Plant Ecology (2026) 227:49
https://doi.org/10.1007/s11258-026-01618-1

Forest structure and soil conditions influence the potential for drought-induced mortality in *Vaccinium myrtillus*

Per-Ola Hedwall[1] · **Joachim Strengbom**[2]

Received: 28 August 2025 / Accepted: 13 February 2026 / Published online: 12 March 2026
© The Author(s) 2026

Abstract
Vaccinium myrtillus is a foundation species and of high importance for ecosystem functions and services in many ecosystems of boreal Europe. Climate change now threatens the integrity of these cold-adapted ecosystems, with droughts and heat waves expected to increase in both frequency and intensity. In this study we investigated the occurrence of drought damage (desiccated twigs and mortality) on *V. myrtillus* ramets following several years with spring and/or summer droughts in southern Sweden. From the 26 524 ramets that were classified according to vitality, 21% were either dead or had more than 50% dead biomass. The proportion of damaged ramets varied according to forest structure and soil moisture. The impact of forest density was strongly dependent on tree species composition. While the proportion of damage decreased with forest density in forest dominated by *Pinus sylvestris*, it increased with density in forest dominated by *Picea abies*. Additionally, the proportion of damaged ramets was higher on elevated microhabitats such as rocks or stumps, and lower where *V. myrtillus* co-occurred with hygrophytic bryophytes. Damage was also inversely related to thickness of the humus layer. While the long-term effects on both *V. myrtillus* and the ecosystem remain largely unknown, our results indicate that climate change may have considerable direct impacts on this species. Importantly, our results indicate an interaction between climate change and forest composition, suggesting that forest management could potentially mediate the effects of droughts by altering tree species composition.

Keywords Bilberry · Dwarf shrub · Global change · Understory vegetation · Taiga

Introduction

Ericaceous dwarf shrubs are recognized as foundation species in the boreal biome due to their high copiousness and importance for ecosystem functions and services (Nilsson and Wardle 2005). In northern Europe, the forest floor vegetation is often dominated by *Vaccinium myrtillus* (bilberry). For example, it accounts for approximately 28% of the total ground cover of vascular plants on forestland in Sweden (SLU 2023). Due to its high abundance, this species plays an important role in multiple ecosystem functions and processes and provides a wide range of ecosystem services. For example, it can contribute substantially to net primary production and ecosystem-level carbon sequestration (Nilsson and Wardle 2005; Wardle et al. 2012). Further, it provides sustenance for many forest species (Atlegrim 1989; Lakka and Kouki 2009; Selås et al. 2011). For example, *V. myrtillus* constitutes a substantial share of the diet of large wild ungulates (Felton et al. 2020; Spitzer et al. 2023), and the quantity and quality of this species can influence population growth of these animals (Selås et al. 2011; Spitzer et al. 2021). Additionally, it produces berries of large economical and recreational value (Miina et al. 2010; Pouta et al. 2006). However, during recent decades, the cover of this shrub species has declined dramatically in southern Sweden (Hedwall et al. 2019, 2021), and its ecosystem functions may now be further threatened by global climate change, particularly through more frequent and intense summer droughts (Ma et al. 2012; Gutierrez Lopez et al. 2021).

The life-history traits of *V. myrtillus*, such as slow growth and nutrient conservatism, likely make it sensitive to changes in disturbance regimes and nutrient cycling.

✉ Per-Ola Hedwall
per-ola.hedwall@slu.se

[1] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Lomma, Sweden

[2] Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

Declines in dwarf-shrub-dominated heathlands across Western Europe over the last century are associated with high levels of anthropogenic nitrogen deposition (Bobbink et al. 2010), but nitrogen deposition is probably only one of several factors contributing to the decline of *V. myrtillus* in southern Sweden (Hedwall et al. 2016; Hedwall et al. 2019; Hedwall et al. 2021). Because declines also occur outside areas with high nitrogen deposition, other drivers are likely involved, including intensified forest management (Reinkainen et al. 2000; Hedwall et al. 2016; Hedwall et al. 2019). For example, forest density and tree species composition typical of conifer production forests strongly influence both the abundance (Hedwall et al. 2025) and growth (Juvany 2023) of this species. Much less is known about the effects of climate change, but these effects likely depend on where the species is positioned within the species' climatic envelope. In the (sub-)Arctic, at the cold end of its climatic envelope, warming has been shown to have positive effects on fitness and growth (Taulavuori et al. 2013; Ndah et al. 2024), whereas further south in the boreal zone, responses to increasing temperatures appear to be more variable (e.g. Hedwall et al. 2015; Hedwall et al. 2021).

Climatic anomalies, including extreme events such as droughts and prolonged heat waves, are expected to become more common under global warming (IPPC 2023). Despite the observed effects of increasing frequency and severity of droughts on boreal ecosystems (Ma et al. 2012; Gutierrez Lopez et al. 2021), the knowledge on their ecological consequences is limited to the effects on trees, while research elucidating the effects on understory plants is essentially missing. The few existing studies indicate that the photosynthetic apparatus of dwarf shrubs is considerably more drought-sensitive than that of the tree component of boreal forests (Palmroth et al. 2019; Mielke et al. 2022). Additionally, two studies report changed chemical composition as an effect of drought stress. These changes include increasing carbon concentration, while many other macro elements decrease (Urbina et al. 2015), and increased degradation of chlorophyll and oxidized proteins (Taulavuori et al. 2013), most likely as an effect of accelerated leaf senescence in this deciduous plant (Fig. 1). Overall, these findings suggest that dwarf shrubs exhibit high drought sensitivity and may be more strongly influenced by global warming than trees.

