



Effects of forest structure, soil, and macroclimate on specific leaf area of foundational *Vaccinium* plants

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Abstract

Bilberry (*Vaccinium myrtillus*) and cowberry (*V. vitis-idaea*) are foundational species in Northern Europe. Specific leaf area (SLA) is a key trait because it specifies the relative thickness of the leaves, indicating both the plant's response to environmental conditions and its effects on the environment. Identifying factors influencing SLA is therefore essential for understanding how these plants respond to environmental perturbations like climate change and forest management, as well as feedback effects on the plant's environment. Here, we test how the SLA of these two plant species responds to overstory density and tree species composition across an extensive climatic gradient. We focused on two forest types in Sweden: dominated by an overstory of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*); hereon spruce-pine, and an overstory of Norway spruce and birch (*Betula* sp.); hereon spruce-birch. Our results show that the SLA of both bilberry and cowberry increases (thinner leaves) significantly with higher forest density, whereas it declines with a greater proportion of pine or birch. Increasing soil moisture had a negative effect on SLA of both species in the spruce-birch context, whereas soil fertility never was a significant determinant. Additionally, we observed that the species-specific response in SLA was related to macroclimate and leaf age, with lower SLA in colder climate and older leaves. These findings highlight the importance of considering the effects of forest structure and composition on the SLA in forest management, as shifts in SLA may have implications for ecosystem functioning under present and future climates.

Keywords Dwarf shrub · Ericaceae · Forest floor vegetation · Functional ecology · Latitudinal gradient · Trait-environment relationships

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Introduction

Understory plants play a significant role in maintaining forest structure and ecosystem functioning. Numerous studies have demonstrated the role of these plants in regulating soil temperature, increasing soil organic carbon and moisture (Zhang et al. 2022), maintaining the diversity of soil bacterial communities (Xiao et al. 2022; Duan et al. 2023), and providing food and habitat for animals (Dagan and Izhaki 2019; Deng et al. 2023). Among understory plants, certain species function as foundational species because of their disproportionately strong influence on ecosystem processes, community composition, and biodiversity (Ellison 2019). Through their stabilizing and facilitative roles, they help sustain biodiversity and regulate ecosystem dynamics across multiple scales (Ellison and Degrassi 2017; Borst et al. 2018; Ellison 2019; Forzieri et al. 2020; O'Brien et al. 2020; Lortie et al. 2022). Despite their ecological significance, foundation species are often overlooked in conservation planning until their decline begins to compromise the interactions and ecosystem services they support (Ellison and Degrassi 2017; Borst et al. 2018). The loss of such species can trigger cascading effects across trophic levels and lead to the simplification of ecological networks, as species dependent on them, and on their mutualists, face a heightened extinction risk (Losapio and Schöb 2017; Ellison 2019).

Two foundational species in Northern European forests are bilberry (*Vaccinium myrtillus* L.) and cowberry (*Vaccinium vitis-idaea* L.) (Sjörs 1999; Nilsson and Wardle 2005). Both species often dominate the understory layer, where they provide critical ecological functions such as habitat for invertebrates, supply edible fruit to many taxa, forage for wild ungulates, affect tree seedling regeneration and contribute to carbon sequestration (Nilsson and Wardle 2005; Felton et al. 2020; Spitzer et al. 2021, 2025; Wozniwoda et al. 2021). The occurrence and abundance of bilberry and cowberry is closely linked to the structure of the forest overstory and other environmental drivers (Hedwall et al. 2013, 2025; Eldegard et al. 2019). Consequently, the cover of these dwarf shrubs has decreased in Sweden due to, among other factors, increasing forest density resulting from changing land-use and forest management practices, such as the promotion of even-aged and dense Norway spruce (*Picea abies* (L.) H.Karst., hereafter spruce) stands (Hedwall et al. 2013, 2019a, b, 2021; Hedwall and Brunet 2016). The extent to which these changes to dwarf shrubs affect ecosystem functions and services remains largely unknown. Moreover, research on how forest density and tree species composition influence bilberry and cowberry properties beyond cover, such as plant functional traits, has only recently begun to

emerge, offering new insights into potential functional effects (Juvany et al. 2023; Juvany 2023; Felton et al. 2026).

Understory plants adapt to changes in environmental conditions by morphological, physiological, or phenological adaptations (Funk et al. 2017; Blondeel et al. 2020; Kemppinen and Niittynen 2022). For example, plants may adjust their specific leaf area (SLA; Cornelissen et al. 2003) in response to environmental conditions such as light, nutrient availability, and moisture levels. SLA is the quotient of leaf area to leaf dry mass and can be measured in units of square mm per mg (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). In environments with low light availability, and/or high accessibility of soil resources, plants generally have higher SLA (indicating thinner, less dense leaves), which support higher growth rates through more efficient light capture. In contrast, stress-tolerant species in high light/poor soil environments often have a lower SLA (indicating thicker leaves), which confers durability and reduced water loss (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). Additionally, the intra-specific plasticity of SLA enables plant species to adapt to disturbances and changing climates (Schlickmann et al. 2020) with potential effects on ecosystem processes. Plant species and individuals with high SLA exhibit greater photosynthetic capacity, faster litter decomposition, and enhanced nutrient cycling, but are often associated with lower carbon storage due to higher carbon and nutrient turnover rates (Garnier et al. 2004; Mokany et al. 2008; Bu et al. 2019). Hence, SLA is positively linked to biomass production but negatively correlated with soil carbon and the ratio of soil carbon to nitrogen (C: N; Garnier et al. 2004; Ordoñez et al. 2009; Shome et al. 2023). Additionally, leaves with higher SLA are more palatable, therefore influencing herbivory and trophic interactions (Funk et al. 2017). As such, SLA serves as a key trait for assessing understory plant-environment interactions, adaptation strategies, and the ecosystem-level impacts of environmental change.

