Multivariate analysis of risk factors associated with Scots pine blister rust in Northern Sweden

Ke Zhang [a,*], Henrik Svennerstam [b]

[a] *Department of Forest Mycology and Plant Pathology, Swedish University of Agricultural Sciences, Uppsala, Sweden*
[b] *The Forestry Research Institute of Sweden, Skogforsk, Sävar, Sweden*

ARTICLE INFO

ABSTRACT

Scots pine blister rust (SPBR), caused by the rust fungus *Cronartium pini*, has existed in Swedish pine forests for approximately 200 years. However, recent outbreaks have led to substantial damage in young Scots pine stands, particularly in northern Sweden. A better understanding of the current epidemics and the environmental factors influencing their occurrence is essential for sustainable forest management. In 2021 and 2022, field surveys were conducted in young forest stands across northern Sweden to assess SPBR incidence, alongside the collection of geographical, topographical, and vegetation data. Additionally, to investigate climate impact on SPBR, historical and projected climate data were obtained from public databases. The surveys revealed frequent presence and high incidence of SPBR in Norrbotten, with the highest observed disease incidence reaching 48.8 %. Using logistic regression with generalized linear mixed models and beta regression, we found that SPBR prevalence and higher incidence were significantly associated with higher elevation, moist soil conditions, and higher abundance of the telial host *Melampyrum* spp. Moreover, warmer temperatures combined with higher precipitation were also positively correlated with higher disease incidence. Based on future climate projections under various Representative Concentration Pathway (RCP) scenarios, we estimated the potential impact of climate change on SPBR dynamics. The results suggest that rising temperatures and precipitation levels may have a greater impact on SPBR risk in Norrbotten, the estimated absolute increase in disease incidence may reach 20 % by the end of the 21st century with RCP8.5. In other RCP scenarios, the climate impact on SPBR incidence increase is generally modest, typically below 5 %.

1. Introduction

Scots pine (*Pinus sylvestris*) is one of the most important tree species in Sweden, comprising 39.4 % of the total growing stock in Swedish forests in 2022 (SLU National Forest Inventory, 2023). Scots pine can thrive in less fertile, acidic, and nutrient-poor soils due to its deep root system (Ostonen et al., 2007). In northern Sweden, Scots pine is claimed to have significantly higher gross stem-wood production than Norway spruce (*Picea abies*) (Nilsson et al., 2012). However, forests in northern Sweden, particularly young pine forests, face multiple threats from abiotic and biotic disturbances, including moose browsing and fungal pathogens (Wulff et al., 2022). Scots pine blister rust (SPBR) is among the most severe forest diseases in this region, causing substantial damage and economic losses (Skogsstyrelsen, 2017).

SPBR is caused by the rust fungus *Cronartium pini;* this pathogen has two different life-cycle forms (Samils and Stenlid, 2022). The autoecious (non-host-alternating) form has a simple life-cycle on pine. The heteroecious (host-alternating) form has a complex macrocyclic life-cycle that requires two different hosts: an aecial host, such as the Scots pine, and a telial host, such as *Melampyrum* spp. The small cow-wheat (*M. sylvaticum*) is one of the most important telial hosts in northern Fennoscandia (Kaitera and Hantula, 1998). Both forms infect pine through the current year's needles or shoots and grow towards the stem, eventually forming perennial cankers on branches and stems that produce aeciospores during summer. Infected branches and stems exhibit excessive resin exudation and deformation (Kaitera et al., 2021), with up to 70 % reduction in radial increment (Martinsson and Nilsson, 1987). Severe infections may girdle stems and kill the top or entire tree, posing significant risks to both production and natural forests in northern Sweden. SPBR has long been present in the forests of Fennoscandia, occasionally causing severe damage during the past century (Kaitera et al., 1994; Rennerfelt, 1947). Over the past few decades, increasing

---

* Corresponding author.
   E-mail address: ke.zhang@slu.se (K. Zhang).

SPBR outbreaks in young Scots pine forests have been reported, leading to considerable forest damage (Wulff and Hansson, 2013, 2009). The causes of recent SPBR epidemics in Sweden remain unclear.

Efforts to control SPBR include selective breeding (Persson et al., 2024), but resistant Scots pine material has not yet been released. Several silvicultural strategies, such as pruning infected branches and thinning susceptible trees, have been tested (Kaitera, 2002; Samils and Stenlid, 2022). However, these methods can be labour-intensive, time sensitive (Kim et al., 2021; Schnepf and Schwandt, 2006), and sometimes ineffective due to the pathogen's latent growth (Zeglen and Diprose, 2021). Given the importance of *M. sylvaticum* in the pathogen's life cycle, prescribed burning has been tested as a control measure. Nevertheless, studies have reported rapid reappearance of *M. sylvaticum* (Marozas et al., 2007; Ruokolainen et al., 2006) and no significant reduction in disease incidence (Tillberg, 2010).

These challenges, increasing SPBR epidemics and the lack of effective management strategies, highlight the importance of epidemiological studies on this disease. Advances in statistical tools, such as generalized linear mixed models and beta regression, have enabled the analysis of complex multivariate data in plant pathology (Garrett et al., 2004; Martínez-Minaya et al., 2021). These methods can identify key variables associated with disease epidemics, support disease prediction at various spatial scales, and inform decision-making (Garrett et al., 2004). In multivariate analysis studies, forest disease epidemics are often associated with topographical factors and meteorological/climate factors (Iturritxa et al., 2015; Dudney et al., 2021), the latter is especially crucial to investigate due to climate change. The impact of climate change on plant disease epidemics has been widely discussed, both globally with many plant pathogens (Chaloner et al., 2021; Rosenzweig et al., 2014) and locally with specific pathogens (Dudney et al., 2021; Robin et al., 2017). This issue is particularly relevant for Sweden and other Nordic countries, where higher latitudes are warming more rapidly and may experience more severe ecological impacts (Post et al., 2019). A recent study found that most crop diseases were projected to increase in Scandinavia under climate change, especially under high carbon emission scenarios (Strandberg et al., 2024). Increased temperature and precipitation, both of which are predicted for Sweden, are likely to favor the growth and spread of many forest pathogens, including rust fungi. For instance, Samils and Stenlid (2022) proposed changing climate conditions to be one of the potential explanations of rising SPBR epidemics in Sweden.

To analyse the relationship between environmental factors and SPBR, high-quality, complete, and reliable data of disease assessment is essential (Nutter et al., 2006). SPBR in Swedish forest is easiest to diagnose in June and July, when orange-yellow spore-bearing aecia are visible (Samils and Stenlid, 2022). If assessments are done outside this optimal time window, inactive cankers may be confused with other diseases, and survey errors can occur. In addition, the telial host *M. sylvaticum* is most easily recognized in northern Sweden from late June to early July by its yellow flowers and clustered growth (Dalrymple, 2007). In the summers of 2021 and 2022, the Forestry Research Institute of Sweden (Skogforsk) conducted extensive surveys to assess SPBR distribution and severity in young Scots pine forests in northern Sweden (Svennerstam, 2023). These surveys collected comprehensive data on geographic, topographic, and vegetation conditions, providing an excellent basis for identifying SPBR risk factors. Additionally, historical climate reanalysis and future climate projections with suitable spatial resolutions are available to explore the relationships between climate conditions and SPBR absence/presence and incidence.

By integrating field survey data with historical climate records and applying multivariate analysis methods, this project aims to identify the risk factors associated with SPBR. Our primary hypothesis is: the presence and high disease incidence of SPBR are associated with geographical, topographical, vegetation and climate factors. Furthermore, based on the disease models, we also aim to assess the potential impact of future climate scenarios on SPBR dynamics in northern Sweden.

2. Methods

2.1. Surveys of young Scots pine forest stands in northern Sweden

Surveys were conducted between June and July in both 2021 and 2022, encompassing 420 Scots pine stands in northern Sweden, specifically in the counties of Norrbotten (BD), Västerbotten (AC), Jämtland (Z), and Västernorrland (Y). Data from Jämtland and Västernorrland were pooled together, so the data covered three regions with similar sizes. The stand age in the survey year was calculated based on the pine planting year. Most stands were 10–30 years old, with one exception of nine years. Stands in this age-span are considered to be relatively young given a 100-year rotation time on average in northern Sweden (SLU National Forest Inventory, 2023). In each stand, six to ten circular plots (100 m^2) were arbitrarily selected from a pre-determined 40 m × 40 m grid projected over each stand. Hence, plots were spatially independent with a minimum distance of 40 m between the centre of adjacent plots. In total, 3373 plots were surveyed. The field assessments followed a tailored protocol specifically developed for the inventory project (Svennerstam, 2023).

A detailed list of the variables included in the analyses is in Supplementary Table 1. Data collected from each plot included disease absence/presence, geographical information, topographical characteristics, and vegetation characteristics. Plot-level data were aggregated to the stand level: the number of infected and healthy pines from all plots were used to summarize the SPBR disease incidence in each stand; other numerical variables were averaged; while categorical or ranked variables were represented by the most frequently occurring value.