Southern Sweden has recently experienced several years with relatively low precipitation and some severe droughts during spring and early summer (Fig. 2). Associated with this an increased frequency of wilted *V. myrtillus* ramets (Fig. 1) has been observed in subsequent years (authors'

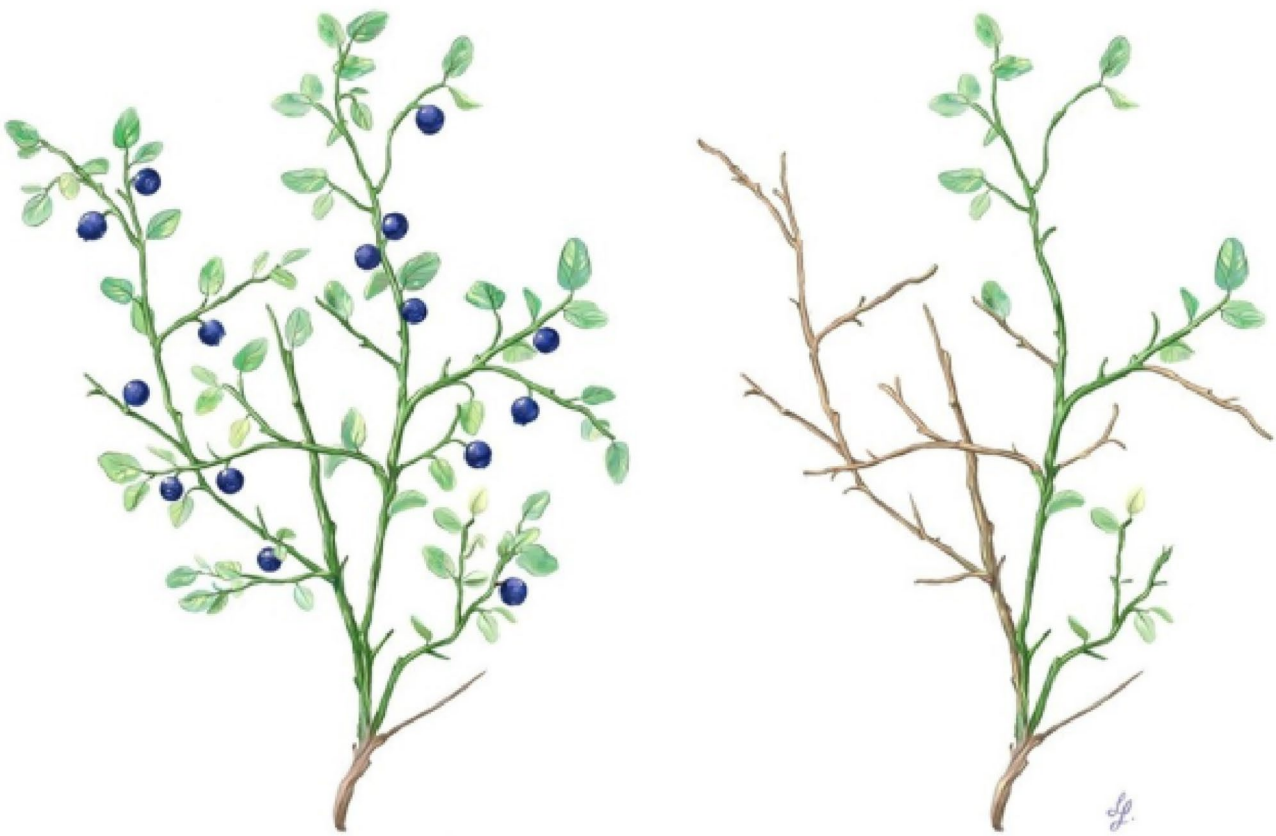

Fig. 1 A healthy *Vaccinium myrtillus* ramet (left), and a ramet with desiccated twigs (right). Illustration: Linnea Felton

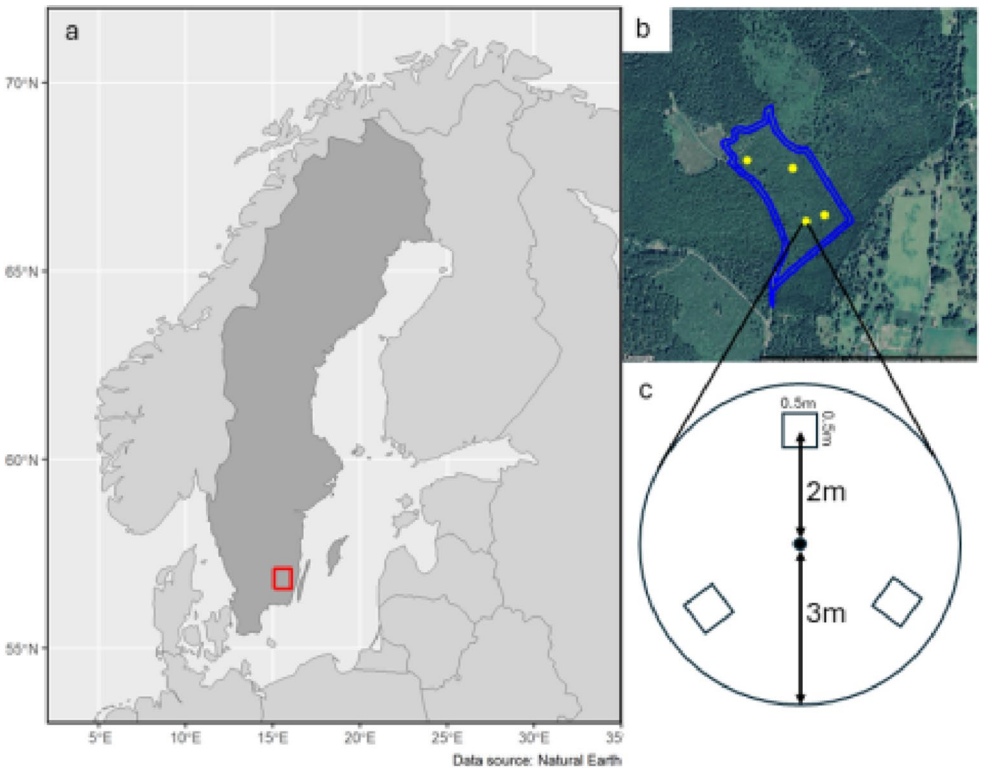

Fig. 2 Map of northwest Europe (Natural Earth 2025) showing Sweden in dark grey and the study area within the red frame (**a**); satellite photo of a landscape window (Google 2025) with one of the stands used in the study (**b**); and a diagram of the plot layout (c). In (b), the blue lines indicate the stand borders and the 10 m buffer inside of which the plots (yellow points) were randomly allocated. In (**c**), three subplots were placed at 2 m distance from the plot centre in a systematic way within each plot. In case there were less than 10 ramets in any 0.5 by 0.5 m area in these predefined locations, the plot and subplots were moved to the closest place that fulfilled this requirement

personal observations). Although direct evidence for a causal relationship between the measured low precipitation and the wilted *V. myrtillus* ramets is lacking, this nevertheless provides a unique opportunity to quantify the occurrences of wilted ramets.

