species *Calluna vulgaris*, *Vaccinium myrtillus*, and *V. vitis-idaea* often dominate forest understories as well as more open habitats such as bogs, heathland, and rocky outcrops (Esseen

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et al. 1997; Gimingham 1960; Ritchie 1955, 1956). As such, they make a significant contribution to net primary production (Nilsson and Wardle 2005; Wardle et al. 2012), and to ecosystem-level carbon sequestration due to their effects on turnover rates of soil carbon (Nilsson and Wardle 2005). Further, dwarf shrubs provide food for many forest species (Atlegrim 1989; Lakka and Kouki 2009; Selås et al. 2011) and constitute a considerable share of the diet of large wild ungulates (Felton et al. 2020a; Spitzer et al. 2023), with resulting effects on ungulate population growth and ecosystem processes (Selås et al. 2011; Spitzer et al. 2021). Additionally, *V. myrtillus* and *V. vitis-idaea* produce berries of large economical and recreational values (Miina et al. 2010; Pouta et al. 2006). Hence, these species influence multiple ecosystem functions and processes and contribute with manifold ecosystem services.

The three dwarf shrubs are all stress tolerant, relatively strong competitors, nutrient conservative, and generally adapted to less frequent disturbances (Ellenberg et al. 2001; Grime et al. 2007; Tyler et al. 2021). Further, they are strongly clonal through vegetative propagation from horizontal rhizomes in *Vaccinium*, and from adventitious rooting in *Calluna* (Gimingham 1960; Ritchie 1955, 1956). Their ramets and clones reach ages of at least several decades, which together with abundant seed banks, especially in *Calluna* (Granström 1988), can induce considerable legacy effects from previous environmental conditions and disturbances on their abundances. They regenerate well vegetatively after light or intermediately severe fires, while more severe fires that cause rhizome and seed-bank mortality can have long-term negative effects on their abundance (Schimmel and Granström 1996). Similar legacy effects have been indicated by Gustafsson et al. (2021) who found that the starting point for postfire succession of *V. myrtillus* is dependent on previous disturbance intervals. Specifically, this study found that the recovery of *V. myrtillus* in the years directly after a fire was positively related to the time span since the last stand-replacing disturbance before the fire event, while negatively related with tree canopy cover.

Despite these interspecific similarities, and that they often grow in mixtures (Gimingham 1960; Ritchie 1955, 1956), these species are distinct along the leaf economics spectrum. The specific leaf area of the deciduous *V. myrtillus* is two to three times that of the other two species, which are evergreen, and the leaf size is much smaller in *Calluna* than in *Vaccinium* (Kleyer et al. 2008). Due to this we would expect the three species to respond differently to gradients of light and nutrient availability with *V. myrtillus* being more shade-adapted and nutrient-demanding than *Calluna*, and with *V. vitis-idaea* being intermediate. This has been confirmed for the *Vaccinium* species (Hedwall et al. 2013) and is also supported by indicator values for light and nitrogen/nutrients for all species (Ellenberg et al. 2001; Tyler et al. 2021).

The life history of these dwarf shrubs makes them vulnerable to alterations in disturbance regimes and the nutrient cycle. During the last century, considerable changes in their abundance have been observed in Europe. For example, changes in management and elevated deposition of anthropogenic nitrogen caused a decline in *Calluna* heathlands in Western Europe during the last century (Bobbink et al. 2010). Nitrogen deposition is probably also one of the reasons behind the decline of these species in southern Sweden (Hedwall and Brunet 2016; Hedwall, Gustafsson, et al. 2019, 2021). However, the species have declined also outside areas with high deposition of nitrogen such as documented by National Forest Inventories (NFI) in northern Sweden and Finland, likely as an effect of intensified forestry (Reinkainen et al. 2000; Hedwall and Brunet 2016; Hedwall, Gustafsson, et al. 2019; Hedwall, Holmström, Lindbladh and Felton 2019; Hedwall, Brunet and Diekmann et al. 2019). Interactions between large-scale (e.g., nitrogen deposition) and local drivers (e.g., forest structure) have been reported for temperate plant community composition (Perring et al. 2018; Depauw et al. 2020) but not yet for these ericaceous shrubs (Hedwall et al. 2021).

Boreal forestry largely relies on clear-cutting and regeneration with conifer tree species in rotations considerably shorter than the trees' natural life spans (Esseen et al. 1997; Roberge et al. 2016). This type of management generally results in forests that are younger and more homogenous, with a larger share of conifer species, than forests under natural disturbance regimes (Esseen et al. 1997; Axelsson and Östlund 2001). In some regions, such as Sweden, forest management has also led to an increasing share of late-successional shade-tolerant tree species such as Norway spruce (*Picea abies*), which has considerably stronger negative effects on the understory light availability than early-successional, shade-intolerant tree species (Lindbladh et al. 2014; Hedwall, Holmström, Lindbladh and Felton 2019). The detailed relationships between the abundance of the *Vaccinium* species and forest structural variables such as forest density, tree species composition, and forest age, have been parameterized in several studies (Miina et al. 2009; Hedwall et al. 2013; Turtiainen et al. 2013, 2016; Eldegard et al. 2019) but, to our knowledge, not for *Calluna* (see however e.g. Tonteri et al. 2016, Itter et al. 2024) which limits our possibilities to predict its response to future changes in forest structure.