2.2. Curation of climate data

Historical and projected climate data were retrieved from the CORDEX regional climate model dataset (Copernicus Climate Change Service and Climate Data Store, 2019), using the global climate model CNRM-CERFACS-CM5 and the regional climate model CNRM-ALADIN63. The dataset covered the European domain with a spatial resolution of 0.11° × 0.11° (approximately 10 km × 5 km) and included both historical reanalysis and future climate projections.

Based on previous studies on *Cronartium* spp. and other rust pathogens (Dudney et al., 2021; Newcomb et al., 2010; Samils and Stenlid, 2022), we selected temperature, precipitation, and relative humidity (RH) as the key climate variables. These were represented in the dataset as 2-meter temperature (K), mean precipitation flux (kg m^{-2} s^{-1}), and 2-meter relative humidity (%), respectively. Daily averages for these variables were retrieved for the period 1990–2100, but only data from May 1 to October 30 were used, as this corresponds to the vegetation season in northern Sweden.

Historical Climate Data: For each stand, historical climate data were averaged over the period from the year of stand establishment up to the year prior to the survey. For example, for a stand established in 2001 and surveyed in 2021, climate data from 2001 to 2020 were included. Twenty-seven variables were generated, representing the three climatic factors across nine time periods (May–October, May–July, August–October, and individual months from May to October).

Climate Projection Data: Future climate conditions were summarized for two time windows: 2041–2070 and 2071–2100, under three Representative Concentration Pathway (RCP) scenarios: RCP2.6, RCP4.5, and RCP8.5 (van Vuuren et al., 2011). This generated six climate projection datasets, each containing the same 27 climate variables as in the historical data, calculated as 30-year averages for May to October.

2.3. Multivariate analysis

Two datasets—plot-level of disease absence/presence and stand-level of disease incidence—were generated from the survey data. After removing entries with missing data, 3321 plots and 415 stands were included in the final analysis. Climate data were merged with the survey data based on geographic coordinates. All statistical analyses were conducted using R software in RStudio. All data visualizations were processed with the package *ggplot2*.

2.3.1. Plot-level analysis with logistic regression of SPBR absence/presence

The total number of trees affected by SPBR (including production/main stem and potentially developable/secondary stem) was converted into a binary response variable, *Cron*, to represent SPBR absence/presence (1 = positive/presence of SPBR, 0 = negative/absence). All numeric explanatory variables were standardized to have a mean of 0 and a standard deviation of 1 using the *scale* function.

Logistic regression using generalized linear mixed models (GLMMs) with a binomial logit-link function was used to identify significant predictors of SPBR absence/presence. *Cron* was the response variable, Stand ID (*ID*) was treated as the random variable. The dataset was split into training (80 %) and testing (20 %) subsets using the *createDataPartition* function for model validation.

Prior to the regression analyses, pairwise correlations between explanatory variables were assessed using Pearson's r. Variables with high correlation (r > 0.5) were reviewed, and only one from each correlated pair was retained to reduce multicollinearity. For example, longitude (lon) is highly correlated with latitude (lat) and elevation (E), and stand age (Age) is highly correlated with pine height (Hp) and pine diameter (Dp); therefore, only lon, E, and Age were included in the regressions. Initial models were constructed using geographical, topographical, and vegetation variables. Variance inflation factors (GVIF and GVIF^(1/(2*Df))) were calculated for each model using the *vif* function from the *car* package. The best-fitting, most parsimonious model was selected based on Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), area under the curve (AUC), sensitivity, specificity, and overall accuracy. The latter four indices were calculated by the *confusionMatrix* function in *caret* package and the *roc* function in the *pROC* package. Climate variables—including average temperature, precipitation, and RH of different time windows in the stand where the plot was located—were then added to assess their effects. The best model was selected as mentioned above.

2.4. Stand-level analysis with beta regression of SPBR incidence

SPBR disease incidence (DI) was defined as the proportion of main stems and secondary stems infected with SPBR. DI was transformed using the formula: $DI_T = \frac{DI \times (N-1) + 0.5}{N}$, where N was the number of forest stands included in the analysis. DI_T was treated as the response variable in the analysis. All numeric explanatory variables were standardized to have a mean of 0 and a standard deviation of 1 using the *scale* function. Historical climate data were standardized together with climate projection data, then only historical climate data were used in the modelling, and the climate projection data were used in the later prediction.

The distribution of DI_T was tested with *fitdist* function in the *logspline* package and Goodness-of-fit statistics in the *fitdistrplus* package. DI_T was modelled using beta regression, as it followed a beta distribution (Supplementary Figure 1). Model selection followed the same approach as in Section 2.3.1: a core panel of geographical, topographical, and vegetation variables was established first, followed by the inclusion of climate variables. The optimal model was chosen based on AIC, likelihood, and pseudo R² values. The DI_T predicted from the best-performed beta regression model were back transformed to predicted DI using the formula $DI = \frac{DI_T \times N - 0.5}{N-1}$, and then plotted on the map together with the observed DI based on the survey. Stands were classified as SPBR-negative if the predicted DI was below 0.005 (0.5 %).

2.5. Predicting the climate change impact on SPBR incidence

To assess the impact of climate change on SPBR incidence, other explanatory variables from the stand-level survey data were combined with each of the six climate projection datasets (two time periods with three RCP scenarios) based on the coordinates of the stands. The climate projection data were standardized as mentioned in Section 2.4.

Predictions were made using the best-fit beta regression model identified in Section 2.4. Predicted DI_T were back-transformed to predicted DI using: $DI = \frac{DI_T \times N - 0.5}{N-1}$. Stands were classified as SPBR-negative if the predicted incidence was below 0.005 (0.5 %). The absolute and relative increase of predicted DI caused by future RCP scenarios were calculated by comparing the current predicted DI and future predicted DI, the increase under different RCP scenarios and time windows were plotted on the map. Density graphs were plotted to summarize the absolute and relative increase of DI in the three regions in northern Sweden.

3. Results

3.1. Summary of SPBR epidemics in surveyed stands

Most surveyed plots in Västerbotten, Jämtland, and Västernorrland were free of SPBR, whereas approximately half of the plots in Norrbotten were positive (Fig. 1A). At the stand level, 87.1 % of surveyed stands in Norrbotten were SPBR-positive, compared to 59.5 % in Västerbotten and 33.6 % in Jämtland and Västernorrland. The highest recorded disease incidence (DI) was 48.8 % in a single stand in Norrbotten, although DI was generally below 10 % across most stands (Fig. 1B).

Preliminary correlation analyses revealed a positive correlation between DI and elevation in all three regions (Fig. 1C). Stands in which the telial host *Melampyrum* spp. was present during the survey (rare to very frequent) tended to have higher DI. Stands with dry soil generally showed lower DI values (Fig. 1E). Due to the small number of stands categorized as having wet soil (n = 4), these wet soil stands were pooled with moist soil stands for subsequent analyses.

3.2. SPBR absence/presence in plots was associated with soil moisture and climate conditions in June

The coefficients and performance of various generalized linear mixed models (GLMMs) in logistic regression were compared in Table 1 (with climate variables) and Supplementary Table 2 (without climate variables).

The presence of SPBR was not significantly associated with soil type (S_{TY}), soil texture (S_{TE}), the presence of mobile soil water (MBS), ground (Gr), or slope (Sl). The SPBR presence was geographically aggregated towards the east (higher longitude, lon), which also suggested aggregation towards the north due to the survey data set and the geography of Sweden. SPBR presence was also associated with forest stands with higher elevation (E) and older age (Age). Among topographic factors, soil moisture (S_M) was the most influential, with drier soils corresponding to a lower likelihood of disease. Vegetation variables, particularly higher pine proportion (P_P) and *Melampyrum* abundance (Mel), were also significant predictors.