The forest tree layer, including tree density or forest canopy cover and tree species composition, has a strong influence on the understory microclimate (Díaz-Calafat et al. 2023; Zhang et al. 2024), with anticipated effects on the survival and fitness of understory plants during extreme climatic events like droughts. For instance, *V. myrtillus* usually has its lowest coverage in young forest (Hedwall et al. 2025), likely related to stress induced by the extreme climatic conditions during the years immediately following stand-replacing disturbances such as clear-felling. Likewise, small-scale variation in soil moisture content and microtopography can be expected to influence the drought effects on understory plants (Koelemeijer et al. 2024).

The objective of this study was to improve our understanding of the effects of drought on *V. myrtillus*, and more specifically, how drought-related damage may vary along gradients of forest structure and soil conditions. We expected wilted ramets to be less common in sites with higher soil moisture, in older forests, and under denser, and more shade-casting tree canopies, due to the protection against direct sun light and buffering from extreme temperatures (Díaz-Calafat et al. 2023).

Methods

Study area

This study was conducted in the central parts of southern Sweden (Figs. 2a and 15°E 57°N), at the border between the hemiboreal and southern boreal vegetation zones according to Ahti et al. (1968). The study area is dominated by coniferous tree species (*Picea abies*, *Pinus sylvestris*) commonly mixed with varying amounts of deciduous tree species (e.g., *Betula* sp., *Populus tremula*, *Salix* sp.) and most forest is managed by rotational clear-cutting or by shelterwood cutting and regenerated either by planting or natural regeneration.

Climate data were accessed from the Swedish Meteorological and Hydrological Institute (smhi.se), and the two closest weather stations, Kosta and Orrefors, depending on variable and data availability. Both stations are located within 30 km from all forest stands used in this study (see below). The yearly precipitation sum is 647 mm and mean annual temperature 6.9 °C (average 1991–2020). During the winters 2018–2023 snow cover was highly variable, with long snow free periods, and the snow depth rarely exceeded 25 cm (Fig. 3a). During this period the precipitation patterns were characterized by less-than-normal precipitation in spring and early summer (Fig. 3b). The monthly precipitation sums for April, May, or June in these six years slightly exceeded the 1981–2010 average at only three occasions:

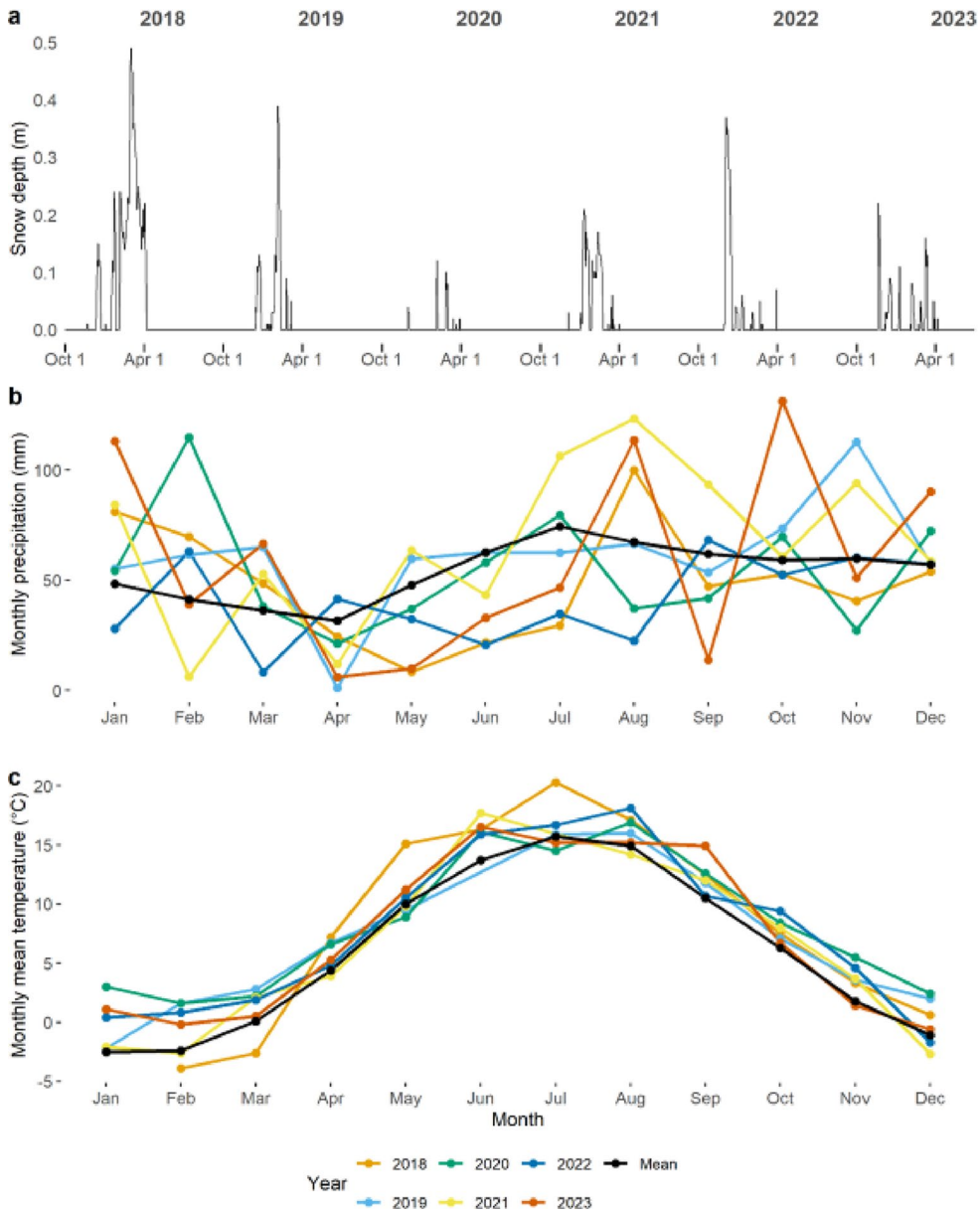

Fig. 3 Daily snow depth (**a**), monthly precipitation sums (**b**), and monthly mean temperatures during 2018–2023. The mean values indicate the 30-year averages for precipitation (1981–2010) and temperature (1971–2000)

May 2019, May 2021 and April 2022. The monthly mean temperatures during these years were generally warmer than the average for 1971–2000, especially during the winters (Fig. 3c).

Data collection

Stands were randomly selected from a database of 7 343 stands located on mineral soils excluding sites on peaty soils (>50 cm peat depth) supplied by the forest company Sveaskog, the largest forest owner in the region. Based on information about the stand basal area and tree species composition the selection of stands was stratified with the aim of including stands representing gradients in basal area (0–40 m^2) and tree species composition (0-100% of spruce), and all combinations of these gradients. This resulted in a final set of 162 stands.

Prior to the inventory, four plots per stand were randomly selected, each ensuring a 10 m buffer from the stand borders (Fig. 2b). In most cases the three plots per stand that were closest to a road were used, but the number of plots varied between one and four to use the time as efficiently as possible. All data were collected by one person during the period from the end of May until the end of June 2023. Plots were localized by a hand-held GPS. When the centre of the plot was identified, the surroundings were visually inspected to ensure that there was at least one 0.5 by 0.5 m area with at least ten ramets of *V. myrtillus* within a three m radius from the plot centre. If this criterion was not fulfilled, the plot centre was adjusted until the aforementioned criteria were

fulfilled, while maintaining the 10-meter buffer to the stand edge. In cases adjustments were made, the new coordinates for the plot centre were noted. Once the centre of the plot was located, the basal area per tree species was estimated with a relascope for each plot and used to calculate total basal area and relative tree species composition.

At each plot ramets were inventoried in a maximum of three 0.5 by 0.5 m subplots per plot (Fig. 2c). If there were more than three potential places for subplots within 3 m from the plot centre, they were systematically placed in three directions, each at a distance of 2 m from the plot center. If there were fewer than three positions fulfilling the criteria within the plot, one to two subplots were placed wherever the criteria (≥10 ramets) were fulfilled. In total, this resulted in data collected from 87 stands, 259 plots and 671 subplots.

In each subplot, we visually classified all ramets according to their level of damage into four classes: less than 10% of the ramet biomass dead, 10–49% dead, 50–99% dead, and 100% dead. Classification was based on whether the ramet had leaves, and on the coloration of the ramet stem and twigs (Fig. 1). As *V. myrtillus* ramets sometimes take red or brown colours without being dead, calibration was done by cutting and breaking ramets of different colouration to estimate their vigour. This was also repeated during the inventory whenever there were uncertainties about ramet status. In connection to the classification of ramets, the proportion of browsed ramets was estimated, and humus layer thickness was measured with a steel scale in the centre of the subplot. It was also noted if the subplot was placed in a clearly elevated microhabitat, such as a rock or old tree stump, and if there were bryophytes of the species *Polytrichum commune* and/or genus *Sphagnum* in the subplot as these are easy to identify and good indicators of moist microhabitats (hereafter referred to as hygrophytic bryophytes). Additionally, data on soil moisture were extracted from the SLU Soil Moisture Map (Lidberg et al. 2017), which is based on different field and remote sensing data sources. This map gives a soil moisture value from zero to 100, where 100 indicates the wetter end of the gradient. The resolution of the index is 2 by 2 m and here we used the average value for the 3 m radius around the plot centre.

Data analysis

All data management and analyses were done in R version 4.3.0 (R_Core_Team 2023). We used a Generalized Linear Mixed Model (GLMM) to estimate the effect of a set of predictors on the drought damage. This model was built as a Hurdle model combining a set of predictors for the proportion of damaged ramets larger than one, and a set of predictors for the presence/absence of damage due to the abundance of zeros in the response variable. The GLMM was performed by the glmmTMB function in the package with the same name (Brooks et al. 2017), with a beta error distribution for the proportional part of the model, and with a binomial distribution for the presence/absence part (formula for zero inflation in glmmTMB), all with logit link-functions. The full model contained the same set of predictors in both the beta and binomial parts. Continuous predictors were forest density estimated by the basal area of trees and the proportion of *P. abies*, both on plot level, as well as the interaction between these two variables, the total number of ramets in the plot, the proportion of browsed ramets in the plot, soil moisture, humus layer thickness, and forest age (extracted from the stand database). The proportion of *P. abies* and the interaction with forest density were included in the model as we expected the positive effect of forest density to be stronger under the more shade casting *P. abies* than under *P. sylvestris* and most broadleaf species (dominance by *Betula* sp.) in our stands (Verheyen et al. 2012). Additionally, the presence of hygrophytic bryophytes and whether the subplot was located on an elevated spot or not were used as factorial variables to test for variation among dry and moist microhabitats. All continuous variables were standardized prior to modelling by subtracting the mean and dividing by the standard deviation. To not over-parameterize the binomial part we simplified the model in a backward selection procedure ($\alpha = 0.05$), while all variables were kept in the beta part. Both stand and plot were initially evaluated as random effects. Stand did, however, account for a minor part of the variance, which is why this variable was excluded.