The strong effect of forest management on ericaceous dwarf shrubs, and their importance for boreal forest ecosystems, calls for tools to estimate the outcomes of different management strategies on their abundances (e.g., Miina et al. 2010). One way of providing such tools is to implement functions for estimating cover or biomass of the understory species in decision support systems (DSS) for forest management. A forest DSS is a "computer-based system that supports forest management planning and analysis involving multiple objectives by integrating analytical methods and models for projecting the future development of forests and their production of ecosystem services based on assumptions about, e.g., forest management and price trends" (Lämås et al. 2023). So far, the modeling work done on these species has used nonparametric model frameworks (Hedwall et al. 2013) or was adapted to local site and soil classification schemes (Turtiainen et al. 2013, 2016; Eldegard et al. 2019). This calls for a more general approach with parametric models, as implementing nonparametric models in DSS is much more challenging than parametric models due to data requirement and computational complexity.

The objective of this study was to create empirical and parametric models for estimating cover of the three ericaceous shrubs *C. vulgaris*, *V. myrtillus*, and *V. vitis-idaea* as affected by forest structure and soil conditions on forest land, comprising time-lags in response to the overstory and legacy effects of previous environmental conditions. The models were based on > 2800 data points from the Swedish NFI (Fridman et al. 2014) including information on vegetation and soil, and designed for implementation in forest DSS to facilitate the evaluation of different management strategies from the perspective of ecosystem functioning and services. We expected that all three dwarf-shrub species increase in cover with stand age due to recovery from disturbance and that all species will increase with decreasing soil fertility due to their adaptation to relatively poor soils, but with interspecific differences due to their placement on the leaf economics spectrum. Further, we expected that the effects of forest density will differ between the three dwarf-shrub species depending on their shade tolerance, and that the effects of forest density are largely dependent on tree species composition due to differences in light transmittance (Verheyen et al. 2012). We assumed plant cover to be related to our presumed drivers in a curvilinear fashion as plant species responses to extensive environmental gradients almost exclusively are nonlinear (e.g., Jansen and Oksanen 2013), which also has been shown for our focal *Vaccinium* species (Hedwall et al. 2013; Eldegard et al. 2019).

2 | Method

2.1 | Study Area

In Sweden, the understory vegetation is commonly dominated by dwarf shrubs (mainly *C. vulgaris* and *Vaccinium* spp.), which increase in abundance along gradients from south to north and from fertile to infertile soils (SLU 2011; Hedwall et al. 2013). The narrow-leaved grass *Avenella flexuosa* is very common, especially on moderately fertile and newly disturbed sites, while fertile soils often are dominated by forbs and broadleaved grasses (SLU 2011).

Sweden extends over almost 14° of latitude (55.3°–69.1° N), with annual mean temperatures ranging from c. 8°C in the very south to −3°C in the far north. During the period 1991–2013, the annual mean temperature across Sweden has increased by 0.9°C and the mean annual precipitation by 8%, when compared to the period 1961–1990 (Kjellström et al. 2014). There is a south–north gradient in nitrogen deposition ranging from ~12.5 kg ha^{-1} year^{-1} in the southernmost parts to close to ambient levels (< 2 kg ha^{-1} year^{-1}) in the far north (Akselsson et al. 2010). The forests of Sweden belong to the temperate, boreal and subarctic biomes. Forests cover 279,000 km^2 of a total land area of 407,000 km^2 (SLU 2023). Of the total forest area, 44,000 km^2 consist of low-productive forests, including subalpine mountain *Betula pubescens* subsp. *czerepanovii* forests, peatlands dominated mainly by *Pinus sylvestris* (nomenclature according to: www.dyntaxa.se), and woodland on rocky outcrops. The remaining forests, covering 235,000 km^2, are considered as productive forest land, with a potential annual increase in woody biomass of at least 1 m^3 ha^{-1} year^{-1}. The southern third of the country (67,000 km^2 productive forest) is part of the temperate vegetation zone (comprising the temperate zone *sensu stricto* according to Ahti et al. (1968), and the hemiboreal zone forming a transition towards the boreal zone). The northern part of the country (168,000 km^2 productive forest) belongs to the boreal zone and is dominated by *Picea abies* and *P. sylvestris*. Because of active forest management, these two species also dominate the forests of southern Sweden and together currently make up 79% of the country's standing timber volume (SLU 2023). However, the temperate zone still contains c. 2500 km^2 of temperate broadleaf forest dominated by *Quercus robur*, *Fagus sylvatica* and other temperate broadleaf tree species. These deciduous tree species are also often admixed to conifer-dominated forests in temperate southern Sweden. The most common soil types are podsols (45%), but arenosols (20%) are also relatively common (SNA 1994). The bedrock is dominated by gneisses, granites and other siliceous bedrock, while dolomites and limestones are rare (Sjörs 1999).