In this study we aimed to increase the understanding of the drivers of SLA in bilberry and cowberry. First, we examined how forest overstory structure and tree species composition influence SLA, focusing on the role of the overstory as a key determinant of light availability and resource competition in understory vegetation. To do so, we sampled both *Vaccinium* species along a broad latitudinal gradient in Sweden and across two dominant overstory types: spruce-pine (Scots pine (*Pinus sylvestris* L.) and spruce-birch (*Betula* spp.) mixed forest stands. Second, we assessed the effects of soil C: N and moisture on SLA, and evaluated whether these effects interact with overstory characteristics to shape trait expression. Finally, we investigated how macroclimate influences SLA by sampling along an extensive climatic gradient and determined whether this relationship is modified

by local overstory and soil conditions. Collectively, these efforts enabled us to start disentangling the relative and interactive effects of biotic and abiotic factors on SLA, thereby advancing our understanding of plant adaptation strategies and ecosystem functioning in boreal forest ecosystems. Specifically, we expected SLA to increase with increasing forest density and an increasing proportion of spruce, which casts relatively more shade than, for example, pine or birch (Hedwall et al. 2025). Furthermore, we expected decreasing nutrient availability to have negative effects on SLA, as plants develop more nutrient-conservative strategies under nutrient limitation (Wright et al. 2004; Ordoñez et al. 2009). We also expected *Vaccinium* species in the environmentally harsher northern regions to express more conservative resource-use strategies due to the shorter growing season and colder climate (Frenne et al. 2013), as reflected in lower SLA (Chelli et al. 2019; Cubino et al. 2021).

Methods

Study area and design

Sweden extends from 55.3° N to 69.1° N, covering areas of boreal and hemi-boreal biomes with a forest area of 280,000

km² (Ahti et al. 1968; Sjörs 1999). The growing season varies from 100 days in northern Sweden to 200 days in Southern Sweden (Sjörs 1999). To increase the generalizability of our findings across different forest types and climatic conditions, we designed two surveys along Sweden's latitudinal gradient, covering both the boreal and hemi-boreal zones. The first survey was conducted at three sites distributed along a latitudinal gradient from 57° N to 64° N, hereafter referred to as the spruce-pine survey (Fig. 1). At the southern, and central (hereafter mid) site, 16 forest stands were selected at each site, while 15 stands were chosen at the northern site. Forest stand selection was based on available metadata from the respective Swedish University of Agricultural Sciences (SLU) field stations at each of the sites, incorporating criteria such as tree species composition, stand age, and site fertility. Stands were classified into four age categories: early (6–15 years), young (16–48 years), middle-aged (49–75 years), and old (> 76 years). The stands had mixed species overstories with pine or spruce in varying degrees of dominance (Table 1). Within each stand, three circular plots served as replicates. The plot radius was 5 m in young stands and 8 m in all other age categories. At the centre of each plot, a 4 m² square sub-plot was established, divided into sixteen 0.25 m² squares. From these, three squares were randomly selected for understory vegetation

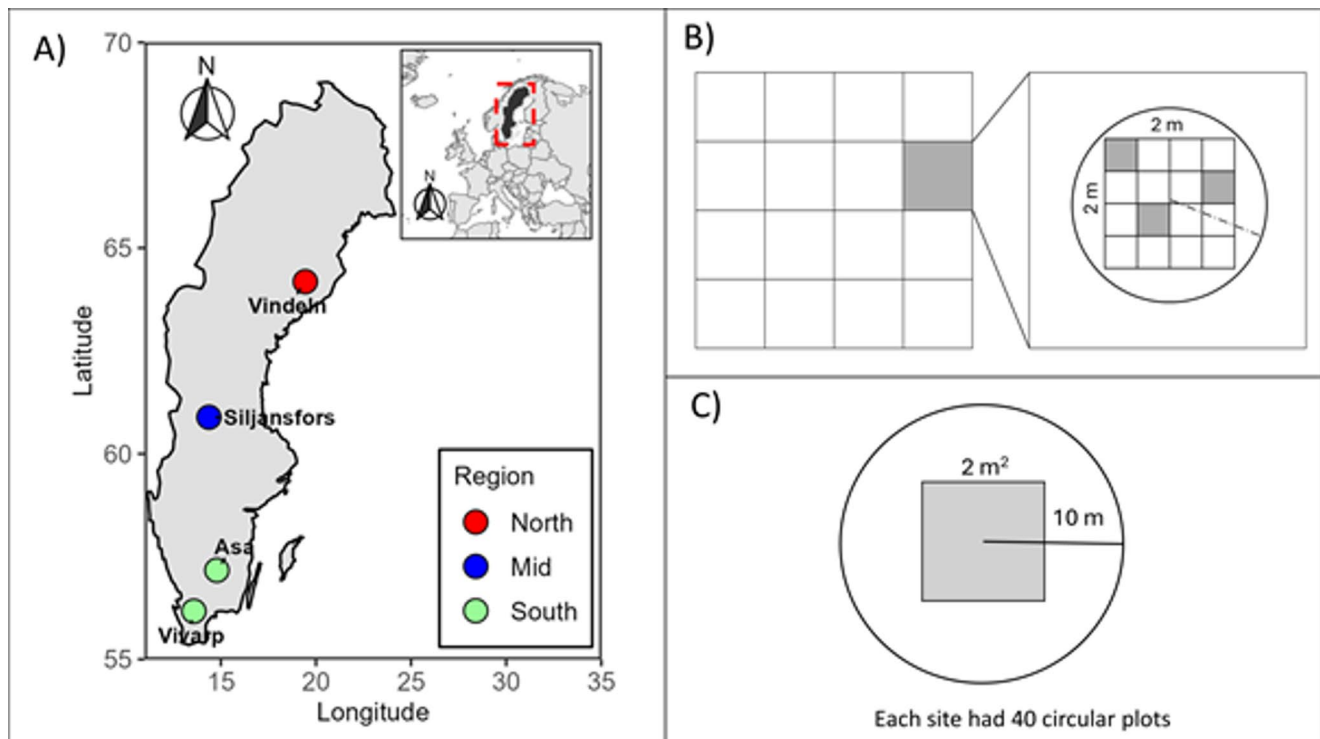


Fig. 1 Panel A shows study sites across Sweden along a latitudinal gradient representing the South, Mid, and North regions, and Sweden's location in northern Europe. The study sites Vindeln, Siljansfors, and Asa were used for the spruce-pine survey, whereas only the sites Vin-

deln and Vivarp were used for the spruce-birch survey. Panel B shows plot design for the spruce-pine survey. Panel C shows plot design for the spruce-birch survey