The model was evaluated by plotting the residuals from the simulateResiduals function in the DHARMa package (Hartig 2018). Prior to modelling, we ran correlation tests between all our continuous variables, and performed a t-test of these as an effect of the factor variables to detect potential multi-collinearity issues. Later we also calculated variance inflation factors for both the full and final models. None of these analyses revealed any problems due to multi-collinearity. As we were mainly interested in damage with considerable functional and fitness implications, we decided to include only the damage classes with ≥50% desiccated biomass. Models based on the proportion of ramets with >50% desiccation (the two most damaged classes together), or the proportion with 100%, were very similar, but the former showed slightly better residuals, which is why we decided to present results from this model only.

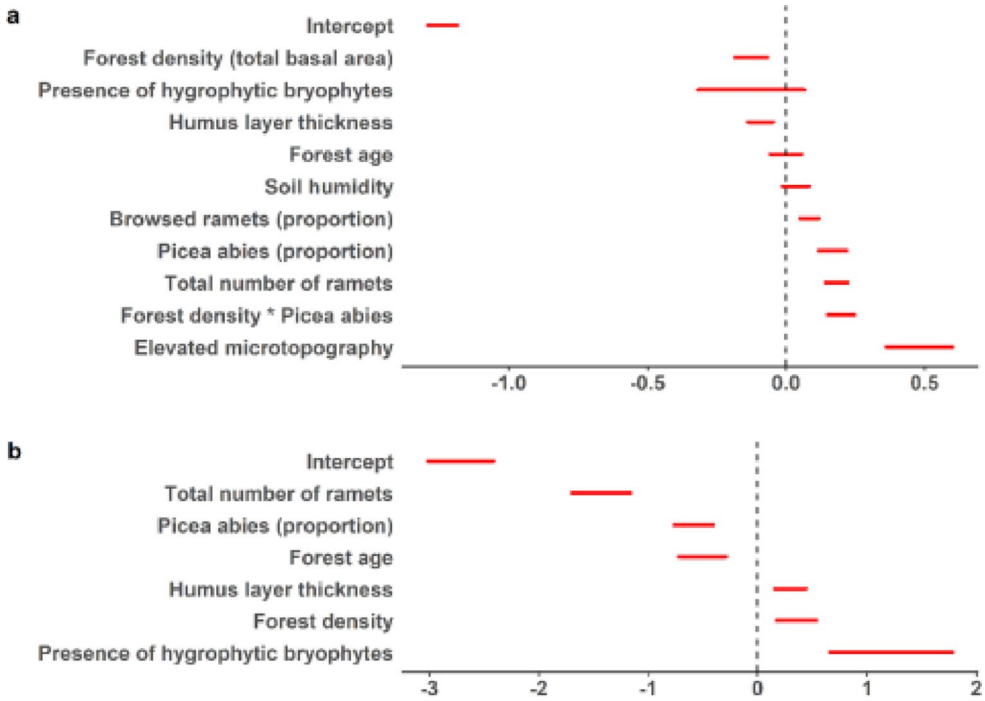

Fig. 4 Estimated model coefficients ± 1 SE (on the logit scale) for terms included in the beta part of the model (**a**) and terms in the binomial part (**b**). Observe that that the latter predicts the probability of zero occurrences of damage, and that this part of the model was reduced by backward selection of significant variables (α = 0.05). For the exact coefficients see Table SI1

Results

In total 26 524 ramets were classified according to vitality. The maximum number of ramets in a subplot was 181. Across all subplots on average 67% (range min-max: 0-100) of the ramets had less than 10% dead biomass, 11% (range: 0–70%) were moderately damaged (10–50% dead), and 5% (range: 0–50%) were more severely damaged (50–99% dead), while 16% (range: 0–94%) were entirely dead.

Our results show that severe desiccation damage (50–100% of ramet dead) was less likely to occur when bilberry co-occurred with hygrophytic bryophytes ($P = 0.029$, Fig. 4b, Online information Table SI 1)), while the proportion of damaged ramets was unrelated to their occurrence ($P = 0.516$, Fig. 4a). The proportion of damaged ramets increased with the proportion of browsed ramets ($P = 0.013$) and was higher at elevated microtopography ($P < 0.001$), while it tended to decrease with increasing thickness of the humus layer ($P = 0.051$). Both the proportion of damaged ramets ($P < 0.001$) and the probability of damage ($P < 0.001$) increased with the total number of ramets in the subplot. There was no significant effect of forest age ($P = 0.996$) or soil humidity ($P = 0.487$) on the proportion of damaged ramets, while the probability of finding damaged ramets increased with forest age ($P = 0.020$). The probability of finding damaged ramets increased with the proportion of *P. abies* ($P = 0.001$) and decreased with forest density, although this main effect was only borderline significant ($P = 0.049$). Moreover, there was a significant interactive effect between trees species composition and forest density ($P < 0.001$) on the proportion of damaged ramets. The proportion of damaged ramets decreased with forest density in forests dominated by *P. sylvestris* (supplemented by small amounts of broadleaf trees), while the proportion increased with density in forest dominated by *P. abies* (Fig. 5).