2.2 | Data Collection

This study is based on data on plant cover, forest structure, and soils from the Swedish NFI (Fridman et al. 2014; SLU 2011). The Swedish NFI collects data on forest structure and environmental variables in a nationwide network of permanent sample plots in five regions. The plots are aggregated in square-shaped clusters with 4–8 plots in each square, all of which are located along the border of the square. The edge of each square is 300–1200 m long, and the distance between squares varies between the five regions, with on average 14,800 m between the square centers in the northernmost region and 6200 m in the south of Sweden. The five NFI regions coincide well with the vegetation zones in Sweden and thus are located along a biogeographic gradient ranging from northern temperate to northern boreal (Ahti et al. 1968). In the vegetation survey, circular permanent plots with a radius of 5.64 m (100 m^2) are used. The cover of 72 species or groups of species, including vascular plants, bryophytes and lichens, is noted according to a predetermined list of species (Odell and Löfgren 2009). For this study three species, *C. vulgaris*, *V. myrtillus* and *V. vitis-idaea*, were selected for analysis. In a subplot (3.14 m^2), selected as representative of the main plot, 1–9 soil samples (depending on humus layer thickness) are taken with a 100 mm diameter soil corer and aggregated to a minimum of 1.5 L sample. In sample plots with mor or moder humus or peat, the samples are taken from the whole O-horizon (humus layer), after litter was removed, down to a maximum depth of 30 cm (max. 50 cm for peat). In sample plots with mull or mull-like moder, samples are taken to a soil depth of 10 cm. The soil samples are dried (35°C) to constant weight and then homogenized and sieved (< 2 mm), after living and dead roots (> 1 mm diameter) are removed. Total C and N content (%) are analyzed using an elemental analyzer (LECO CNS-1000 and LECO TruMac CN). Detailed information on the ground vegetation and soils is collected recurrently in plots with intervals of 10 years (SLU 2011; Fridman et al. 2014). For this study, we used plots surveyed between 2007 and 2016 on productive forest land that included information about both soil and vegetation.

2.3 | Data Treatment and Modeling

In the NFI, cover of individual plant species is estimated in m^2 (maximum 100). Additionally, they estimate the area where plants can't grow, like newly disturbed soil and larger boulders. We calculated the proportion (0–1) of the plot covered by one of our three focal plant species as the number of m^2 covered by this species divided by the total plot size minus the unsuitable area. In our statistical modeling (see below) we used the total basal area ($m^2\,ha^{-1}$) of all trees growing on the plot as an indicator of forest density, and the basal area percentage of *P. abies* or deciduous broadleaved trees as indicators of tree species composition. We assume that these variables account for recent changes to the overstory by forestry operation or other disturbances. Density and tree species composition of overstories are however in constant change due to both natural and anthropogenic disturbances, growth, competition and succession. Our focal plant species are slow growing and, therefore, we assume their abundance to never be in equilibrium with their environment, but rather also dependent on one or several disturbance events that can be far back in time. Likewise, do we assume that the resulting effects of a disturbance may be dependent on the pre-disturbance conditions (Gustafsson et al. 2021). To account for these time-lags and legacy effects, the cover of the focal plant species on the same plot, at the preceding inventory, 10 years earlier was included in our models. The humus layer C:N ratio was used as an indicator of soil nitrogen availability (the higher the ratio, the lower nitrogen availability), while the forest age was included as an indicator of time since disturbance and successional stage. As neither the cover of the focal plants, nor the C:N ratio, always are available in DSSs, we formulated four different starting models per plant species (i.e., 12 final models in total) for model selection (see below) that either included (1) all available explanatory variables, (2) all variables except the previous cover, (3) all variables except the C:N ratio, or (4) all variables except the previous cover and the C:N ratio. Note that when models are implemented in a DSS they do not require data on plant cover prior to the starting point for predictions, just from a time point prior to the time point for which the DSS should predict. Due to insufficient amounts of data points for reliable predictions in parts of the environmental gradients, we excluded total basal areas $>50\,m^2$, forest ages >180 years and C:N ratios <10 and >50, respectively, from the analyses (which reduced n from the original 2970 to 2869). For the same reason we excluded cover proportions larger than 0.5 for *V. myrtillus* ($n=2853$), 0.3 for *V. vitis-idaea* ($n=2826$) and 0.25 for *C. vulgaris* ($n=2843$). To account for expected nonlinear effects of the explanatory variables we included the first, second, and third degree polynomials of all variables except the previous cover which was log-transformed (natural logarithm($X+0.1$)). As we expected the effect of forest density to be dependent on tree species composition (Juvany Canovas 2023) we included interactions between the total basal area and percentage of *P. abies* or deciduous broadleaved trees. This was done by including all possible combinations of the different levels of polynomials for the two variables in the starting models. Additionally, we checked if large-scale variables such as climatic indicators or N deposition contribute to the explanatory power of the models in addition to the variation already explained by the stand-level variables. For this purpose, we used data on mean annual temperature and precipitation, as well as the mean temperature of the warmest month (July) in addition to total deposition of N. These values were extracted from maps of modeled mean deposition between 2005 and 2014, and climate for the reference period 1961–1990. Data on climate and nitrogen deposition were provided by the Swedish Meteorological and Hydrological Institute (SMHI 2015). All explanatory variables were centered and standardized by subtracting the mean and dividing by the standard deviation of that specific variable. The means and standard deviations can be found in Appendix S1.