Table 1 Summary of SLA, overstory composition, and environmental variables by site (South, Mid, North) and species group (Bilberry, Cowberry new, Cowberry old) used in the spruce-pine survey. Values are presented as mean $\pm$ SD, with ranges in parentheses. SLA is measured in $\text{mm}^2 \text{mg}^{-1}$; plot basal area (Plot BA), pine basal area (Pine BA), spruce basal area (Spruce BA), and broadleaf basal area (Broadleaf BA) is measured in $\text{m}^2 \text{ha}^{-1}$. N and n denote the number of unique plots and stands, respectively. C:N and SM is the soil carbon-nitrogen ratio and soil moisture, respectively.

Site	Species group	n	N	SLA	Plot BA	Pine BA	Spruce BA	Broadleaves BA	C: N	SM
South	Bilberry	16	46	9.2 $\pm$ 5.51 (1.6–20.65)	27.18 $\pm$ 11.42 (6.88–55.81)	14.13 $\pm$ 12.22 (0–37.2)	12.49 $\pm$ 13.43 (0–45.26)	0.55 $\pm$ 0.97 (0–3.52)	29.97 $\pm$ 3.01 (24.35–36.4)	14.01 $\pm$ 4.29 (7.32–26.52)
	Cowberry (new leaves)	13	28	3.41 $\pm$ 2.09 (0.73–7.87)	23.64 $\pm$ 11.15 (4.6–44.36)	17.74 $\pm$ 12.48 (0–37.2)	5.41 $\pm$ 8.16 (0–29.11)	0.49 $\pm$ 0.86 (0–3.52)	30.39 $\pm$ 2.86 (24.35–36.4)	14.71 $\pm$ 4.65 (7.32–26.52)
	Cowberry (old leaves)	13	28	3.42 $\pm$ 2.17 (1.02–8.16)	23.64 $\pm$ 11.15 (4.6–44.36)	17.74 $\pm$ 12.48 (0–37.2)	5.41 $\pm$ 8.16 (0–29.11)	0.49 $\pm$ 0.86 (0–3.52)	30.39 $\pm$ 2.86 (24.35–36.4)	14.71 $\pm$ 4.65 (7.32–26.52)
Mid	Bilberry	16	47	6.93 $\pm$ 5.35 (1.01–23.32)	22.7 $\pm$ 14.97 (0.21–47.25)	10.41 $\pm$ 12.37 (0–39.04)	11.65 $\pm$ 16.24 (0–43.06)	0.64 $\pm$ 1.83 (0–10.69)	33.81 $\pm$ 7.91 (18.57–47.15)	12.93 $\pm$ 7.06 (3.02–31.23)
	Cowberry (new leaves)	16	40	3.81 $\pm$ 3.42 (0.96–14.41)	21.49 $\pm$ 15.06 (0.21–47.25)	11.03 $\pm$ 12.59 (0–39.04)	9.87 $\pm$ 15.8 (0–43.06)	0.59 $\pm$ 1.84 (0–10.69)	34.6 $\pm$ 7.16 (18.8–47.15)	12.81 $\pm$ 7.27 (3.02–31.23)
	Cowberry (old leaves)	16	40	3.19 $\pm$ 2.24 (1.00–9.11)	21.49 $\pm$ 15.06 (0.21–47.25)	11.03 $\pm$ 12.59 (0–39.04)	9.87 $\pm$ 15.8 (0–43.06)	0.59 $\pm$ 1.84 (0–10.69)	34.6 $\pm$ 7.16 (18.8–47.15)	12.81 $\pm$ 7.27 (3.02–31.23)
North	Bilberry	15	42	7.04 $\pm$ 5.18 (1.86–21.84)	22.44 $\pm$ 18.01 (0.08–67.25)	10.63 $\pm$ 10.67 (0–31.66)	10.94 $\pm$ 14.45 (0–47.36)	0.88 $\pm$ 1.55 (0–6.52)	32.64 $\pm$ 5.38 (20.95–46.26)	10.03 $\pm$ 3.29 (3.3–18.12)
	Cowberry (new leaves)	15	45	3.46 $\pm$ 2.45 (0.89–11.05)	22.7 $\pm$ 17.43 (0.08–67.25)	11.68 $\pm$ 11.06 (0–31.66)	10.21 $\pm$ 14.22 (0–47.36)	0.82 $\pm$ 1.51 (0–6.52)	33.02 $\pm$ 5.43 (20.95–46.26)	9.98 $\pm$ 3.19 (3.3–18.12)
	Cowberry (old leaves)	15	45	2.86 $\pm$ 1.57 (0.91–7.91)	22.7 $\pm$ 17.43 (0.08–67.25)	11.68 $\pm$ 11.06 (0–31.66)	10.21 $\pm$ 14.22 (0–47.36)	0.82 $\pm$ 1.51 (0–6.52)	33.02 $\pm$ 5.43 (20.95–46.26)	9.98 $\pm$ 3.19 (3.3–18.12)

sampling. All understory measurements and biomass collections were carried out within these sub-plots. Samples were collected in August and early September 2020 starting from the northernmost sites.