Inclusion of climate variables improved model fit in most cases, with the exception of models using climate data from July and August. Models with climate factors in June and September (precipitation, temperature and relative humidity) had the best AIC and accuracy; the most parsimonious model included precipitation (P) in June (Table 1). However, the model with September climate variables was abandoned due to high collinearity and multicollinearity (GVIF > 5). The result suggested higher amount of rain in June was associated with disease
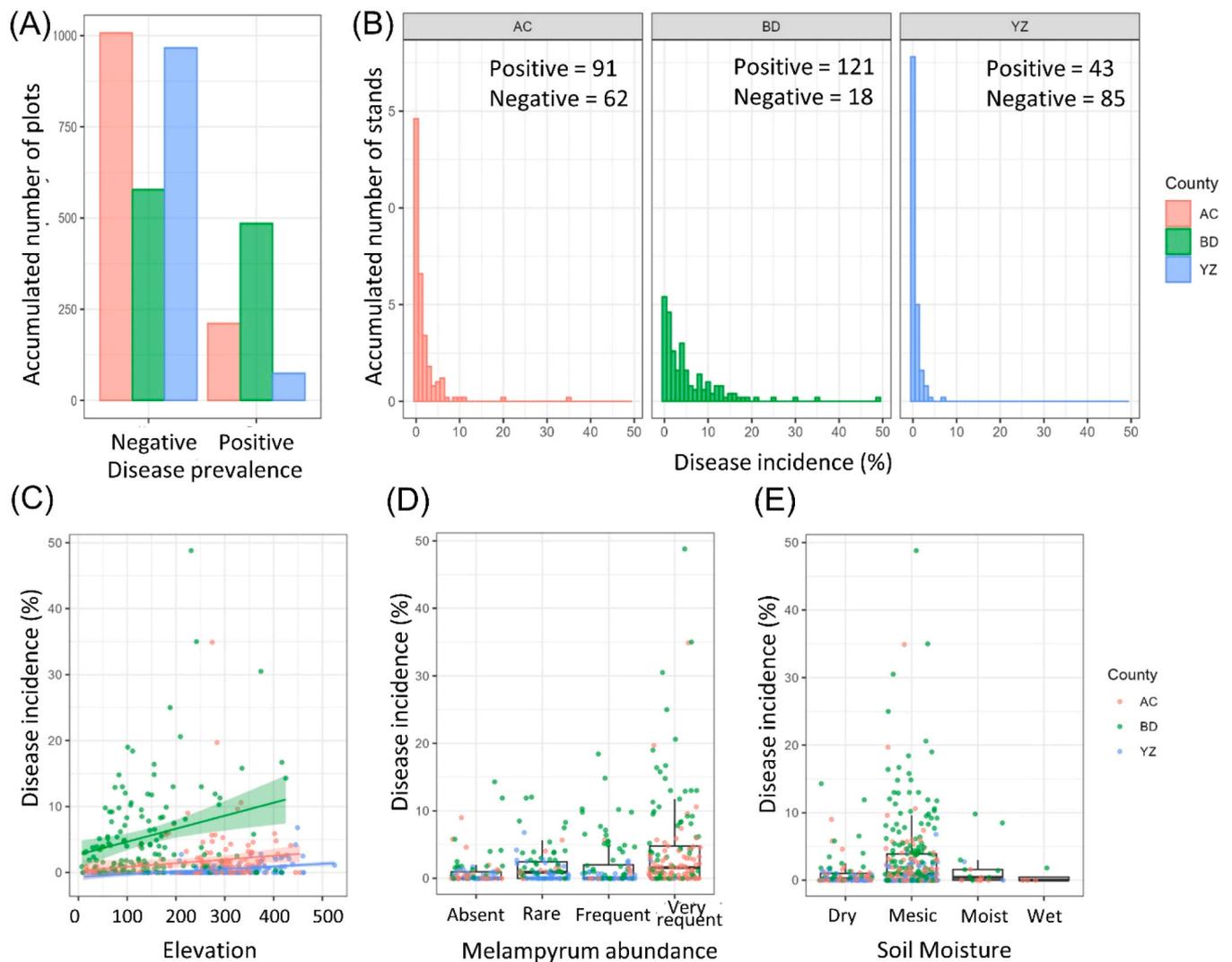
Fig. 1. Summary of Scots pine blister rust (SPBR) prevalence and incidence in surveyed plots and stands in the three counties in northern Sweden. (A) The number of SPBR positive and negative plots in each county. (B) Histogram of SPBR disease incidence in stands in each county. (C) Scatter plot with linear regression (95 % confidence interval) of disease incidence and elevation. (D) Box plot of disease incidence in stands with various levels of *Melampyrum* abundance. (E) Box plot of disease incidence in stands with various level of soil moist. AC: Västerbotten. BD: Norrbotten. YZ: Jämtland & Västernorrland.

presence.

Standardization of the variables allowed cross-comparison of the level of impacts among the factors. Besides the aggregated distribution of SPBR (longitude), elevation had the strongest positive impact on the SPBR presence among all the variables, while dry soil had the strongest negative impact (Fig. 2). Other variables included in the model had similar positive association with SPBR presence.

3.3. High SPBR incidence was associated with Melampyrum abundance and June climate conditions

The coefficients and performance of various beta regression models are shown in Table 2 (with climate variables) and Supplementary Table 3 (without climate variables). Stands with high SPBR incidence were geographically concentrated in the Norrbotten county, especially in the east (higher lon). In addition, stands with higher elevation (E) and older age tended to have higher disease incidence. Very frequent *Melampyrum* abundance (Mel) was another risk factor that would increase the disease incidence. Soil moisture (S_M) did not improve model performance and was thus excluded from the final model. Notably, pine proportion (P_P) exhibited a consistent negative association with disease incidence across all models. This inverse relationship might reflect a secondary effect, where severe SPBR infections reduce pine density over time.

In models with climate factors, climate variables in May and June outperformed the other time periods (Table 2). The most parsimonious model with temperature and precipitation in June produced the lowest AICc and highest likelihood (LL). It suggested that higher temperature and precipitation in June were associated with higher disease incidence. June temperature had the strongest impact on the SPBR incidence together with elevation and *Melampyrum,* besides the location of the stand (Fig. 2).

This most parsimonious model with climate factors was used to generate spatial predictions of SPBR incidence and compare the results with the observed SPBR incidence in the survey (Fig. 3). The predicted SPBR incidences were similar to observed SPBR incidences in northern Sweden: the incidences were much higher in Norrbotten county (BD); while in Jämtland and Västernorrland counties (YZ), more stands were SPBR negative. However, the model did not predict a few stands that were SPBR negative in Västerbotten (AC) and the one stand with extremely high incidence (48.8 %) in Norrbotten (BD).

Table 1
Parameter estimates of logistic regression with generalized linear mixed model of Scots pine blister rust (SPBR) absence/presence in each plot. The response variable was SPBR presence/absence. Stand ID was assigned as the random effect. Other geography, topography, vegetation, and climate variables were used as fixed effects. AIC: Akaike information criterion. BIC: Bayesian information criterion. AUC: Area under the curve of receiver's operating characteristic (ROC). lon: longitude. E: elevation. Age: stand age. S_M: soil moisture. Mel: *Melampyrum* abundance. P_P: pine percentage. T: temperature. RH: relative humidity. P: precipitation.

Models	Basic model	Basic model + May to October climate	Basic model + May to July climate	Basic model + August to October climate	Basic model + May climate	Basic model + June climate	Basic model + July climate	Basic model + August climate	Basic model + September climate	Basic model + October climate	**Basic model + June precipitation**
(Intercept)	-2.0352 ***	-2.4617 ***	-1.559 ***	-3.1796 ***	-2.0445 ***	-1.1058 **	-2.0797 **	-2.594 ***	-2.5568 ***	-3.0868 ***	**-1.8291 ***
lon	1.82929 ***	1.77125 ***	1.88725 ***	1.75016 ***	1.6288 ***	2.23114 ***	1.58954 ***	1.6877 ***	1.77951 ***	1.91773 ***	**2.01488 ***
E	1.02654 ***	0.79525 ***	0.81696 ***	0.81899 ***	0.77193 ***	1.1011 ***	0.76506 ***	0.78637 ***	0.76896 ***	1.14886 ***	**0.86641 ***
Age	0.28168 **	0.28125 **	0.34982 ***	0.30732 ***	0.17508 .	0.43114 ***	0.2983 **	0.28154 **	0.1276	0.34444 ***	**0.43067 ***
S_M-wet	-0.134	-0.1497	-0.1381	-0.16	-0.1263	-0.1597	-0.1345	-0.1324	-0.1558	-0.1367	**-0.1675**
S_M-dry	-0.8883 ***	-0.8224 ***	-0.805 ***	-0.8361 ***	-0.844 ***	-0.8206 ***	-0.8316 ***	-0.8755 ***	-0.7816 ***	-0.8269 ***	**-0.8595 ***
Mel-rare	0.4563 *	0.46704 *	0.43971 *	0.48093 *	0.48008 *	0.42628 *	0.45272 *	0.48113 *	0.46201 *	0.4716 *	**0.4499 *
Mel-frequent	0.22891	0.25421	0.22167	0.28003	0.26114	0.20438	0.24962	0.26526	0.25102	0.28968	**0.2451**
Mel-very frequent	0.52081 *	0.53925 *	0.56645 **	0.54837 *	0.56075 **	0.51644 *	0.60228 **	0.55564 **	0.55615 **	0.57316 **	**0.56483 **
P_P	0.37804 ***	0.36452 ***	0.37002 ***	0.3614 ***	0.35473 ***	0.38196 ***	0.37166 ***	0.36657 ***	0.35088 ***	0.34857 ***	**0.39153 ***
T		-0.8152 *	0.14176	-1.0843 ***	-0.3565	0.71399	-0.0963	-0.5833	-1.3843 ***	-0.4463 *	
RH		-0.5917 **	-0.2402	-0.5779 **	-0.4786 **	-0.0222	-0.0054	-0.1933	-0.8467 ***	-0.5095 ***	
P		0.50059 **	0.61793 **	0.3625 *	0.27618 *	0.61988 ***	0.27813	0.0351	0.59714 ***	0.00025	**0.41575 **
AIC	2269.9	2263.9	2264.4	2262.8	2266.6	2262.1	2271	2272.9	2252.8	2260.6	**2263.1**
BIC	2334.6	2346.3	2346.8	2345.2	2349	2344.5	2353.4	2355.3	2335.2	2343	**2333.7**
AUC	0.853	0.855	0.854	0.853	0.854	0.854	0.854	0.853	0.854	0.855	**0.852**
Sensitivity	0.8377	0.7987	0.8312	0.8506	0.8247	0.7078	0.8182	0.8117	0.8117	0.8506	**0.8442**
Specificity	0.7216	0.7608	0.7294	0.7059	0.7412	0.8451	0.7412	0.7431	0.7471	0.7078	**0.7157**
Accuracy	0.7485	0.7696	0.753	0.7395	0.7605	0.8133	0.759	0.759	0.762	0.741	**0.7455**

Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, .: $p < 0.1$
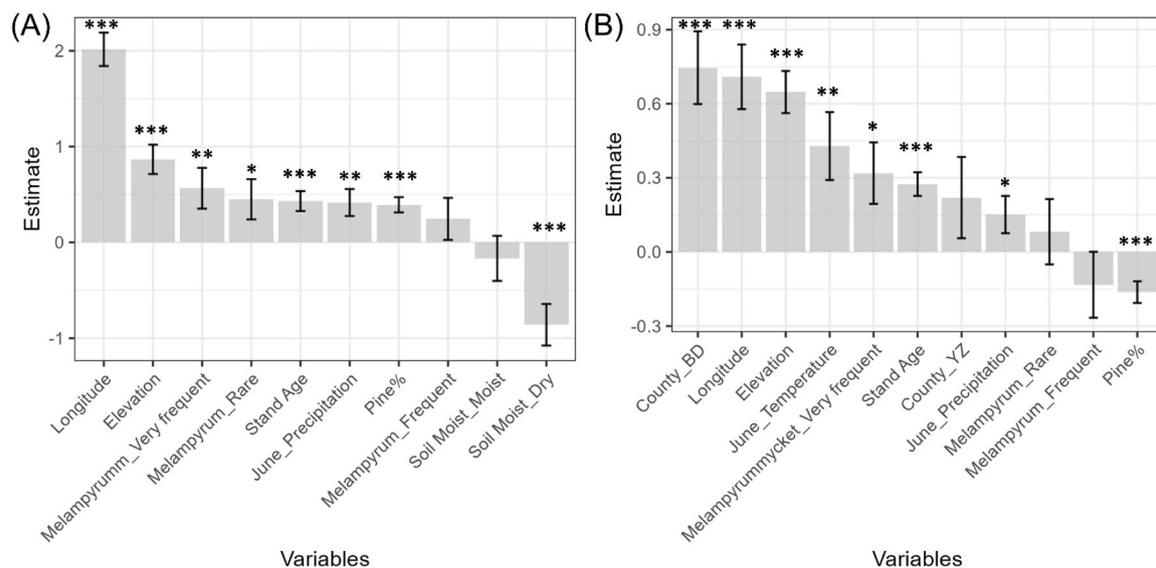
Fig. 2. Coefficient estimates of Scots pine blister rust (SPBR) presence/absence and incidence models. (A): logistic regression with generalized linear mixed model of SPBR presence/absence. (B): beta regression of SPBR incidence. The variables were rescaled/standardized with a mean of 0 and a standard deviation of 1 and ranked based on the coefficients. Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$.

Table 2

Parameter estimates of beta regression models of Scots pine blister rust (SPBR) disease incidence in each stands. The models included climate variables from indicated time periods. The response variable is transformed disease incidence. AICc: Akaike information criterion. LL: likelihood The highlighted model with best performance is used in analysis with climate data. lon: longitude. County-BD: Norrbotten. County-YZ: Jämtland and Norrbotten. E: elevation. Age: stand age. Mel: *Melampyrum* abundance. P$_P$: pine percentage. T: temperature. RH: relative humidity. P: precipitation.

Models	Basic model	Basic model + May to October climate	Basic model + May to July climate	Basic model + August to October climate	Basic model + May climate	Basic model + June climate	Basic model + July climate	Basic model + August climate	Basic model + September climate	Basic model + October climate	Basic model + May temperature	Basic model + June temperature and precipitation
(Intercept)	-4.2156 ***	-3.8999 ***	-3.5538 ***	-4.2512 ***	-3.92 ***	-3.7103 ***	-4.2071 ***	-4.0306 ***	-4.2387 ***	-4.0828 ***	-3.9237 ***	**-3.791 *****
lon	0.59548 ***	0.647 ***	0.62488 ***	0.65912 ***	0.64188 ***	0.70801 ***	0.63495 ***	0.58848 ***	0.68323 ***	0.66944 ***	0.63985 ***	**0.70884 *****
County-BD	0.67807 ***	0.86564 ***	0.8674 ***	0.73935 ***	1.01454 ***	0.78134 ***	0.73587 ***	0.96361 ***	0.64665 ***	0.7359 ***	0.74175 ***	**0.74585 *****
County-YZ	0.27522	0.14494	0.01349	0.28369	-0.0009	0.18055	0.23861	0.1708	0.26656	0.23532	0.15148	**0.21992**
E	0.52623 ***	0.64686 ***	0.66019 ***	0.58044 ***	0.67654 ***	0.67572 ***	0.58026 ***	0.57471 ***	0.537 ***	0.61541 ***	0.6481 ***	**0.64731 *****
Age	0.25332 ***	0.26935 ***	0.30184 ***	0.26346 ***	0.33177 ***	0.27718 ***	0.24942 ***	0.30247 ***	0.23343 ***	0.24646 ***	0.27865 ***	**0.27468 *****
Mel-rare	0.09958	0.07283	0.06265	0.08503	0.09733	0.07048	0.12081	0.08193	0.23343	0.08625	0.11009	**0.08182**
Mel-frequent	-0.1025	-0.1328	-0.1456	-0.1174	-0.1274	-0.1437	-0.0936	-0.1186	-0.1179	-0.1083	-0.1003	**-0.1329**
Mel-very frequent	0.3505 **	0.31336 *	0.31317 *	0.33313 **	0.31201 *	0.31711 *	0.33727 **	0.33589 **	0.33383 **	0.32768 **	0.3275 **	**0.31914 ***
P$_P$	-0.1581 ***	-0.1589 ***	-0.1607 ***	-0.1562 ***	-0.1688 ***	-0.1584 ***	-0.1687 ***	-0.1476 ***	-0.1631 ***	-0.1625 ***	-0.1725 ***	**-0.1626 *****
T		0.2102	0.64407	-0.0352	0.51382 *	0.58362 *	-0.0299	0.16455	-0.2494	0.10842	0.29701 *	**0.4285 *****
RH		-0.1021	0.09783	-0.0908	0.1051	0.1045	-0.1185	-0.0661	-0.2294 *	-0.0198		
P		0.1423 *	0.17611 *	0.07095	0.08499	0.13185	0.01657 .	0.19109 *	0.16147 *	-0.0417		**0.15113 ***
Pseudo R-squared	0.4324	0.4429	0.4482	0.4375	0.4457	0.4467	0.4309	0.4419	0.4433	0.4348	0.4364	**0.444**
AICc	-2495.4	-2495.7	-2498.2	-2491.1	-2499.1	-2498.7	-2491.7	-2494.8	-2495.2	-2490.7	-2498.9	**-2500.2**
LL	1259.01	1262.35	1263.61	1260.05	1264.09	1263.87	1260.37	1261.94	1262.13	1259.89	1261.81	**1263.53**

Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$,.: $p < 0.1$
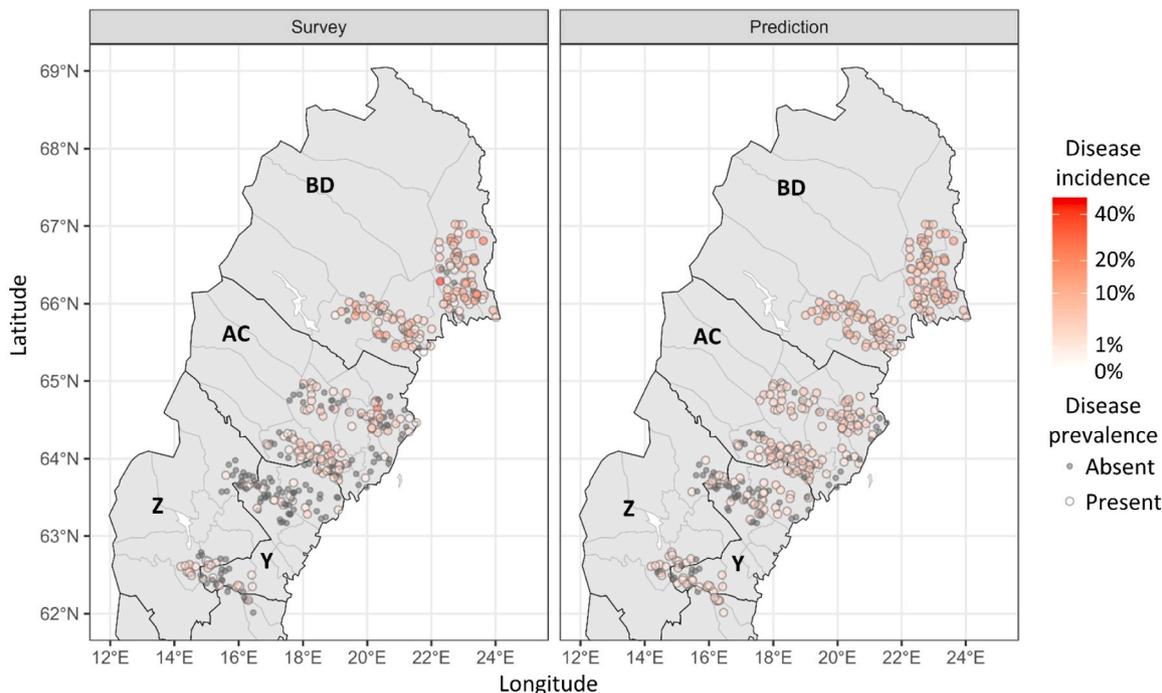
Fig. 3. Scots pine blister rust disease incidence observed in the surveys (left) and predicted based on the beta regression model (right). AC: Västerbotten. BD: Norrbotten. YZ: Jämtland & Västernorrland.

3.4. Climate change is predicted to increase the SPBR incidence in northern Sweden

With climate projection data in June from 2041 to 2070, and from 2071 to 2100 under RCP2.6, RCP4.5 and RCP8.5 scenarios, the predicted future SPBR incidence is shown in Supplementary Figure 2. The increase of SPBR disease incidence is shown in Fig. 4. It is important to note that these projections reflect only the influence of climate variables. Other potentially dynamic factors (e.g. stand age, *Melampyrum* abundance) were held constant in the analysis.

Under RCP2.6, minimal increases in SPBR incidence were projected. The absolute increase of stands in all three counties was expected to be less than 5 % by 2070 and 2100 (Fig. 5). Under RCP4.5, small absolute increases (<5 %) in SPBR incidence were predicted in Västerbotten (AC), Jämtland and Västenorrland (YZ), while moderate increases (5 % — 10 %) were projected in some stands in Norrbotten (BD) by 2070 and 2100. Under RCP8.5, more substantial increases in SPBR incidence were predicted, including increases of up to 20 % in several stands in Norrbotten (BD).

In all RCP scenarios, the most pronounced absolute increases in SPBR incidence were expected to occur in northern regions, particularly Norrbotten (BD), while southern areas were projected to experience small absolute increases (Fig. 5 A). However, the relative increases of the incidence would be higher in Jämtland and Västernorrland (YZ) by 2070, and Västerbotten (AC), Jämtland and Västernorrland (YZ) by

2100, where climate change might double or triple the SPBR incidence (Fig. 5 B).

4. Discussion

4.1. Geographical distribution of SPBR in Northern Sweden

The four counties included in the study— Norrbotten (BD), Västerbotten (AC), Jämtland (Z), and Västernorrland (Y) have 5.7, 3.9, 3.4, and 1.8 million hectares of forestland, which is equivalent to 58 %, 72 %, 70 % and 88 % of the total land area. Scots pine accounts for 58 %, 47 %, 39 % and 37 % of the standing volume in the production forest in these counties (SLU National Forest Inventory, 2023). Survey data confirmed earlier reports from the Swedish National Forest Inventory showing that SPBR causes the most severe damage in Norrbotten, the northernmost county (SLU National Forest Inventory, 2023). Both GLMM and beta regression results showed that SPBR presence and incidence increased toward the northeast (higher longitude and latitude) and with higher elevation. A similar trend has been reported for white pine blister rust (WPBR) caused by *C. ribicola* in North America, where higher latitude was linked to greater disease risk (Dahir and Carlson, 2001; White et al., 2002). In addition, WPBR incidence was also significantly correlated with higher topographic position (Dahir and Carlson, 2001) or increased until it peaked at around 2800 m (Thoma et al., 2019). This association is potentially due to lower evaporation
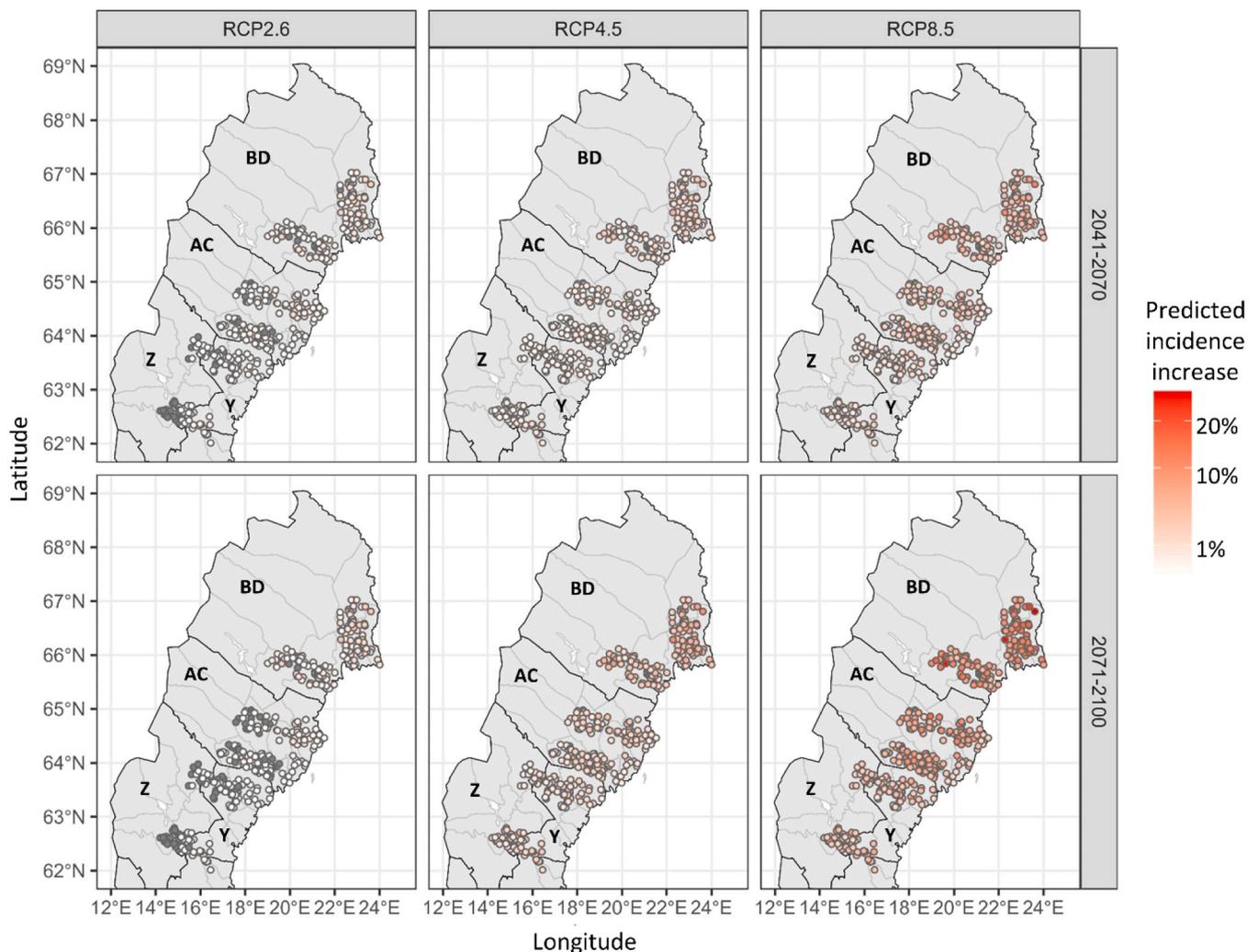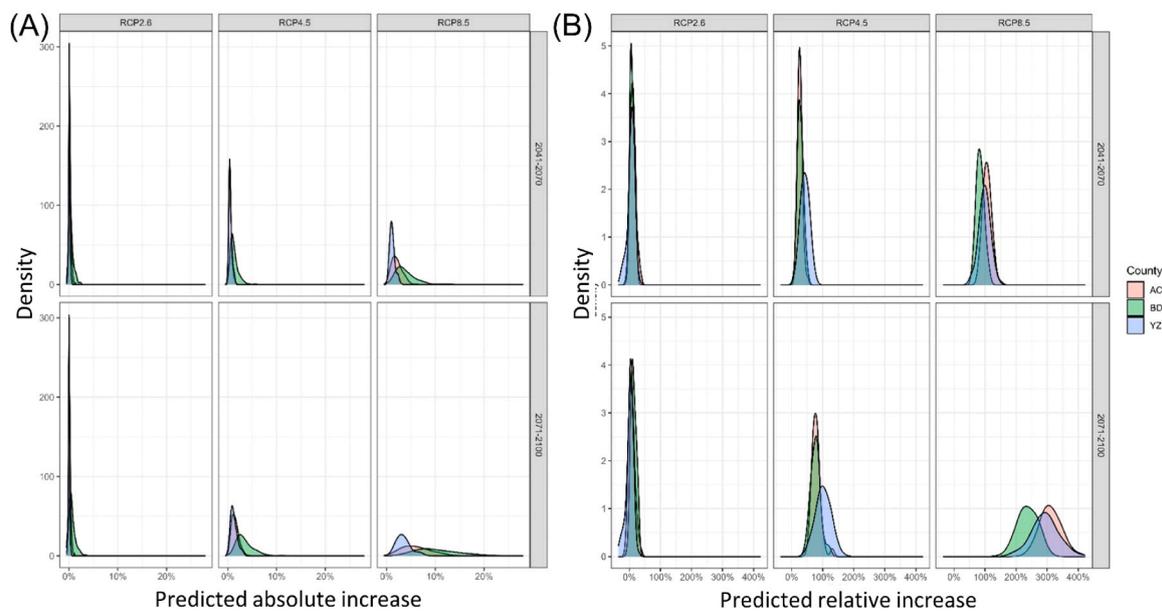