All data management and statistical modeling were done in R (R Core Team 2023). We fitted Generalized Linear Mixed Models (GLMM) with cluster ID as a random intercept effect, by applying the glmmTMB function in the glmmTMB package (Brooks et al. 2017). To account for the abundant observations with null cover of the response plant species, we fitted Hurdle models (Cragg 1971) by incorporating a zero-inflation formula including the main effects (first degree polynomial) of previous plant cover, C:N ratio, total basal area, percentages of Norway spruce and deciduous broadleaved trees. We applied a beta error distribution for the part of the model fitting observations larger than zero and a binomial distribution for the part that predicts the probability of zero cover, both with a logit link. Model selection was performed in two steps. First we used the buildglmmTMB function in the buildmer package (Voeten 2023), with the default settings, on the continuous part of the data (observations with zero cover of the focal plant excluded). Then we added the zero-inflation formula to the selected GLMM and ran this model on all data, including the zero-observations. As there is no automatic way of selecting variables for this formula, we performed a backwards stepwise exclusion of the variables with $p>0.05$. The models were evaluated by looking for patterns in the residuals and heteroscedasticity in residual plots and QQ-plots based on simulated residuals from the simulateResiduals function in the DHARMa package (Hartig 2022). We also performed tests of zero-inflation by the testZeroInflation function in this package, and of spatial autocorrelation by the moranNP.randtest function in the adespatial package (Dray et al. 2023). None of these tests were significant ($\alpha=0.05$). The models were evaluated for overfitting by 10-fold cross-validation by the cv function in the cv package (Fox and Monette 2024). This method randomly divides the sample data into 10 equally large subsamples and refits the model one time for each subsample using the remaining 90% of the data for training the model and the subsample for evaluating the model. Each refit and evaluation generates a cross-validation criterion (CVC, mean squared error) and a mean and 95% confidence interval of these criteria is calculated. If the criteria for the full sample (FSC) lay within the 95% CI of the CVC, the model is considered not to be overfitted but to predict equally well on new data, which was the case in 11 of the 12 models. The exception was *V. myrtillus* and the model resulting from the starting model with all variables except the previous cover and the C:N ratio, for which the FSC was lower than the CSC (Appendix S3). Marginal R^2s were calculated with the r2_nakagawa function in the performance package (Lüdecke et al. 2021) for the continuous parts (lacking zeros) of all models and the presented R^2s of the models therefore should be considered as conservative estimates of the explanatory power of the models. We fitted GLMMs to the residuals of the final models with the largest R^2s for each species to check how much of the remaining variation is explained by the large-scale variables annual mean temperature, mean July temperature, annual precipitation, and nitrogen deposition, by calculating R^2s as described above. We used the average modeled total deposition (NO_x+NH_x) from the period 2005–2014 and the average climatic data for the period 1961–1990, both acquired from the Swedish Meteorological Institute (SMHI 2015). Because the two mean temperatures and N deposition were

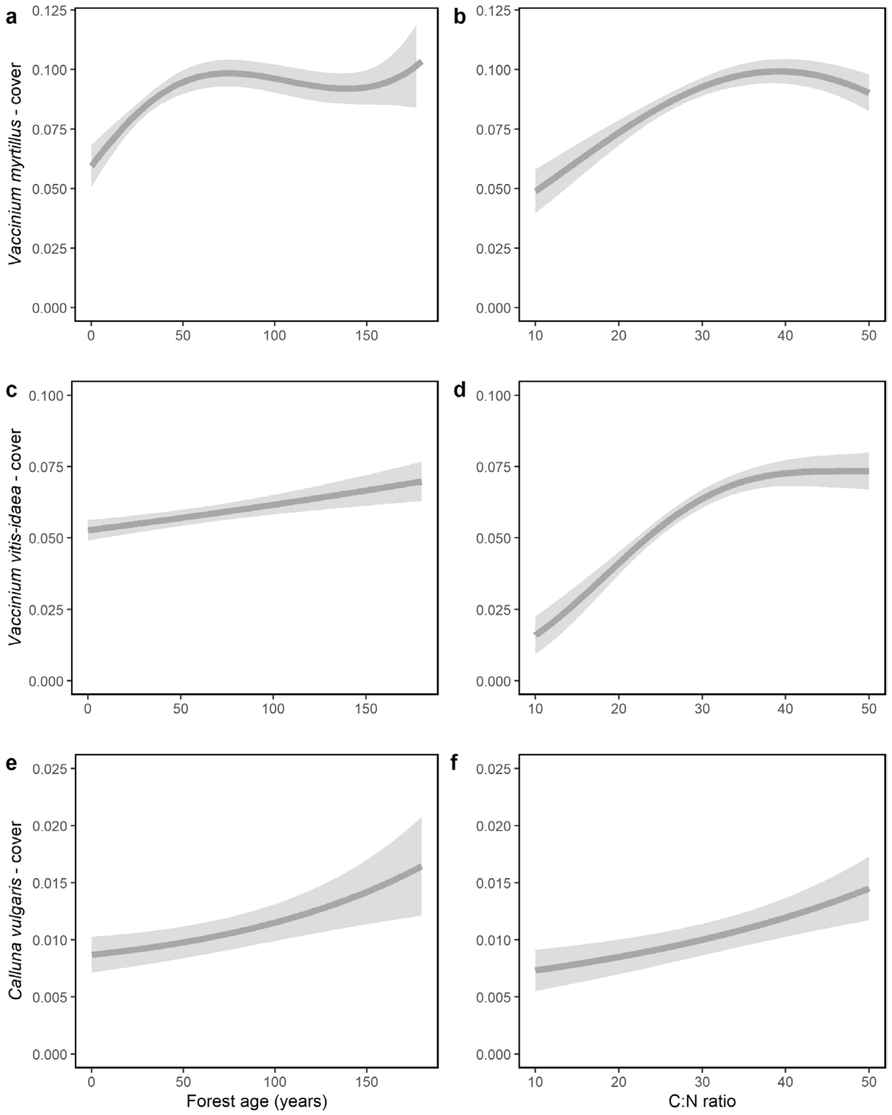

FIGURE 1 | Predicted proportional (0–1) cover (±95% CI) of *Vaccinium myrtillus* (a, b), *V. vitis-idaea* (c, d) and *Calluna vulgaris* (e, f) from Generalized Linear Mixed Models. Panels in the left column (a, c and e) show the effect of the forest age, while the panels in the right column (b, d and f) show the effect of the C:N ratio. The other variables were kept to their mean. Note that the scale of the *y*-axes differs between the species. The full range of the *Y*-axes and raw data points can be seen in Appendix S19.