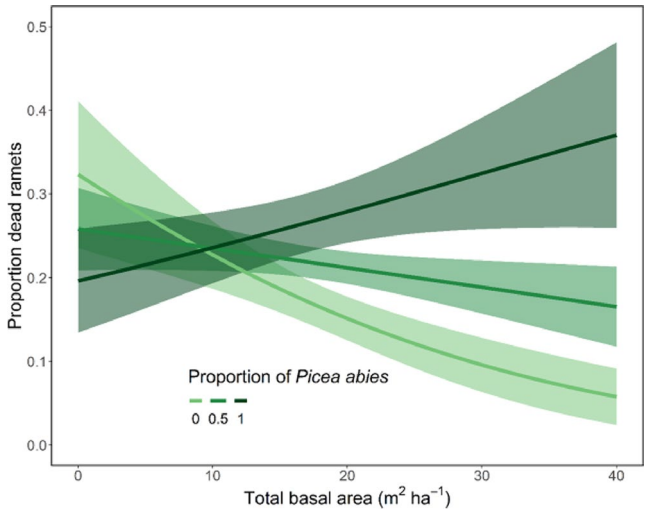

Fig. 5 Predicted proportions of >50% dead *Vaccinium myrtillus* ramets (±95 CI) depending on tree basal area and proportion of Norway spruce. The other continuous variables were kept at their mean, while the factors were set to no raised elevation and no hygrophytic bryophytes

Discussion

This study shows that *V. myrtillus* ramets, at least locally, have suffered from considerable mortality or biomass loss during recent years. Additionally, it demonstrates, for the first time, that this mortality varied across a forest landscape along gradients in soil moisture and overstory density, as well as tree species composition, which has implications both for our interpretation of the potential causes of this damage and for management recommendations.

The microclimatic buffering of forest overstories on the understory environment, i.e. the extent to which the maximum temperature under tree canopies is lower than in an open area, is largely dependent on the density or canopy cover of the overstory, with a larger buffering effect in dense forests (Díaz-Calafat et al. 2023). Hence, we expected less frequent damage under closed canopies than in more open environments, and that the positive effect of forest density is stronger under more shade casting tree species (Verheyen et al. 2012). In our case, this would mean greater buffering effect in forest dominated by *P. abies* than in forest dominated by *P. sylvestris* (and to a small extent *Betula* sp.). This expectation was only partly confirmed. While the proportion of damaged ramets decreased with increasing forest density in plots dominated by *P. sylvestris*, the opposite pattern was found for *P. abies*. The effects on understory communities from tree canopies goes, however, far beyond the easily observed effects on the light environment and microclimate (Balandier et al. 2022). Trees can exhibit strong asymmetrical competition (i.e., amensalism) for water on understory plants, and trenching in *P. abies* forest can mitigate drought effects on seedlings growing beneath the tree canopy (Ammer 2002). Competitive effects from trees do, however, vary considerably depending on the tree species due to differences in water use, rainwater interception, as well as root morphology and distribution. Although both our dominant tree species are water conservative evergreen conifers, and intercept relatively large proportions of the rainfall in comparison to most broadleaf trees, there is no clear evidence that our tree species differ in these aspects (Barbier et al. 2009; Pflug et al. 2021). Their root systems are, however, morphologically different with *P. abies* having more shallow root systems than *P. sylvestris* (Kalliokoski et al. 2008), which may imply that the former is a stronger competitor for soil resources in the rooting zone of *V. myrtillus*. The two tree species also differ largely in light transmittance with much higher light availability for the understory community in *P. sylvestris* than *P. abies* forests (Barbier et al. 2008). We can therefore not exclude that part of the observed mortality in *P. abies* dominated plots is due to light deprivation.

Snow removal experiments have shown that *V. myrtillus* can suffer from desiccation when unprotected by snow during cold weather (Taulavuori et al. 2013). As snow depth often is smaller in dense forest than open (Winkler et al. 2005) there is a possibility that the effects in our study, with more damage in dense forest, are an effect of less protection by snow during frost events rather that drought. Our study area had very little snow also in open areas (often none or less than 10 cm) during the years prior to our inventory and it is thus unlikely that this may have caused the observed variation in damage. In addition, dense canopies buffer extreme temperatures like frost events (Díaz-Calafat et al. 2023) which would counteract an increased exposure due to lower snow cover beneath such canopies. Nevertheless, these uncertainties call for controlled experiments on drought effects on *V. myrtillus*, as well as on other boreal plant species, preferably under varying light availability and belowground competition.

In addition to the tree layer, variation in ramet damage was also associated to soil moisture conditions, and we found less damage in subplots with thicker humus layer (higher water holding capacity) and where hygrophytic bryophytes occurred, while more damage was found in elevated microhabitats such as rocks or old tree stumps. These results indirectly support our assumption that the damage observed was mainly a result of drought. In contrast, damage was unrelated to the soil moisture index. This may seem surprising, but it is possible that damage varies on a finer scale than the resolution of this remote sensing derived index, or that this index does not reflect the actual water availability that understory plants experience, especially during drought. To our knowledge, this is also the first time this index has been used in relation to understory plants.

The likelihood of finding damaged ramets increased with the total number of ramets in the subplot. Including ramet density accounts for potential stochasticity in the occurrence of damaged ramets, and that the probability of finding a damaged ramet just by chance will increase with increasing abundance of ramets. However, since the proportion of damaged ramets also increased with ramet density, it is more likely that this is an effect of competition, and that damage may be elevated by intra-specific competition for water, or by high density of ramets from the same individual plant.

Damage was greatest in forest types that typically have low cover of *V. myrtillus* (Hedwall et al. 2025). As such, the damage may have less functional impact (e.g., for herbivores) on the landscape level than if more widely distributed. However, if successional recovery of *V. myrtillus* following stand-replacing disturbances (e.g., clear-felling) is severely constrained in suboptimal habitats, this slow-dispersing species may fail to recolonize sites before the next harvest cycle, leading to local extinction and reduced landscape-level occupancy.

The long-term effects of drought damage on *V. myrtillus* and associated ecosystem services will depend on the ability of the clones to compensate for the lost biomass. *Vaccinium myrtillus* has shown relatively strong potential to recover from other types of disturbances (Nielsen 2007), but as far as we know its potential to recover from drought damage has not been studied and remains a knowledge gap.et al.