Fig. 4. The impact of climate change on the absolute increase of the Scots pine blister rust disease incidence in different Representative Concentration Pathway (RCP) scenarios in 2041–2070 and 2071–2100. Solid gray dots indicate no increase. AC: Västerbotten. BD: Norrbotten. YZ: Jämtland & Västernorrland.

Fig. 5. Density plot of the number of stand distribution of Scots pine blister rust disease incidence increase in different Representative Concentration Pathway (RCP) scenarios in 2041–2070 and 2071–2100. A: Absolute increase; B: Relative increase. AC: Västerbotten. BD: Norrbotten. YZ: Jämtland & Västernorrland.

rates and higher moisture availability in higher latitude (White et al., 2002) and frequent water condensation at elevated sites, which provides free water for spore germination and infection.

4.2. SPBR epidemics are associated with stand age, host availability, and soil moisture

SPBR presence and incidence are higher in older stands, which likely reflects the cumulative nature of infections over time rather than age-related susceptibility in pine trees. SPBR infection occurs primarily in current-year needles and shoots (Samils and Stenlid, 2022). After infection through the stomata, the pathogen grows towards the stem and needs two to six years to develop aecia with aeciospores (Kaitera, 2000). Previous studies based on naturally infected pine stands and field trials in Sweden and Finland showed that fresh aecia could occur in shoots 3–20 years of age (Kaitera, 2000; Persson et al., 2024). Earlier studies (Rennerfelt, 1947; Van Der Kamp, 1970) found that *C. pini* aecia were most frequent in 2 – 4-year-old pine shoots; the cankers would stay active for several years and might produce aeciospores every summer to start the new life cycle.

GLMM results indicated that SPBR presence was positively associated with higher pine proportion, reflecting higher host availability to the pathogen. Higher tree diversity in a mixed forest usually improves forest resilience to tree diseases (Roberts et al., 2020). More frequent occurrences of non-hosts (spruce and birch in the case of SPBR) can interrupt the spread of pathogen inoculum. For example, Californian coastal forests with lower densities of tanoaks in mixtures with non-host neighbour species had lower *Phytophthora ramorum* transmission and reduced tanoak mortality (Cobb, 2022). In contrast, beta regression revealed an inverse relationship between pine proportion and disease incidence. This may be due to SPBR-induced mortality, which has reduced pine density in highly infected areas, since early infection in young trees leads to canker in the main stem that can girdle and kill the whole tree (Kim et al., 2021).

Due to the critical role of *Melampyrum* as the telial host in *C. pini* life cycle, its presence is evidently a risk factor for SPBR. Both GLMM and beta regression confirmed that frequent presence of *Melampyrum* was strongly associated with higher SPBR incidence, supporting its important role in SPBR epidemiology (Kaitera and Hantula, 1998). This correlation is not always found between conifer rust and alternate (telial)

host distribution. For instance, Maloney (2011) found no association between the abundance of *Ribes* and the presence or absence of WPBR, which could be explained by the disconnection between *Ribes* leaf development and *C. ribicola* sporulation (Maloney, 2000) and the long dispersal distance of *Cronartium* basidiospores (van Arsdel et al., 2006). In our surveyed regions, *Melampyrum* is most abundant in June to July, which is a compatible timing with *C. pini* sporulation.

Soil moisture was among the strongest predictors of SPBR absence/presence. Drier soils were associated with a lower likelihood of disease, consistent with earlier observations (Dufberg and Lundholm, 2013). Scots pine is known to reduce transpiration and close stomata during drought stress to reduce transpiration and prevent substantial xylem embolism (Bucholz et al., 2020; Irvine et al., 1998; Panek and Goldstein, 2001), which likely inhibits spore entry and infection through stomata (Ragazzi et al., 2005). In WPBR inoculation tests, Patton and Spear (Patton RF and Spear RN, 1980) reported that the closure of stomata was important in preventing entry by the *C. ribicola* basidiospore germ tube into the substomatal tissue. In addition, drought can reduce the atmospheric relative humidity in the microclimate, which causes the failure of spore germination and colonization (Jactel et al., 2012). In a recent study of WPBR distribution modelling, Dudney et al. (2021) reported that drought might decrease WPBR infection risk at low elevations while simultaneously increasing infection risk at high elevations. However, the elevation of their study site was between 1300 m and 3000 m, while the highest elevation in our survey data was 525 m. Unlike disease absence/presence, soil moisture was not retained in the beta regression models for incidence. The cause behind this could be that these two analysis model two different types of data, the binary data at the plot level and the incidence in the open interval (0,1) after transformation. Soil moisture had more impact on "any disease (1) vs no disease (0)", but in beta regression with transformed 0, this predictor might not be significant enough to differentiate a low disease incidence and a high disease incidence. It could also reflect more complex or delayed effects of soil moisture on disease development in stands, or confounding from other variables such as elevation and climate.

4.3. Climate change is predicted to promote SPBR epidemics in northern Sweden

The weather in the recent decades in Sweden has become more

humid, especially in summer (SMHI, 2023); this could be one of the factors that caused the increase of SPBR epidemics (Samils and Stenlid, 2022). Year-round climate data (Dudney at al. 2021) or summer climate data (Shepherd et al., 2025) have been used in previous WPBR modelling in North America. We aimed to identify the time window when climatic conditions had the most critical impact on SPBR, therefore, the monthly average temperature, RH, and precipitation were tested in the models. In northern Sweden, the monthly temperature in late autumn to spring (November to April) is generally below zero, with precipitation falling as snow. The vegetation season starts in mid-spring when the average temperature has been above 5°C for four consecutive days and ends in mid-autumn when the average temperature has been below 5°C for four consecutive days (Häggström et al., 2021). Assuming that *C. pini* grows in the host tissue actively during the vegetation period, we only included climate data from May to October in the modelling.

The GLMM and beta regression identified that higher precipitation and higher temperature in June were associated with SPBR presence and higher incidence. This conclusion corresponds with the life cycle of *C. pini* in northern Sweden. In mid to late June, the aeciospores from autoecious *C. pini* infect pine through wounds (Kaitera and Nuorteva, 2008); the aeciospores from heteroecious *C. pini* infect the telial host (such as *Melampyrum* spp.) leaves. The upper and lower temperature limits for aeciospore germination are 5 °C and 30 °C, with an optimal temperature of 25 °C (Olembo, 1971). Therefore, there may be a mechanistic connection between increased temperatures and the increased disease incidence through the promotion of aeciospore germination. Currently, we lack information on the optimal temperature for the colonization of *C. pini* mycelium in pine or *Melampyrum* tissue; nonetheless, higher temperatures usually favour the growth and reproduction structure development of fungi, including some conifer rust species (Zhang et al., 2022). More frequent and higher amount of precipitation creates a moist condition that is essential for *C. pini* aeciospore germination and infection. The positive correlation between higher temperature and/or precipitation and disease incidence has also been reported in WPBR. In Canada, high WPBR incidences in white bark pine and limber pine were associated with high precipitation in spring and the cool/wet condition in summer, while the white bark pine mortality was higher in areas with higher summer heat moisture index (Shepherd et al., 2025). In the US, Dudney et al. (2021) developed a quadratic model of WPBR based on yearly average vapour pressure deficit (VPD); higher VPD suggests higher temperature and drought. The strong association between high precipitation and high humidity and basidiospore release has been known in many conifer rust, such as SPBR (Ragazzi, 1989, 1983), WPBR (Arsdel, 1967), and cherry spruce rust (Zhang et al., 2022). *Cronartium pini* basidiospores are dispersed from July to September in Italy and Finland (Kaitera et al., 2005; Moriondo, 1980). Interestingly, weather conditions in July to September were less predictive of SPBR outcomes in this study, but early summer conditions played a more critical role.