correlated ($r = 0.71$–0.90), we fitted three sets of these variables separately: N deposition and precipitation; mean annual temperature and precipitation; mean July temperature and precipitation. In all cases the models included the first, second, and third degree polynomials of these variables.

3 | Results

The marginal R^2 varied between 0.12 and 0.60 for the 12 final models (Appendix S2). R^2 dropped considerably when the previous plant cover was excluded from the model ($\Delta R^2 = 0.18$–0.31), and even further when additionally also the C:N ratio was excluded ($\Delta R^2 = 0.32$–0.40). All models overpredicted at low cover values and underpredicted at higher values to varying degrees (Appendices S16–S18). This pattern was however stronger for the models which didn't include the previous cover. Due to the better fit of the models based on all available explanatory variables we chose to present the specifics of these here below, while model summaries for all models are presented in Appendices S4–S7 for *V. myrtillus*, Appendices S8–S11 for *V. vitis-idaea*, and Appendices S12–S15 for *C. vulgaris*.

3.1 | *Vaccinium myrtillus*

The R^2 of the final model for *V. myrtillus* cover was 0.6. The continuous part of the model included the previous cover of *V. myrtillus* and nonlinear effects of the variables age, C:N ratio, total basal area, and basal area percentages of *P. abies* and broadleaved trees (Appendix S4). Additionally, it included interactions between basal area and percentage of *P. abies*, and between basal area and percentage of broadleaved trees. The binomial part included the previous cover of *V. myrtillus*, C:N ratio and percentage of *P. abies*, all predicting a decreasing probability of zero cover with increasing values of these variables (Appendix S4). The model predicts an initial steep increase in cover with age which levels off between 50 and 100 years′ age and then does not change (Figure 1a). The predicted cover along the C:N gradient shows an unimodal trend with increasing cover at low C:N values and decreasing at a high values (Figure 1b). The effect of the total basal area was strongly dependent on tree species composition (Figure 2a,b). The predicted cover initially increased with basal area at low (i.e., in *Pinus*-dominated forest) or intermediate percentages of *P. abies* and then turned downwards with increasing basal area if the percentage of *P. abies* was intermediate, while there was no such change at a low percentage of *P. abies* (Figure 2a). In contrast, the effect of basal area was continuously negative at a high percentage of *P. abies*. The effect of basal area was initially positive, independently of percentage of broadleaved trees (Figure 2b). At low (i.e., in *Pinus*-dominated forest) and intermediate percentages of broadleaved trees, the increase in cover leveled off at intermediate basal areas, whereafter no change was predicted. On the other hand, the trend along the basal area gradient was unimodal for broadleaved-dominance with a predicted decrease in cover at high basal areas. None of the combinations of climatic variables, or climate combined with N deposition, explained more than 1% of the residual variation in *V. myrtillus* cover, why these variables were not included in the model structure.

3.2 | *Vaccinium vitis-idaea*

The R^2 of the final model for *V. vitis-idaea* cover was 0.49. The continuous part of the model included the previous cover of *V. vitis-idaea* and age, and nonlinear effects of the variables C:N