Vaccinium myrtillus have decreased in abundance in Fennoscandian forests during the last half-a-century and increasing forest density and higher proportion of *P. abies* are suggested to be important drivers of this change (Reinkainen et al. 2000; Hedwall et al. 2019). Besides direct effects on the light regime from increased canopy cover, our results also stress the potential importance of changed belowground competition, and that such effects may be exacerbated by drought. Whether the potential interaction between climate change and forest management contributes to the observed declining abundance of *V. myrtillus* in Sweden is unknown, but it may well be something to consider in future management decisions. As our results indicate considerably less damage in mixed or pure *P. sylvestris* forests than in pure *P. abies* forests, even at high stand density, management that promotes a high proportion of pine or results in mixed forest stands may better maintain ecosystem services associated with *V. myrtillus*.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11258-026-01618-1.

Acknowledgements We are in debt to Henrik Johansen for his efforts collecting the field data for this study, and to Sveaskog for making their forest stand data available. Special thanks go to David Ventorp at Sveaskog for his valuable support in stand selection and to Lukas Graf for his help retrieving the soil moisture data.

Author contributions Both authors contributed to the study conception and design. Data treatment and analysis were performed by Per-Ola Hedwall. The first draft of the manuscript was written by Per-Ola Hedwall and Joachim Strengbom jointly. Both authors read and approved the final manuscript.

Funding Open access funding provided by Swedish University of Agricultural Sciences. The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Data availability Data supporting the findings of this study will be made available on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Ahti T, Hämet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. Ann Bot Fenn 5:169–211

Ammer C (2002) Response of *Fagus sylvatica* Seedlings to Root Trenching of Overstorey *Picea abies*. Scand J Res 17:408–416. https://doi.org/10.1080/028275802320435423

Atlegrim O (1989) Exclusion of birds from bilberry stands: impact on insect larval density and damage to the bilberry. Oecologia 79:136–139. https://doi.org/10.1007/BF00378251

Balandier P, Mårell A, Prévosto B, Vincenot L (2022) Tamm Review: Forest understorey and overstorey interactions: so much more than just light interception by trees. Ecol Manag 526:120584. https://doi.org/10.1016/j.foreco.2022.120584

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. Ecol Manag 254:1–15. https://doi.org/10.1016/j.foreco.2007.09.038

Barbier S, Balandier P, Gosselin F (2009) Influence of several tree traits on rainfall partitioning in temperate and boreal forests: a review. Ann Sci 66:1–11. https://doi.org/10.1051/forest/2009041

Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M, Bustamante M, Cinderby S, Davidson E, Dentener F, Emmett B, Erisman J, Fenn M, Gilliam F, Nordin A, Pardo L, De Vries W (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol Appl 20:30–59. https://doi.org/10.1890/08-1140.1

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker B (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Díaz-Calafat J, Uria-Diez J, Brunet J, De Frenne P, Vangansbeke P, Felton A, Öckinger E, Cousins SAO, Bauhus J, Ponette Q, Hedwall PO (2023) From broadleaves to conifers: The effect of tree composition and density on understory microclimate across latitudes. Agric Meteorol 341:109684. https://doi.org/10.1016/j.agrformet.2023.109684

Felton AM, Holmström E, Malmsten J, Felton A, Cromsigt JPGM, Edenius L, Ericsson G, Widemo F, Wam HK (2020) Varied diets, including broadleaved forage, are important for a large herbivore species inhabiting highly modified landscapes. Sci Rep 10:1904. https://doi.org/10.1038/s41598-020-58673-5

Google (2025) Google Maps. https://www.google.com/maps

Gutierrez Lopez J, Tor-ngern P, Oren R, Kozii N, Laudon H, Hasselquist NJ (2021) How tree species, tree size, and topographical location influenced tree transpiration in northern boreal forests during the historic 2018 drought. Glob Change Biol 27:3066–3078. https://doi.org/10.1111/gcb.15601

Hartig F (2016) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. contributed packages, CRAN

Hedwall PO, Brunet J (2016) Trait variations of ground flora species disentangle the effects of global change and altered land-use in Swedish forests during 20 years. Glob Change Biol 22:4038–4047. https://doi.org/10.1111/gcb.13329

Hedwall PO, Skoglund J, Linder S (2015) Interactions with successional stage and nutrient status determines the life-form specific effects of increased soil temperature on boreal forest floor vegetation. Ecol Evol 5:948–960. https://doi.org/10.1002/ece3.1412

Hedwall PO, Gustafsson L, Brunet J, Lindbladh M, Axelsson AL, Strengbom J (2019) Half a century of multiple anthropogenic stressors has altered northern forest understory plant communities. Ecol Appl 29:e01874. https://doi.org/10.1002/eap.1874

Hedwall PO, Uria-Diez J, Brunet J, Gustafsson L, Axelsson AL, Strengbom J (2021) Interactions between local and large-scale drivers determine long-term trends in boreal forest vegetation under global change. Glob Ecol Biogeogr 30:1765–1780. https://doi.org/10.1111/geb.13324

Hedwall PO, Felton A, Öhman K, Juvany L, Brunet J (2025) Modeling the Abundance of Boreal Foundation Species: The Impact of Forest Structure, Soils, and Legacy Effects on Ericaceous Shrubs. Appl Veg Sci 28:e70014. https://doi.org/10.1111/avsc.70014

IPCC (2023) In: Lee H, Romero J (eds) Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team. IPCC, Geneva, Switzerland, p 184. doi: https://doi.org/10.59327/IPCC/AR6-9789291691647

Juvany Canovas L (2023) The puzzle of forestry and cervid interactions. Acta Universitatis Agriculturae Sueciae 2023(76). https://doi.org/10.54612/a.4g9uebego0

Kalliokoski T, Nygren P, Sievänen R (2008) Coarse root architecture of three boreal tree species growing in mixed stands. Silv Fenn 42:189–210

Koelemeijer IA, Severholt I, Ehrlén J, De Frenne P, Jönsson M, Hylander K (2024) Canopy cover and soil moisture influence forest understory plant responses to experimental summer drought. Glob Change Biol 30:e17424. https://doi.org/10.1111/gcb.17424