Climate change will have a greater impact at higher latitudes than lower latitudes (Deutsch et al., 2008) (IPCC 2025). The temperature increase since the end of 19th century in Sweden is two times higher than the global average (Schimanke et al., 2022). In the next decades, the temperature in June will continue to increase in Sweden (Strandberg et al., 2024). The precipitation indices, such as the number of rainy days in summer (June to August) will also increase in Northern Sweden (Chen et al., 2015). Based on the current trend, the emission scenario RCP4.5 is most likely to occur by the end of this century (Sarofim et al., 2024). In previous studies, the increasing temperature is projected to increase the plant disease risk at higher latitudes in the future (Chaloner et al., 2021; Dudney et al., 2021; Strandberg et al., 2024). Less attention has been drawn to the impact of future moisture conditions (water vapor, evaporation, and precipitation). Our models included both temperature and precipitation projections. Under the intermediate-emission scenario (RCP4.5), the model predicted relatively modest increases of SPBR incidences (<5 %) by the end of the century. However, under high-emission scenario (RCP8.5), SPBR incidence could increase by as much as 20 % in certain stands—primarily in Norrbotten. The high relative increase of SPBR in both scenarios, about 50–300 %, suggests the forestry sector needs to deploy effective disease management strategies, such as breeding pines with better resistance and avoiding regeneration with pine in regions with high SPBR risk.

4.4. Limitations in modelling

Cronartium pini has two life cycle forms that are morphologically indistinguishable. During the survey, aeciospore samples were occasionally collected to determine which form was prevalent in different regions. In general, heteroecious form dominates in Norrbotten, whereas autoecious form is more prevalent in Jämtland and Västernorrland; these two forms can coexist in the same stand, especially in Västerbotten (Zhang and Samils, 2024). A significant number of aeciospore samples should be collected from each stand to determine the dominant form of *C. pini*. Therefore, the form information is not included in this project. The differences in their life-cycles suggest these two forms may respond differently to environmental factors; however, this difference is not specifically addressed in our analysis. The beta-regression of SPBR incidence included counties as one of the explanatory variables, which may account for the variance caused by form differences. Future studies should investigate the differences in epidemiology between the two forms.

Our predictions of future SPBR incidences only reflect the direct effects of climate. Future changes in other variables, such as pine density, stand age, and *Melampyrum* abundance, are not accounted for. For instance, *M. sylvaticum* has already expanded upward in elevation over the past several decades (Kullman, 2010), suggesting that host distribution will likely shift with changing climates. Furthermore, long-term climate change could alter host-pathogen interactions in ways that are currently difficult to model. Future studies should address the evolutionary responses and adaptation capacities of *C. pini*, Scots pine, and *Melampyrum* spp. under projected climate conditions. Host resistance, fungal aggressiveness, and vector dynamics may all shift, necessitating ongoing monitoring and updated epidemiological models.

5. Conclusions

In summary, our study provides new insight into the risk factors driving SPBR outbreaks in northern Sweden. Besides natural accumulation of infections in older stands and known geographical aggregation, we identified elevation, moist soil, presence of *Melampyrum*, and high temperature and precipitation in June as the key risk factors for the presence and high incidence of this disease. Climate change is projected to amplify SPBR incidence, particularly in northern regions, but current models likely underestimate the full scope of future epidemics. More knowledge on the broader ecological and evolutionary factors will be valuable to support sustainable forest management and disease mitigation strategies.

CRediT authorship contribution statement

Ke Zhang: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Henrik Svennerstam:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

Generative AI was used in the grammar check of the final draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123603.

Data availability

The datasets are available from both authors upon reasonable request, markdown file of the data analysis is available from KZ upon reasonable request.

References

Arsdel, E.Van, 1967. The nocturnal diffusion and transport of spores. Phytopathology 57, 1221–1229.

Bucholz, E.R., Waring, K.M., Kolb, T.E., Swenson, J.K., Whipple, A.V., 2020. Water relations and drought response of *Pinus strobiformis*. Can. J. For. Res. 50, 905–916.

Chaloner, T.M., Gurr, S.J., Bebber, D.P., 2021. Plant pathogen infection risk tracks global crop yields under climate change. Nat. Clim. Change 11, 710–715. https://doi.org/10.1038/s41558-021-01104-8.

Chen, D., Achberger, C., Ou, T., Postgård, U., Walther, A., Liao, Y., 2015. Projecting future local precipitation and its extremes for sweden. Geogr. Ann. Ser. A Phys. Geogr. 97, 25–39. https://doi.org/10.1111/GEOA.12084.

Cobb, R.C., 2022. The intertwined problems of wildfire, forest disease, and climate change interactions. Curr. For. Rep. 8, 214–228. https://doi.org/10.1007/s40725-022-00161-2.

Copernicus Climate Change Service, Climate Data Store, 2019. CORDEX regional climate model data on single levels. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). DOI: 10.24381/cds.bc91edc3 (Accessed on 31-3-2023).

Dahir, S.E., Carlson, J.E.C., 2001. Incidence of white pine blister rust in a high-hazard region of Wisconsin. North. J. Appl. For. 18, 81–86. https://doi.org/10.1093/njaf/18.3.81.

Dalrymple, S.E., 2007. Biological flora of the British Isles: *Melampyrum sylvaticum* L. J. Ecol. 95, 583–597. https://doi.org/10.1111/J.1365-2745.2007.01234.X.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. USA 105, 6668–6672. https://doi.org/10.1073/PNAS.0709472105/SUPPL_FILE/SD1.XLS.

Dudney, J., Willing, C.E., Das, A.J., Latimer, A.M., Nesmith, J.C.B., Battles, J.J., 2021. Nonlinear shifts in infectious rust disease due to climate change. Nat. Commun. 12, 1–13. https://doi.org/10.1038/s41467-021-25182-6.

Dufberg, J., Lundholm, A., 2013. Förekomst av törskate (*Cronartium flaccidum*, *Peridermium pini*) på tall (*Pinus sylvestris*) i relation till markfuktighet och fältskikt. URL ⟨http://urn.kb.se/resolve?urn=urn:nbn:se:slu:epsilon-s-2181⟩.

Garrett, K.A., Madden, L.V., Hughes, G., Pfender, W.F., 2004. New applications of statistical tools in plant pathology. Phytopathology 94, 999–1003. https://doi.org/10.1094/PHYTO.2004.94.9.999.

Häggström, B., Domevscik, M., Öhlund, J., Nordin, A., 2021. Survival and growth of Scots pine (*Pinus sylvestris*) seedlings in north Sweden: effects of planting position and arginine phosphate addition. Scand. J. For. Res. 36, 423–433. https://doi.org/10.1080/02827581.2021.1957999.

Irvine, J., Perks, M.P., Magnani, F., Grace, J., 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. Tree Physiol. 18, 393–402. https://doi.org/10.1093/TREEPHYS/18.6.393.

Iturritxa, E., Mesanza, N., Brenning, A., 2015. Spatial analysis of the risk of major forest diseases in Monterey pine plantations. Plant Pathol. 64, 880–889. https://doi.org/10.1111/ppa.12328.

Jactel, H., Petit, J., Desprez-Loustau, M.L., Delzon, S., Piou, D., Battisti, A., Koricheva, J., 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. Glob. Change Biol. 18, 267–276. https://doi.org/10.1111/J.1365-2486.2011.02512.X.

Kaitera, J., 2000. Analysis of Cronartium flaccidum lesion development on pole-stage Scots pines. Silva Fenn. 34, 21–27.

Kaitera, J., 2002. Short-term effect of thinning on *Pinus sylvestris* damage and sporulation caused by *Cronartium flaccidum*. Scand. J. Res 17, 158–165. https://doi.org/10.1080/028275802753626809.

Kaitera, J., Aalto, T., Jalkanen, R., 1994. Effect of resin-top disease caused by *Peridermium pini* on the volume and value of *Pinus sylvestris* saw timber and pulpwood. Scand. J. For. Res. 9, 376–381. https://doi.org/10.1080/02827589409382854.

Kaitera, J., Hantula, J., 1998. *Melampyrum sylvaticum*, a new alternate host for pine stem rust *Cronartium flaccidum*. Mycologia 90, 1028–1030. https://doi.org/10.1080/00275514.1998.12027001.

Kaitera, J., Nuorteva, H., Hantula, J., 2005. Distribution and frequency of *Cronartium flaccidum* on *Melampyrum* spp. in Finland. Can. J. For. Res. 35, 229–234. https://doi.org/10.1139/X04-167.