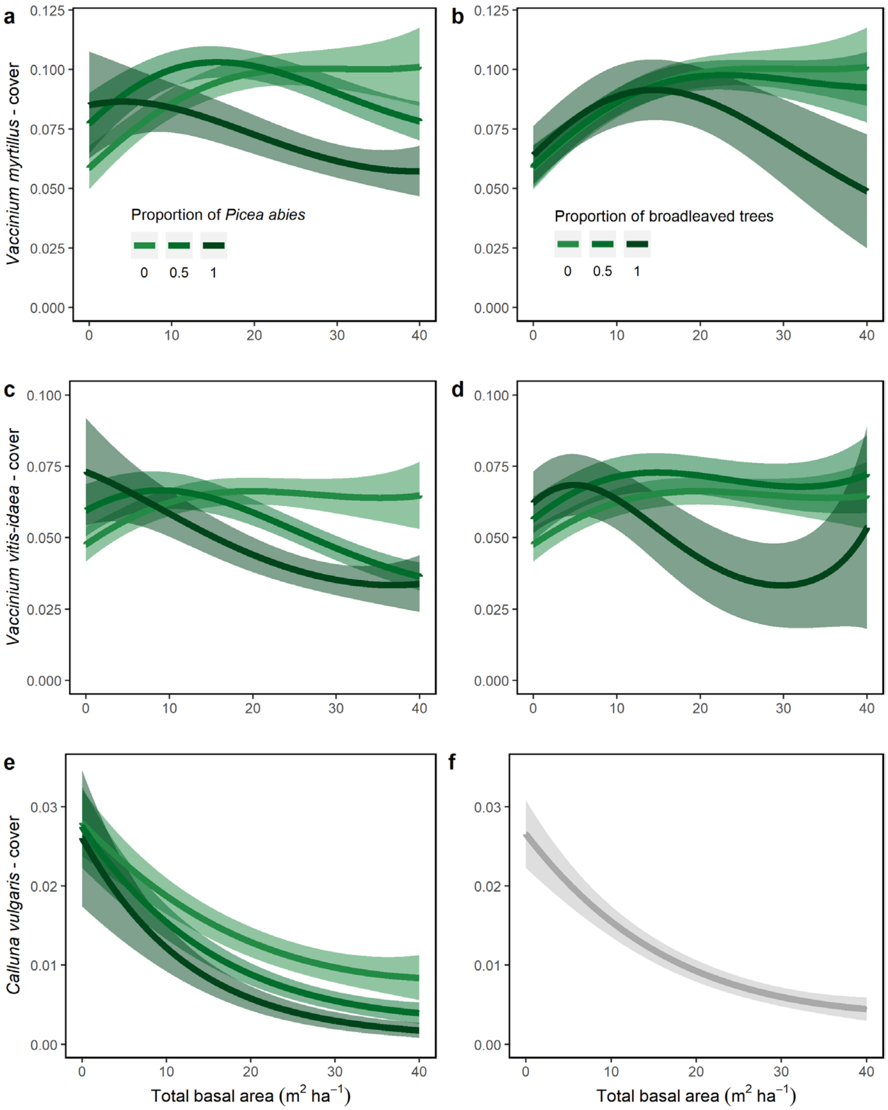

FIGURE 2 | Predicted proportional (0–1) cover (±95% CI) of *Vaccinium myrtillus* (a, b), *V. vitis-idaea* (c, d) and *Calluna vulgaris* (e, f) from Generalized Linear Mixed Models. Panels in the left column (a, c and e) show the effect of the total basal area of trees depending on the proportion of *Picea abies*, while the two upper panels in the left column (b, d) show the effect of the basal area depending on the proportion of broadleaved trees. Panel (f) shows the main effect of basal area as no interaction with the proportion of broadleaves was included in the final model. The other variables were either kept to their mean (previous cover, forest age and C:N ratio) or set to zero (proportion of spruce or broadleaved trees, respectively). This implies that the lines for zero spruce or broadleaves represent *Pinus*-dominated forest (mainly *Pinus sylvestris*), and that the lines for 50% *P. abies* or broadleaves are mixtures of *Pinus* sp. and *P. abies* or *Pinus* sp. and broadleaves, respectively. Note that the scale of the *y*-axes differs between the species. The full range of the *Y*-axes and raw data points can be seen in Appendix S20.

ratio, total basal area, and basal area percentages of *P. abies* and broadleaved trees (Appendix S8). Additionally, it included interactions between basal area and percentage of *P. abies* and between basal area and percentage of broadleaved trees. The binomial part included the previous cover of *V. vitis-idaea*, C:N ratio, total basal area and percentages of *P. abies* and broadleaves. The model predicted a decreasing probability of zero cover with increasing values of C:N ratio and previous cover of *V. vitis-idaea*, while the probability increased with total basal area, and percentages of broadleaves and *P. abies* (Appendix S8). The predicted cover increased with increasing C:N ratio initially, and then leveled off at intermediate C:N values whereafter no change in cover was predicted (Figure 1d). In contrast, cover increased with age continuously in a linear fashion (Figure 1c). As for *V. myrtillus*, the effect of basal area on the cover of *V. vitis-idaea* was dependent on tree species composition (Figure 2 c-d). The trends along the basal area gradient resembled those of *V. myrtillus* with the differences that the cover peaked at lower basal areas in the case of unimodality, and that the effect of basal area was stronger than for *V. myrtillus* at high percentages of broadleaves (Figure 2d) or *P. abies* (Figure 2c). None of the combinations of climatic variables, or climate combined with N deposition, explained more than 1% of the residual variation in *V. vitis-idaea* cover, why these variables were not included in the model structure.

3.3 | *Calluna vulgaris*

The R^2 of the final model for *C. vulgaris* cover was 0.44. The continuous part of the model included the previous cover of *C. vulgaris* and percentage of *P. abies*, and the nonlinear effects of the variables age, C:N ratio and the total basal area (Appendix S12). Additionally, it included the interaction between basal area and percentage of *P. abies*, while, in contrast to *V. myrtillus* and *V. vitis-idaea*, it did not include the interaction between basal area and broadleaved percentage. The binomial part included age, the previous cover of *C. vulgaris*, C:N ratio, total basal area and percentages of *P. abies* and broadleaves. The model predicted a decreasing probability of zero cover with increasing values of age, C:N ratio and previous cover of *C. vulgaris*, while the probability increased with total basal area, and percentages of broadleaves and *P. abies* (Appendix S12). The predicted cover increased continuously with increasing age (Figure 1c) and C:N ratio (Figure 1d) in a close-to-linear fashion. The effect of the total basal area on cover of *C. vulgaris* was dependent on the percentage of *P. abies* (Figure 2e), but not on the percentage of broadleaves (Figure 2f). Independently of *P. abies* dominance, the effect of basal area was negative with a trend resembling a negative exponential. This negative effect was however stronger at high than at low percentage of *P. abies* (Figure 2e). None of the combinations of climatic variables, or climate combined with N deposition, explained more than 1% of the residual variation in *C. vulgaris* cover, why these variables were not included in the model structure.