The second survey design included forest area from two sites (located at the northernmost and southernmost ends of the latitudinal/climatic gradient), hereafter referred to as the spruce-birch survey (Fig. 1). These sites were dominated by spruce and birch, with large variation in the proportions of the two species (Table 2). Additional broadleaf species (e.g. *Alnus* sp., *Quercus* sp. and *Salix* sp.) occurred, but only in small amounts. At each site, 40 circular plots with a 10 m radius were established. These plots were distributed along a double gradient of forest density (from open to closed canopy) and species composition (from pure spruce to pure birch) to capture maximum variability in structural and compositional conditions. A 2 m² sub-plot was placed at the centre of each plot, from which understory plant biomass was harvested. Samples were collected in July 2020.

Data collection

Collection of understory data

Given the clonal growth forms and rhizomatous structures of our *Vaccinium* species (Ritchie 1955, 1956; Tolvanen 1995), we selected discrete above-ground plant units (hereafter referred to as ramets) that were free from visible damage. In the spruce-pine survey, three ramets per species were randomly sampled within each sub-plot, with a total of 9 ramets per plot and species. In the spruce-birch survey, six ramets per species were collected from each plot. For each ramet, all shoots were subsequently detached and air-dried for further analysis. Cowberry is an evergreen species, while bilberry is deciduous, shedding its leaves annually (Ritchie 1955, 1956). Therefore, in cowberry, leaf samples

were further classified into “old” (previous years' leaves) and “new” (leaves grown in the year of the inventory) based on shoot age, and morphological distinctions in stem and leaf coloration. Bilberry, being deciduous, only produces a single cohort of leaves each year; hence, only newly developed leaves were collected.

Leaf sampling was conducted systematically to ensure representative coverage of leaf size variability within each ramet. For bilberry, 50 leaves were randomly selected per sample. For cowberry, 25 leaves were collected from each growth category (old and new) per sample. In cases where fewer leaves were available, all accessible leaves were sampled. Since not all plots contained both *Vaccinium* species, the sample size varied between sites (Table S1; Table S2).

Overstory measurements

In each plot, all living trees taller than 1.3 m were identified to species, and their diameter at breast height (DBH) was measured. These data were used to calculate the total basal area (BA; m² ha⁻¹) per plot, serving as a proxy for forest density. Additionally, the contribution of individual tree species to plot-level basal area was quantified to derive the percentage of basal area composed of broadleaved species (% broadleaves; used in the spruce-birch survey) and pine (% pine; used in the spruce-pine survey).

Collection of soil data

Soil samples were systematically collected across both the spruce-pine and spruce-birch surveys. A soil corer was used to collect soil samples to a depth of 10 cm, with 4 cores per plot, that included both humus and mineral soil. From each circular plot, four soil samples were extracted from locations just outside the designated sub-plots used for sampling of *Vaccinium* ramets. Before sampling, surface litter was

Table 2 Summary of SLA, overstory composition, and environmental variables by site (South, North) and species group (Bilberry, Cowberry new, Cowberry old) used in the spruce-birch survey. Values are presented as mean ± SD, with ranges in parentheses. SLA is measured in mm² mg⁻¹; plot basal area (Plot BA) is measured in m² ha⁻¹. N denotes the number of plots in each site. C:N and SM is the soil carbon-nitrogen ratio and soil moisture, respectively.

Site	Species group	N	SLA	Plot BA	Pine BA	Spruce BA	Broadleaves BA	C: N	SM
South	Bilberry	31	8.23 ± 3.26 (2.61–17.39)	19.44 ± 5.15 (11.11–33.39)	0.0 0 ± 0.00 (0.00–0.00)	11.91 ± 6.20 (0.22–26.87)	7.53 ± 4.51 (0.66–22.98)	22.42 ± 1.86 (17.69–27.34)	30.32 ± 13.25 (6.12–57.3)
	Cowberry (new leaves)	22	4.07 ± 1.11 (2.74–6.73)	18.67 ± 4.83 (11.11–27.85)	0.0 0 ± 0.00 (0.00–0.00)	11.69 ± 6.47 (0.22–26.87)	6.98 ± 3.22 (0.66–11.33)	22.45 ± 1.93 (17.69–27.34)	34.34 ± 11.58 (12.18–57.3)
	Cowberry (old leaves)	21	5.84 ± 1.82 (2.05–9.44)	19.01 ± 4.68 (11.11–27.85)	0.0 0 ± 0.00 (0.00–0.00)	11.93 ± 6.54 (0.22–26.87)	7.08 ± 3.27 (0.66–11.33)	22.4 ± 1.97 (17.69–27.34)	35.16 ± 11.19 (12.18–57.3)
	Bilberry	40	12.61 ± 6.49 (4.08–30.62)	26.75 ± 8.26 (10.63–41.42)	2.72 ± 1.62 (1.22–6.82)	15.55 ± 7.54 (0.42–28.72)	12.89 ± 6.73 (1.90–24.78)	28.32 ± 3.24 (20.39–34.79)	24.85 ± 13.66 (7.1–58.23)
	Cowberry (new leaves)	40	6.12 ± 2.66 (2.1–14.68)	26.75 ± 8.26 (10.63–41.42)	2.72 ± 1.62 (1.22–6.82)	15.55 ± 7.54 (0.42–28.72)	12.89 ± 6.73 (1.90–24.78)	28.32 ± 3.24 (20.39–34.79)	24.85 ± 13.66 (7.1–58.23)
	Cowberry (old leaves)	39	2.72 ± 1.11 (0.94–5.15)	26.96 ± 8.26 (10.63–41.42)	2.77 ± 1.67 (1.22–6.82)	15.75 ± 7.55 (0.42–28.72)	13.03 ± 6.79 (1.90–24.78)	28.34 ± 3.27 (20.39–34.79)	24.13 ± 13.05 (7.1–58.23)

carefully removed, and rocks or other physical impediments were avoided. Soil moisture (SM) was measured using a Theta Probe (Type ML1; Delta-T Devices, Cambridge, UK) during summer, in 4–5 places per plot, averaged within plot, and expressed as a percentage. The SM measurements were recorded concurrently with vegetation data during a single visit to each spruce-pine plot. For the spruce-birch survey sites, SM measurements were all taken on a single day, the timing of which was chosen to avoid measuring after either rainy or dry periods.