Lakka J, Kouki J (2009) Patterns of field layer invertebrates in successional stages of managed boreal forest: implications for the declining Capercaillie Tetrao urogallus L. population. Ecol Manag 257:600–607. https://doi.org/10.1016/j.foreco.2008.09.042

Lidberg W, Nilsson M, Ågren AM (2017) Using machine learning to generate high resolution wet area maps for planning forest management: a study in a boreal forest landscape. Ambio 49:475–486. https://doi.org/10.1007/s13280-019-01196-9

Ma Z, Peng C, Zhu Q, Chen H, Yu G, Li W, Zhou X, Wang W, Zhang W (2012) Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. PNAS 109:2423–2427. https://doi.org/10.1073/pnas.1111576109

Mielke LA, Ekblad A, Finlay RD, Fransson P, Lindahl BD, Clemmensen KE (2022) Ericaceous dwarf shrubs contribute a significant but drought-sensitive fraction of soil respiration in a boreal pine forest. J Ecol 110:1928–1941. https://doi.org/10.1111/1365-2745.13927

Miina J, Pukkala T, Hotanen JP, Salo K (2010) Optimizing the joint production of timber and bilberries. Ecol Manag 259:2065–2071. https://doi.org/10.1016/j.foreco.2010.02.017

Natural Earth (2025) https://www.naturalearthdata.com/

Ndah FA, Maljanen M, Kasurinen A, Rinnan R, Michelsen A, Kotilainen T, Kivimäenpää M (2024) Acclimation of subarctic vegetation to warming and increased cloudiness. Plant-Environ Interact 5:e10130. https://doi.org/10.1002/pei3.10130

Nilsson MC, Wardle DA (2005) Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Front Ecol Environ 3(8):421–428. https://doi.org/10.1890/1540-9295

Palmroth S, Bach LH, Lindh M, Kolari P, Nordin A, Palmqvist K (2019) Nitrogen supply and other controls of carbon uptake of understory vegetation in a boreal Picea abies forest. Agric Meterol 276:107620. https://doi.org/10.1016/j.agrformet.2019.107620

Pflug S, Voortman BR, Cornelissen JHC, Witte JPM (2021) The effect of plant size and branch traits on rainfall interception of 10 temperate tree species. Ecohydrol 14:e2349

Pouta E, Sievänen T, Neuvonen M (2006) Recreational wild berry picking in Finland – reflection of a rural lifestyle. Soc Nat Res 19:285–304. https://doi.org/10.1002/eco.2349

R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna https://www.R-project.org/

Reinkainen A, Mäkipää R, Vanha-Majamaa I, Hotanen JP (2000) Kasvit Muuttuvassa Mestäluonossa (Changes in the Frequency and Abundances of Forest and Mire Plants in Finland Since 1950). Kustannusosakeyhtiö Tammi, Helsinki

Selås V, Sonerud GA, Hjeljord O, Gangsei LE, Pedersen HB, Framstad E, Spidsø TK, Wiig Ø (2011) Moose recruitment in relation to bilberry production and bank vole numbers along a summer temperature gradient in Norway. Eur J Wildl Res 57:523–535. https://doi.org/10.1007/s10344-010-0461-2

SLU (2023) Forest statistics 2023, Official Statistics of Sweden. Swedish University of Agricultural Sciences Umeå

Spitzer R, Coissac E, Felton AM, Fohringer C, Juvany L, Landman M, Singh NJ, Taberlet P, Widemo F, Cromsigt JPGM (2021) Small shrubs with large importance? Smaller deer may increase the moose-forestry conflict through feeding competition over Vaccinium shrubs in the field layer. Ecol Manag 480:118768. https://doi.org/10.1016/j.foreco.2020.118768

Spitzer R, Coissac E, Cromsigt JPGM, Felton AM, Fohringer C, Landman M, Neumann W, Raubenheimer D, Singh NJ, Taberlet P, Widemo F (2023) Macro-nutritional balancing in a circumpolar boreal ruminant under winter conditions. Fun Ecol 37:1256–1268. https://doi.org/10.1111/1365-2435.14296

Taulavuori K, Laine K, Taulavuori E (2013) Experimental studies on Vaccinium myrtillus and Vaccinium vitis-idaea in relation to air pollution and global change at northern high latitudes: A review. Environm Exp Bot 87:191–196. https://doi.org/10.1016/j.envexpbot.2012.10.002

Urbina I (2015) Shifts in the elemental composition of plants during a very severe drought. Environm Exp Bot 111:63–73. https://doi.org/10.1016/j.envexpbot.2014.10.005

Verheyen K, Baeten L, De Frenne P, Bernhardt-Römermann M, Brunet J, Cornelis J, Decocq G, Dierschke H, Eriksson O, Hédl R, Heinken T, Hermy M, Hommel P, Kirby K, Naaf T, Peterken G, Petřík P, Pfadenhauer J, Van Calster H, Walther GR, Wulf M, Verstraeten G (2012) Driving Factors Behind the Eutrophication Signal in Understorey Plant Communities of Deciduous Temperate Forests. J Ecol 100:352–365. https://doi.org/10.1111/j.1365-2745.2011.01928.x

Wardle DA, Jonsson M, Bansal S, Bardgett RD, Gundale MJ, Metcalfe DB (2012) Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. J Ecol 100:16–30. https://doi.org/10.1111/j.1365-2745.2011.01907.x

Winkler RD, Spittlehouse DL, Golding DL (2005) Measured differences in snow accumulation and melt among clearcut, juvenile, and mature forests in southern British Columbia. Hydrol Process 19:51–62. https://doi.org/10.1002/hyp.5757

Zhang S, Sjögren J, Jönsson M (2024) Retention forestry amplifies microclimate buffering in boreal forests. Agric Meteorol 350:109973. https://doi.org/10.1016/j.agrformet.2024.109973

Nielsen A, Totland Ø, Ohlson M (2007) The effect of forest management operations on population performance of Vaccinium myrtillus on a landscape-scale. Basic Appl Ecol 8:231–241. https://doi.org/10.1016/j.baae.2006.05.009

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.