4 | Discussion

In this study we produced parametric models with the purpose of estimating cover of three ericaceous plant species (*C. vulgaris*, *V. myrtillus* and *V. vitis-idaea*) through information on forest structure, soil fertility, and initial cover of the specific species. These species together constitute a substantial part of the forest floor vegetation in northern Europe (Esseen et al. 1997). In Sweden, for example, they covered 25% of the productive forest area around the year 2000, (*C. vulgaris* 2%, *V. myrtillus* 14%, *V. vitis-idaea* 9%, SLU 2011). Despite this, these three foundation species have, to our knowledge, not previously been considered in a common framework of prediction models. Our models will allow for making projections of the future impact of different management strategies on the individual species and to identify potential tradeoffs between these strategies.

Our fixed effects explained 44%, 49% and 60% of the variation in plant cover for *C. vulgaris*, *V. vitis-idaea* and *V. myrtillus*, respectively. This is considerably more than in previous studies on the two *Vaccinium* species, while no directly comparable studies exist for *Calluna*. The model of Eldegard et al. (2019) for *V. myrtillus* explained 21% of the variation while Hedwall et al. (2013) could explain 31% and 45% of the variation in *V. myrtillus* and *V. vitis-idaea* cover, respectively. Similarly, Turtiainen et al. (2013) explained 43% for *V. vitis-idaea*. The closest to our results in explained variance is the model by Miina et al. (2009), which explained 54% of the variation in *V. myrtillus* cover. In contrast to the other studies, the model from Miina et al. (2009) included variables describing previous land use and management, factors well known to affect vegetation development (Hermy and Verheyen 2007), which may be one reason behind the high explanatory power of this model. These kinds of legacy effects are, together with considerable time-lags in the response to the environment, common drivers of forest vegetation (Flinn and Vellend 2005). However, information on previous land-use and disturbances, among other potential explanatory variables, is often lacking, which may compromise the predictions of models intended for DSSs. Hence, instead of variables directly modeling the effects of land use and management, we included the cover of the same species at previous inventories as an indicator of these effects. The rationale behind the inclusion of this variable was the assumption that the abundance of relatively slow-growing plant species, such as ours, seldom will be in equilibrium with their environment. This is probably true for most forest ecosystems where succession is constant, but maybe especially so for managed forests that are regularly disturbed by harvesting activities. The lag-effect on the cover of our focal plants is verified by the large difference in R^2 between our models with and without the previous plant cover. It is important to point out that when implemented in a forest DSS our models do not require data on plant cover from a time point prior to the starting point for estimations (year zero). This data is just required from a time point that is earlier (i.e., 10 years) than the time point for which the forest DSS should estimate, and all starting data including trees, soil, and ground vegetation can thus be collected at the same time. Later the DSS will use the estimated cover from an earlier time point as the previous cover, for example by taking the estimated value from year 40 when predicting the cover at year 50. The inclusion of the previous cover is also a potential reason behind the insignificant effects of climate and nitrogen deposition, drivers that otherwise have been shown important for the abundance of the three species (Bobbink et al. 2010; Hedwall and Brunet 2016;

Eldegard et al. 2019; Hedwall, Gustafsson, et al. 2019, 2021). As such, the effects of climate and nitrogen deposition are likely already accounted for in the previous cover of the plants. The vegetation survey of the Swedish NFI returns to a specific plot in ten-year intervals, which limited our possibilities to test if this time-point for estimating the previous cover is optimal. Hence, it is an important task for future research to fine-tune this variable, and as data accumulates, test how the dependency of the understory vegetation changes time over longer time-series.

Forest density measured as basal area is, together with tree species composition, a good indicator of canopy cover (Korhonen et al. 2007) and thus light availability on the forest floor in boreal forest. We expected the three shrub species to respond to gradients of light availability and soil nutrient availability (C:N ratio) depending on their position in the leaf economics spectrum. Accordingly, the relative effects of the tree layer on the cover of these species (i.e., relative difference between minimum and maximum predicted cover at any basal area and tree species composition (Figure 2)), were strongest for *Calluna*, intermediate for *V. vitis-idaea*, and weakest for *V. myrtillus*. Our results also stress the importance of tree species composition. Although increasing forest density to some extent can be positive for the cover of both *Vaccinium* species in forest dominated by pine or broadleaved tree species (Hedwall et al. 2013; Eldegard et al. 2019), and so also in our study, this was not the case in forests dominated by *P. abies*. This pattern contradicts the one found by Eldegard et al. (2019) who showed an initial positive response also in forest dominated by *P. abies*. A possible explanation for this difference is that, while we allowed basal area and tree species to interact in a curvilinear fashion (i.e., allowed for all possible two-way interactions between the first to third degree polynomials), Eldegard et al. (2019) did not, which constrains the response shape. In contrast to the *Vaccinium* species, the model for the cover of *Calluna* did not include the percentage of broadleaf trees, and this species responded negatively to increasing forest density independently of tree species composition. This is likely an effect of *Calluna* being more light-demanding than the *Vaccinium* species. However, neither for *Calluna* nor for the *Vaccinium* species, can we rule out other mechanisms related to the tree layer than amensalism for light, such as below-ground competition (Balandier et al. 2022).