All soil samples collected within the same plot were pooled, oven-dried at 60 °C to remove moisture and homogenized before chemical analysis. The total carbon (C) and nitrogen (N) content were determined using an Avio 200 ICP spectrometer (PerkinElmer, Waltham, MA, USA), and the C: N ratio was subsequently calculated.

Data preparation and analysis

For each leaf sample, SLA (in mm²/mg) was determined following standard procedures (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). While the sequence of standard procedures suggests the use of fresh leaf material to get the leaf area before drying, we initially dried leaf samples before scanning leaves to get their area. This approach was necessitated by logistical constraints, as our sampling spanned numerous remote and distant sites over extended periods, making scanning of fresh leaves impractical. Drying allowed us to preserve the samples and maintain consistency across the leaf samples. Further, our objective was to evaluate relative differences in SLA across understory conditions rather than absolute values. Therefore, even if drying the leaves led to a slight underestimation of area (Queenborough and Porras 2014), it should not impact the overall trends or the interpretation of the results in this study.

Leaf samples were oven-dried at 60 °C until reaching a constant weight to determine dry mass. After drying, samples were scanned using a flatbed scanner, and digital images were processed in R version 4.1.3 (R Core Team, 2021) using the *LeafArea* package (version 0.1.8), which batch-processes images through the ImageJ software (Katabuchi 2015). SLA was then calculated using Eq. 1 as follows:

$$SLA = \frac{\text{One sided area of leaf (mm}^2\text{)}}{\text{Oven dry weight of the leaf (mg)}} \quad (1)$$

BA, C:N ratio, SM, percentage of pine (for the spruce-pine study), percentage of broadleaves (for the spruce-birch study), and site were used as explanatory variables, whereas SLA was the response variable in our analysis. Prior to statistical analyses, all explanatory variables were checked for multicollinearity visually using pairwise scatter plots and Pearson correlation coefficients (Table S9). The continuous explanatory variables were standardized by subtracting the mean and dividing by the standard deviation.

Separate models were fitted for each *Vaccinium* species, and for cowberry, models were also fitted separately by leaf age. Generalized linear mixed models (GLMMs) were used for the spruce-pine survey due to the hierarchical structure of our data (i.e., multiple plots present within a stand), and stand was used as a random intercept effect. We fitted two models: one full model with BA, %pine and Site, as well as their two- and three-way interactions and another model without the interaction terms. Both models included the soil variables (Table 3). Generalized linear models (GLMs) were fitted for the spruce-birch survey. The GLMs were used as site was the only level at which plots were clustered, and we aimed to test for differences between the two sites, and for differences in the effects of other variables between the sites (i.e. interactions with site). Here, we followed a similar approach as for the GLMMs where a full model included the interaction between BA and %broadleaves and another model without interaction terms, both including soil variables and site (Table 3). Due to the right skewness of the SLA values, we specified a Gamma distribution with a log-link function for both the GLMMs and GLMs. Model fit was evaluated based on residual diagnostic plots (using DHARMa residuals) (Hartig et al. 2024) and model selection was based on the lowest AIC-value. Variance inflation factor (VIF) was below 3 for the selected models (Table S10).

All the models were fitted using the *glmmTMB* function of the 'glmmTMB' package (Brooks et al. 2017). Finally, SLA was predicted for minimum, mean, and maximum values of

Table 3 Models fitted for both *Vaccinium* species and leaf fractions. Abbreviations: SLA=specific leaf area (mm² mg⁻¹); BA=basal area (m² ha⁻¹); % pine=proportion of pine; % broadleaves=proportion of broadleaves; Site=geographic site (South, Mid, North); C:N=carbon to nitrogen ratio; SM=soil moisture

Survey	Species	Leaf Type	First model structure	Second model structure
Spruce-pine	Bilberry	-	SLA~BA * % pine * Site+C: N+SM + (1 Stand)	SLA~BA + % pine + Site+C: N+SM + (1 Stand)
	Cowberry	New	SLA~BA * % pine * Site+C: N+SM + (1 Stand)	SLA~BA + % pine + Site+C: N+SM + (1 Stand)
	Cowberry	Old	SLA~BA * % pine * Site+C: N+SM + (1 Stand)	SLA~BA + % pine + Site+C: N+SM + (1 Stand)
Spruce-birch	Bilberry	-	SLA~BA * % broadleaves+C: N+SM+Site	SLA~BA + % broadleaves+C: N+SM+Site
	Cowberry	New	SLA~BA * % broadleaves+C: N+SM+Site	SLA~BA + % broadleaves+C: N+SM+Site
	Cowberry	Old	SLA~Site * BA+Site * % broadleaves+C: N+SM	SLA~BA + % broadleaves+C: N+SM+Site

%pine for the spruce-pine survey and of %broadleaves for the spruce-birch survey based on the selected model.

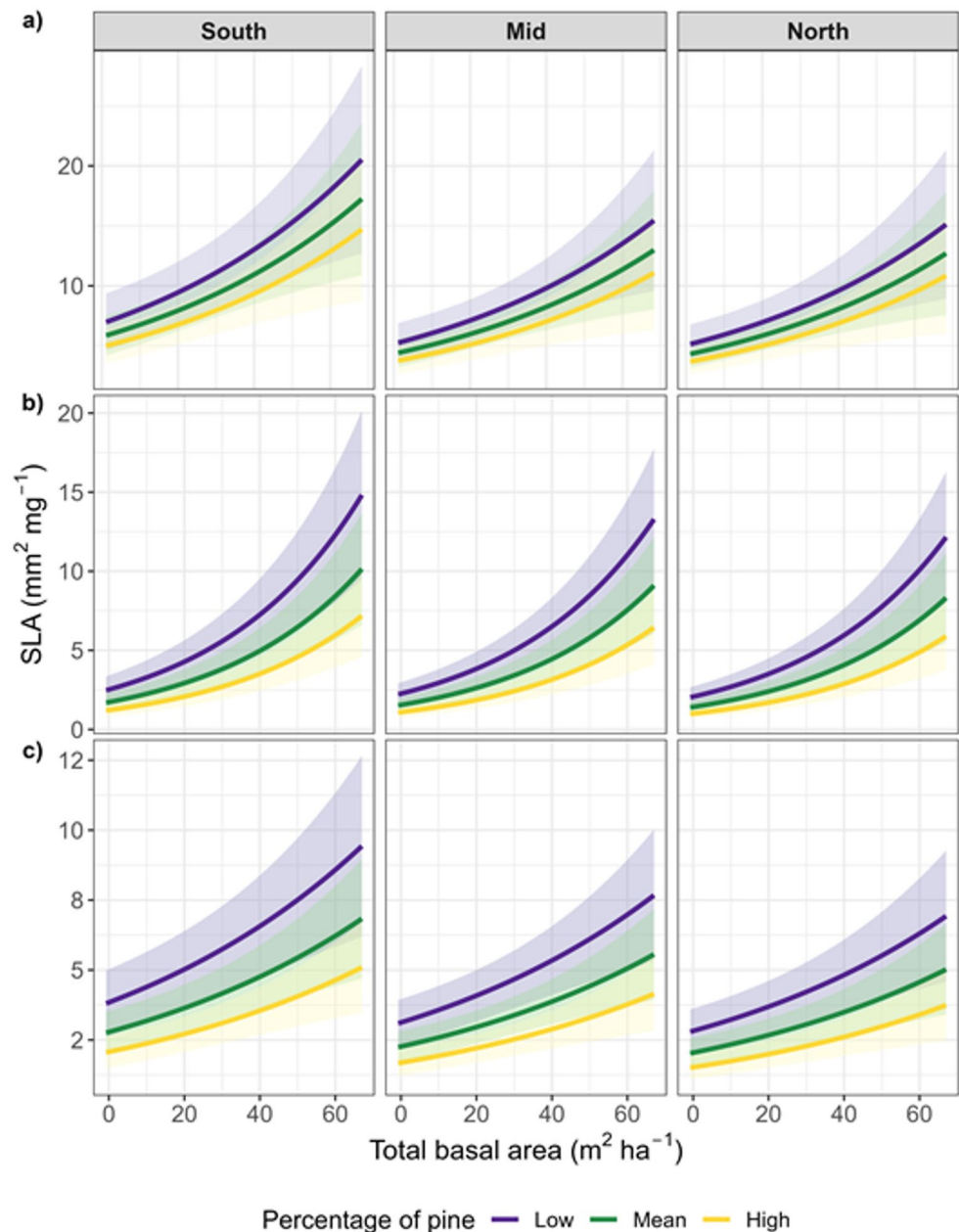
Results

Spruce-pine survey

For both *Vaccinium* species and all leaf fractions, SLA showed a consistent response to overstory structure and pine composition gradient. Specifically, the best model for bilberry ($\Delta AIC = -8.12$), showed a statistically significant effect of BA, the percentage of pine, and site (Table S3). The model explained 30.6% of the variance in SLA due to

fixed effects (marginal effect), and 42.6% when accounting also for random effects (conditional effect). SLA increased significantly with plot BA ($P < 0.001$) and declined with increasing pine proportion ($P = 0.019$) (Fig. 2a, Table S3). SLA was also significantly lower at the Mid ($P = 0.023$) and North ($P = 0.019$) sites relative to the South (Table S3). The best model for cowberry new leaves ($\Delta AIC = -2.02$) had the same structure as for bilberry and explained 66% of the variance in SLA due to fixed effects, and 72% when accounting for both fixed and random effects (Table S4). While SLA increased with BA ($P < 0.001$) and declined with increasing pine proportion ($P < 0.001$), significant site differences were only observed between South and North sites, with SLA being significantly lower at the North site

Fig. 2 Predicted specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$) in response to total basal area ($\text{m}^2 \text{ha}^{-1}$) across a latitudinal gradient (South, Mid, North) and varying levels of pine proportion. (a) bilberry, (b) new leaves of cowberry, (c) old leaves of cowberry in the spruce-pine survey. Solid lines are population-level predictions from Gamma-log GLMMs; ribbons are 95% confidence intervals for the predicted values (± 1.96 SE on the log scale, back-transformed). C: N and SM were held at their means