Similarly to overstory density and composition, the three species showed distinct trends along the C:N ratio gradient. While *V. myrtillus* displayed a unimodal pattern with maximum cover at intermediate C:N ratios, neither *V. vitis-idaea* nor *Calluna* declined at high C:N ratios. Instead *V. vitis-idaea* leveled off and *Calluna* continued to increase in an exponential fashion indicating their adaptation to low nutrient availability. These differences are consistent with our expectations, based on the leaf economics spectrum, that *V. myrtillus* is the most nutrient demanding among the species, followed by *V. vitis-idaea*, and then *Calluna*. Previous studies have used different site quality indicators (site index or site quality classes) to account for differences in site fertility/productivity (Miina et al. 2009; Hedwall et al. 2013; Turtiainen et al. 2013, 2016; Eldegard et al. 2019). The Swedish NFI estimates site index through several site characteristics, including the cover of our three shrub species and modeling the cover based on this site index would thus produce models with potentially biased predictions. Instead we chose to use data on the C:N ratio from the soil inventory done on the NFI plots. Boreal forest ecosystems are generally nitrogen-limited (Högberg et al. 2017) and the C:N ratio is a good indicator of nitrogen availability (Van Sundert et al. 2020) and plant species composition (Hedwall, Brunet and Diekmann et al. 2019), providing us with an unbiased estimate of site fertility and models that allow us to predict the outcome of differences in site fertility.

The forest age used as a predictor in our models can in most cases be seen as time since the establishment of the present stand, with planting or natural regeneration, most often after clear-cutting of the previous stand. This is the result of the prevailing management regime in Swedish forests, but does not exclude that the trees in a minority of plots could have been established after fire or other natural disturbance, or as a result of alternative management regimes. All three species will suffer from physical damage (i.e., biomass removal) and drought/light stress in connection to timber harvest, fire or other stand-replacing disturbances. As mentioned above there are however considerable differences in stress tolerance between the species. While all three species increased with forest age, the response strength and pattern differed. The largest relative effect of the age gradient was found for *V. myrtillus* with a steep increase in cover during the first 50–70 years. Multiple studies have documented the sensitivity of this species to severe canopy disturbances and shown negative effects of clear-cutting on its cover (e.g., Atlegrim and Sjöberg 1996), most likely due to a combination of light and drought stress. However, despite this initial negative effect, *V. myrtillus* shows higher growth and reproduction during early successional stages (Nielsen et al. 2007) which likely explains the fast recovery from disturbance. In contrast, the effect of age on *V. vitis-idaea* was smaller than on *V. myrtillus*. The effects of clear-cutting on the first-mentioned species is usually smaller than for the latter (Kardell 1979), and probably related to differences in life-history traits. The leaves of *V. vitis-idaea* are, in comparison to *V. myrtillus*, thicker and waxy with inrolled margins (Ritchie 1955, 1956) and providing a better protection from drought stress due to lower air humidity and sun exposure after tree canopy removal. Like *V. myrtillus*, *Calluna* showed a relatively large effect of age, but with a slow and continuous recovery from disturbance. The slow recovery of *Calluna* can possibly be a result of its regenerative strategy. While the *Vaccinium* species regrow vegetatively from rhizomes (Ritchie 1955, 1956), *Calluna* is more dependent on its seedbank (Gimingham 1960), which may be abundant but can result in a slower and less certain recovery process. It is, however, important to point out that we cannot determine from our results if the interspecific differences in the patterns along the age gradient are due to differences in their sensitivity to disturbance, in their potential to recover from disturbances, or both. Due to insufficient data we cannot conclude if the increase of *Calluna* and *V. vitis-idaea* would continue beyond a forest age of 180 years. Although most managed forests are well below this limit, a large share of forest in nature reserves and other protected areas is older. Unfortunately, our abilities to predict the development of plant cover in these older forests and their contribution on the landscape level, is limited, which points at an important future research direction. Likewise, future research may also try to include forest environments with more varying C:N ratios and larger basal area values than what our models were able to include, although such forests probably are very rare.

In conclusion, our models imply a step towards a better understanding of the dynamics that drive the cover of *C. vulgaris*, *V. myrtillus* and *V. vitis-idaea*, and towards improved models for evaluation of the impact of different forest management strategies. Forest management directly governs important drivers of the cover of these species by the regeneration methods, choice of tree species, thinning regimes, and rotation periods applied. We can for example infer from our models that selecting for *P. sylvestris* rather than *P. abies*, and increasing rotation periods from today's 45–90 years in for example southern Sweden (Felton et al. 2020b), would benefit all three species. However, as forest landscapes are composed of multiple stands varying in for instance, tree species and age, the impacts of changes in management need to be evaluated by comparing the long-term effects of different management alternatives in a DSS. These models are first of all intended for the Swedish forest DSS Heureka (Lämås et al. 2023) but can also be applied as stand-alone functions or in other similar systems given that the required in-data exist, can be modeled or can be simulated. Besides estimations of cover, these models also open up for the projection of other, functionally more relevant outcomes than cover, such as the biomass, biomass growth as well as ungulate forage availability and quality, by applying already existing functions that predict these from information on the plant cover and forest structure (Juvany et al. 2023; Juvany Canovas 2023). As such, our models open up for analysis aiming for better understanding of the impact of different forest management scenarios on forest ecosystem functions, processes, and services, and constitute a step towards improved multifunctionality of managed forests.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data is available in the Supporting Information of this paper.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.