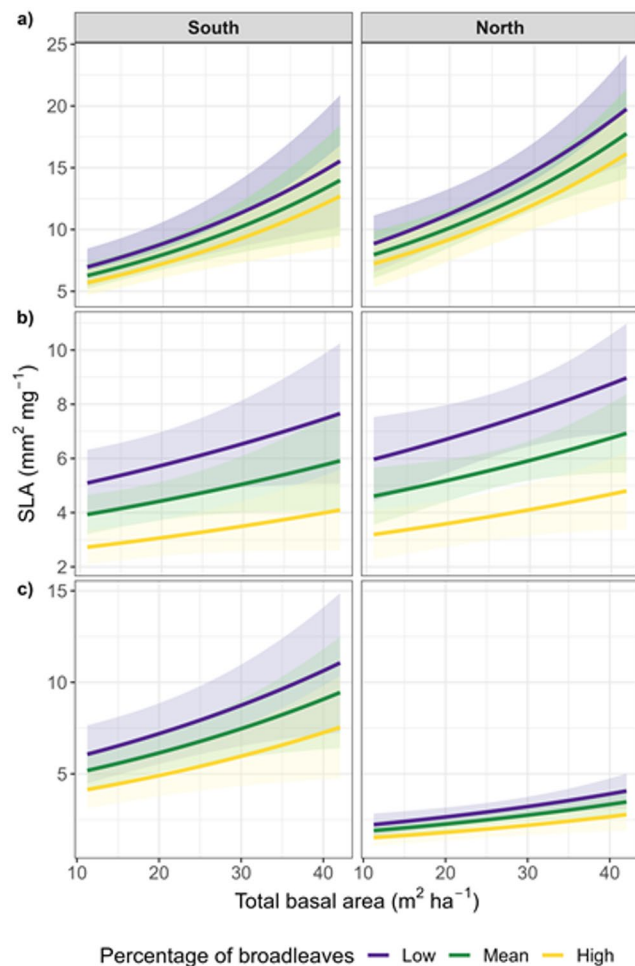


Fig. 3 Predicted specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$) in response to total basal area ($\text{m}^2 \text{ha}^{-1}$) across a latitudinal gradient (South, North) and varying levels of broadleaf in the spruce-birch survey. **(a)** Bilberry, **(b)** New leaves of cowberry, **(c)** Old leaves of cowberry. Solid lines are population-level predictions from Gamma-log GLMs; shaded ribbons are 95% confidence intervals for the predicted values (± 1.96 SE on the log scale, back-transformed). C:N and SM were held at their means. Note the lower values of predicted SLA in the northern site for old leaves of cowberry

($P=0.046$) (Fig. 2b, Table S4). For cowberry old leaves, the best model ($\Delta\text{AIC} = -3.15$) explained 41% of SLA variation. SLA increased with BA ($P<0.001$) and decreased with pine proportion ($P<0.001$, Fig. 2c, Table S5). SLA was significantly lower at the North site ($P=0.008$) than at the South (Table S5). The effect of SM was significant for new leaves of cowberry, where SLA significantly decreased with SM ($P=0.029$; Table S4).

Model predictions revealed consistent patterns across species and sites (Fig. 2). Both bilberry and cowberry had a clear increase in SLA with BA at all three levels (low, mean, and high) of pine percentage. This pattern was consistent across our latitudinal gradient, as interactions with BA, percentage of pine and site were never included in the

best models. Additionally, the predicted SLA values were consistently the highest for bilberry, followed by cowberry.

Spruce-birch survey

SLA in both *Vaccinium* species and all leaf fractions followed a consistent pattern to the spruce-birch compositional gradient. For bilberry, the best model ($\Delta\text{AIC} = -1.21$) included BA, percentage of broadleaved trees, soil C: N ratio, SM, and site (Table S6). SLA increased significantly with BA ($P<0.001$) and decreased with increasing proportion of broadleaved trees ($P<0.001$) (Fig. 3a, Table S6). Further, SLA declined significantly with increasing SM ($P<0.001$), while neither C:N ratio ($P=0.082$) nor site ($P=0.067$) were statistically significant (Table S6). The best model for cowberry new leaves had the same structure as for bilberry ($\Delta\text{AIC} = -1.93$). Moreover, similar results to the bilberry model were obtained, where SLA increased with BA ($P<0.001$) and decreased with increasing proportion of broadleaves ($P<0.001$), and SM ($P=0.027$) (Fig. 3b, Table S7). On the other hand, the effect of C:N ratio ($P=0.640$) and site ($P=0.217$) was non-significant (Table S7).

For cowberry old leaves, the best model ($\Delta\text{AIC} = -1.11$) followed a similar structure to that of bilberry and cowberry new leaves. SLA increased significantly with an increase in BA ($P=0.002$), decreased significantly with increasing proportion of broadleaves ($P=0.016$), and SM ($P=0.04$) (Fig. 3a, Table S8). The North site had significantly lower SLA than the South site ($P<0.001$) (Table S8).

Model predictions showed a similar pattern in SLA across sites (Fig. 3). For both bilberry and cowberry new leaves, SLA increased with BA at all levels of broadleaf composition. SLA was consistently highest at low percentages of broadleaved trees and declined progressively toward high broadleaf dominance, a trend that was more pronounced in cowberry than in bilberry. These patterns were consistent across the latitudinal gradient, with higher SLA values in the South relative to the North. Across all models, the predicted SLA values were again highest for bilberry, followed by cowberry new leaves, and lowest for cowberry old leaves, except for cowberry old leaves in the South site (Fig. 3c), indicating species-specific differences in SLA.

Discussion

Effect of overstory structure and composition

We found that overstory density and tree species composition were strong predictors of SLA for both bilberry and cowberry. The main reason for this association is likely the modulation of light availability on the forest floor by the

overstory structure (Greiser et al. 2018; Govaert et al. 2020; De Pauw et al. 2022), where understory plants increase their SLA under low light conditions. The finding that plants may exhibit large intra-specific variation in SLA is consistent with previous studies of bilberry and cowberry, as well as many other understory plant species (Chelli et al. 2019; Hedwall et al. 2019a; Paž-Dyderska et al. 2020; Sherstiuk et al. 2024). However, studies that quantify such effects for long continuous light gradients are rare. Interestingly, the proportion of pine or broadleaves decreased SLA of both bilberry and cowberry. This observation can be explained by the fact that light transmittance to the understory varies based on overstory tree species composition and that pine and many broadleaved tree species allow more light to enter the understory compared to spruce (Sercu et al. 2017; Hedwall et al. 2019b; Petersson et al. 2019). Additionally, more light can enter the understory of deciduous-dominated stands during winter (Durand et al. 2024), and thus understory plants may get a window in early spring to acquire light resources before leaf-out.

Besides altering light availability on the forest floor, higher density of the forest overstory (Barbier et al. 2008; Yang et al. 2022), and broadleaf dominance can affect SLA by enhancing soil nutrient availability through greater leaf litter input and soil organic matter turnover (Barbier et al. 2008; Sheffer et al. 2015; Pérez-alavez et al. 2023). However, the absence of a significant effect of C: N ratio in our study, which is a good indicator of nutrient availability, indicates that this is of minor importance.

Effect of soil moisture and nitrogen availability

The best model for the spruce-pine survey showed only a significant (negative) effect of SM for new leaves of cowberry (Table S7). Nevertheless, in the spruce-birch survey, SM negatively affected the SLA of both bilberry and cowberry (Table S6, Table S7, Table S8), which contrasts with previous research. For example, a study from the Arctic region indicates that SM is a significant positive predictor of SLA for bilberry, while such a relationship is not observed for cowberry (Kemppinen and Niittynen 2022). Conversely, research on boreal tree species, including *Alnus* and *Picea*, finds that SLA decreases with increasing SM (Anderson et al. 2020). Such contrasting observations may be due to unimodal relationships between moisture and SLA where the effect is largely dependent on the location along the SM gradient (Anderson et al. 2020). In addition, a potential reason for the inconsistency in SM effects on bilberry and cowberry in our different surveys could be the larger variation in weather conditions during the sampling period in the spruce-pine survey, which contrasts with the spruce-birch survey, in which soil measurements were aggregated

in time and under similar conditions. This larger variation in weather conditions is likely to have added noise to the signal of SM implications for SLA in the spruce-pine survey.

In contrast to SM, soil C: N ratio did not have a significant effect on SLA in our study. Although we are not aware of directly comparable studies, previous research on inter-specific variation in SLA from Canadian forests showed SM and the C: N ratio to be key drivers of interspecific SLA variation (Shovon et al. 2019). Likewise, Gong et al. (2019), analysed SLA data of 2,703 species across global biomes and found that the variation in SLA can be largely explained by soil pH and the soil C: N ratio. Ordoñez et al. (2009) used data from 474 species of various growth forms located in 99 sites and found that SLA increased with soil fertility (particularly soil nitrogen availability). However, our study was based on intraspecific SLA variation, resulting in apparently contrasting results. While interspecific patterns often capture broader ecological strategies (e.g., acquisitive vs. conservative), intraspecific plasticity is constrained by species' physiological limits and local environmental heterogeneity (Gong and Gao 2019). Our data included only relatively productive conifer stands, while it excluded both the most nutrient poor coniferous forests and richer often broadleaf-dominated stands; and thereby limited the environmental heterogeneity in the data. This may have constrained our ability to detect effects of soil conditions, while it facilitated our ability to discern overstory effects.

Effect of macroclimate on SLA

Lower SLAs in plants found close to the polar region are an adaptation to harsh conditions with lower temperatures, lower precipitation, and shorter growing seasons (Liu et al. 2016). This pattern aligns with a resource-conservative strategy whereby a plant's leaves maintain low SLA in northern sites where resources are limited, but it is also as a protection against direct climatic stress (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). Our results from the spruce-pine survey confirmed this pattern, while in the spruce-birch survey, a significant macroclimate effect was only detected in old leaves of cowberry. The old leaves of cowberry would have been exposed to the cumulative environmental stress from the previous cold season(s). In contrast, young leaves are primarily shaped by current environmental conditions, such as soil conditions, local light availability and stand structure, which may have been more similar among sites in the spruce-birch survey (Table 2); thereby weakening any detectable latitudinal effect. Another possible explanation for the diverging pattern between our studies, and the absence of a latitudinal effect in the spruce-birch survey, was that the leaves in this study were harvested earlier during the summer than in the spruce-pine survey. Hence, new

leaves may have still been in early developmental stages, reducing the extent to which macroclimatic differences could be expressed.

Changes in SLA along a latitudinal gradient may, besides being the direct outcome of variation in temperature and precipitation, could also be due to indirect climatic effects on soil properties (De Frenne et al. 2013; Gong and Gao 2019). However, because soil conditions were accounted for in our analysis, we infer that this effect was more likely to be driven directly by climatic variation and thus indicates a potential future shift in the leaf economic spectrum under climate change.

Implications for forest management

While previous studies show that changes in overstory density and tree species composition affect the abundance and leaf chemistry of *Vaccinium* species (Hedwall et al. 2013, 2025; Juvany et al. 2023; Felton et al. 2026), our findings reveal that structural changes in the overstory also affect SLA in both species. The importance of these findings is increased by both bilberry and cowberry being foundational plants, playing significant roles in various ecosystem processes, such as the carbon cycling, litter decomposition, and nutrient cycling (Liu et al. 2018; Shome et al. 2023), as well as the provisioning of food for other taxa (Funk et al. 2017; Spitzer et al. 2021). These forest ecosystem services are tightly linked to SLA, which mediates trade-offs between growth rate, tissue longevity, and resource-use efficiency (Shome et al. 2023). For this reason, changes in forest structure can ultimately modify ecosystem functioning via SLA-driven shifts in understory physiology. The outcome of most forest management activities is the regulation of disturbance regimes and the determination of tree species composition and stand density. We found that stand density and the mix of tree species consistently affected the SLA of both bilberry and cowberry. Forest management choices thus have a significant potential impact on understory SLA, and thus, the functional role of the understory vegetation. However, it is important to emphasize that the shift in SLA should not be interpreted as inherently beneficial or detrimental. High or low SLA leaves reflect distinct ecological strategies, and changes in SLA indicate adjustment to local environmental conditions rather than a clear advantage for the species.

Conclusion

Forest density and tree species composition were significant predictors of SLA in bilberry and cowberry, likely mediated by changes in overstory density, which regulated light

transmittance to the understory. Hence, managing forest overstory density and tree species can translate directly into difference in the SLA of both bilberry and cowberry. While soil conditions appear less important for the SLA of these two *Vaccinium* species for the range of contexts assessed, our assessment of macroclimatic differences revealed that plants in resource limited northern sites have more conservative leaf traits; which has implications for our ability to predict ecosystem changes under climate change. The observed plasticity in the SLA of these two understory species, and the strong response of SLA to tree species composition and forest density, highlights the capacity of forest management decisions to alter understory vegetation in ways that go beyond simple changes to plant species composition and prevalence.

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Author contributions Conceptualization: all authors; data collection: JDC, LJ, JUD and AS; data curation: SK, LJ and JDC; formal analysis: SK and POH; writing – original draft: all authors; writing – review and editing: all authors.

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Data availability Data will be made available upon acceptance in Zenodo.

Declarations

Competing interests The authors declare no competing interests.

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