Kaitera, J., Nuorteva, H., 2008. Inoculations of eight Pinus species with *Cronartium* and *Peridermium* stem rusts. Ecol. Manag. 255, 973–981. https://doi.org/10.1016/J.FORECO.2007.10.005.

Kaitera, J., Piispanen, J., Bergmann, U., 2021. Terpene and resin acid contents in Scots pine stem lesions colonized by the rust fungus *Cronartium pini*. Pathol 51. https://doi.org/10.1111/EFP.12700.

Kim, M.S., Hantula, J., Kaitera, J., Zambino, P.J., Woodward, S., Richardson, B.A., Stewart, J.E., Spaine, P., Shaw, D.C., Takeuchi, Y., Klopfenstein, N.B., 2021. Recovery plan for Scots pine blister rust caused by *Cronartium pini*. Plant Health Prog. 23, 105–130. https://doi.org/10.1094/PHP-06-21-0099-RP.

Kullman, L., 2010. A richer, greener and smaller alpine world: review and projection of warming-induced plant cover change in the Swedish Scandes. Ambio 39, 159–169. https://doi.org/10.1007/S13280-010-0021-8/FIGURES/11.

Maloney, P.E., 2000. Topics in forest pathology and ecology in the Sierra Nevada and the Sierra San Pedro Martir. Baja. Dissertation, Davis, CA, p. 122.

Maloney, P.E., 2011. Incidence and distribution of white pine blister rust in the high-elevation forests of California. For. Pathol. 41, 308–316. https://doi.org/10.1111/j.1439-0329.2011.00732.x.

Marozas, V., Racinskas, J., Bartkevicius, E., 2007. Dynamics of ground vegetation after surface fires in hemiboreal *Pinus sylvestris* forests. Ecol. Manag. 250, 47–55. https://doi.org/10.1016/j.foreco.2007.03.008.

Martínez-Minaya, J., Conesa, D., López-Quílez, A., Mira, J.L., Vicent, A., 2021. Modeling inoculum availability of *Plurivorosphaerella nawae* in persimmon leaf litter with Bayesian beta regression. Phytopathology 111, 1184–1192. https://doi.org/10.1094/PHYTO-08-20-0359-R.

Martinsson, O., Nilsson, B., 1987. The impact of *Cronartium flaccidum* on the growth of *Pinus sylvestris*. Scand. J. For. Res. 2, 349–357. https://doi.org/10.1080/02827588709382472.

Moriondo, F., 1980. Features of *Cronartium flaccidum* and its hosts in Italy. Phytopathol. Mediterr. 19, 35–43.

Newcomb, M., Upper, C.D., Rouse, D.I., 2010. Factors contributing to seasonal fluctuations in rust severity on *Ribes missouriense* caused by *Cronartium ribicola*. Phytopathology 100, 986–996. https://doi.org/10.1094/PHYTO-12-09-0349.

Nilsson, U., Elfving, B., Karlsson, K., 2012. Productivity of Norway spruce compared to Scots pine in the interior of Northern Sweden. Silva Fenn. 46, 197–209. https://doi.org/10.14214/sf.54.

Nutter, F.W., Esker, P.D., Netto, R.A.C., 2006. Disease assessment concepts and the advancements made in improving the accuracy and precision of plant disease data. Eur. J. Plant Pathol. 115, 95–103. https://doi.org/10.1007/s10658-005-1230-z.

Olembo, T.W., 1971. A study of some factors of resistance of *Pinus sylvestris* L. to *Peridermium pini* (Pers.) Lev. For. Int. J. For. Res. 44, 81–86. https://doi.org/10.1093/FORESTRY/44.1.81.

Ostonen, I., Lõhmus, K., Helmisaari, H.S., Truu, J., Meel, S., 2007. Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. Tree Physiol. 27, 1627–1634. https://doi.org/10.1093/TREEPHYS/27.11.1627.

Panek, J.A., Goldstein, A.H., 2001. Response of stomatal conductance to drought in ponderosa pine: implications for carbon and ozone uptake. Tree Physiol. 21, 337–344. https://doi.org/10.1093/TREEPHYS/21.5.337.

Patton, R.F., Spear, R.N., 1980. Stomatal influences on white pine blister rust infection on JSTOR. Phytopathol. Mediterr. 19, 1–7.

Persson, T., Hall, D., Barklund, P., Samils, B., Gull, B.A., 2024. The inheritance of resistance to Scots pine blister rust in *Pinus sylvestris*. Ecol. Manag. 568, 122135. https://doi.org/10.1016/J.FORECO.2024.122135.

Post, E., Alley, R.B., Christensen, T.R., Macias-Fauria, M., Forbes, B.C., Gooseff, M.N., Iler, A., Kerby, J.T., Laidre, K.L., Mann, M.E., Olofsson, J., Stroeve, J.C., Ulmer, F., Virginia, R.A., Wang, M., 2019. The polar regions in a 2°C warmer world. Sci. Adv. 5. https://doi.org/10.1126/SCIADV.AAW9883.

Ragazzi, A., 1983. Development of *Cronartium flaccidum* (Alb. et Schw.) Wint. on *Vincetoxicum officinale* Moench in connection with some environmental factors. Phytopathol. Z. 108, 160–171.

Ragazzi, A., 1989. Past, present, and future of *Cronartium flaccidum* in Italy. Phytopathol. Mediterr. 28, 5–9.

Ragazzi, A., Longo, N., Naldini, B., Moricca, S., Dellavalle, I., 2005. Basidiospore-derived penetration by species of *Cronartium* and *Melampsora*: an Outline. In: Pei, M.H., McCracken, A.R. (Eds.), Rust Diseases of Willow and Poplar, 14. CABI publishing, pp. 161–174. https://doi.org/10.1079/9780851999999.0161.

Rennerfelt, E., 1947. The occurrence of the blister-rust stage in Scots pine stands attacked by *Peridermium*. Norrl. Skogsvardsforb. Tidskr. 191, 215.

Roberts, M., Gilligan, C.A., Kleczkowski, A., Hanley, N., Whalley, A.E., Healey, J.R., 2020. The effect of forest management options on forest resilience to pathogens. Front. For. Glob. Change 3, 480727. https://doi.org/10.3389/FFGC.2020.0000.

Robin, C., Andanson, A., Saint-Jean, G., Fabreguettes, O., Dutech, C., 2017. What was old is new again: thermal adaptation within clonal lineages during range expansion in a fungal pathogen. Mol. Ecol. 26, 1952–1963. https://doi.org/10.1111/mec.14039.

Rosenzweig, C., Elliott, J., Deryng, D., Ruane, A.C., Müller, C., Arneth, A., Boote, K.J., Folberth, C., Glotter, M., Khabarov, N., Neumann, K., Piontek, F., Pugh, T.A.M., Schmid, E., Stehfest, E., Yang, H., Jones, J.W., 2014. Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. Proc. Natl. Acad. Sci. USA 111, 3268–3273. https://doi.org/10.1073/PNAS.1222463110.

Ruokolainen, L., Fennici, K.S., 2006. The succession of boreal forest vegetation during ten years after slash-burning in Koli National Park, eastern Finland. Ann. Bot. Fenn. 43, 363–378.

Samils, B., Stenlid, J., 2022. A review of biology, epidemiology and management of Cronartium pini with emphasis on Northern Europe. Scand. J. Res 37, 153–171. https://doi.org/10.1080/02827581.2022.2085322.

Sarofim, M.C., Smith, C.J., Malek, P., McDuffie, E.E., Hartin, C.A., Lay, C.R., McGrath, S., 2024. High radiative forcing climate scenario relevance analyzed with a ten-million-member ensemble. Nat. Commun. 15, 8185. https://doi.org/10.1038/s41467-024-52437-9.

Schimanke, S., Joelsson, M., Andersson, S., Carlund, T., Wern, L., Hellström, S., Kjellström, E., 2022. Observerad klimatförändring i Sverige 1860–2021. Retrieved from ⟨https://urn.kb.se/resolve?urn=urn:nbn:se:smhi:diva-6362⟩.

Schnepf, C.C., Schwandt, J.W., 2006. Silvicultural and economic considerations IN Pruning western white pine: a vital tool for species restoration. Pac. Northwest Ext. Publ.PNW-584. pp 35. Retrieved from ⟨https://verso.uidaho.edu/esploro/outputs/996749742401851⟩.

Shepherd, B., Krakowski, J., Moody, R., Reid, I., Murray, M.P., Stafl, N., Sissons, R., Alger, G., Park, J., McLellan, C., Schwarz, C.J., Smith, C.M., 2025. Climate dominates geographic influences on whitebark pine and limber pine trends and landscape patterns in Canada. Can. J. For. Res. 55, 1–19. https://doi.org/10.1139/cjfr-2024-0114.

Skogsstyrelsen SKADOR PÅ SKOG DEL 2 Gamla och nya epidemier och utbrott Intensiv. skogsbruk och Framt. Tek. Klim. och skogsskador 2017.Retrieved from ⟨https://www.skogsstyrelsen.se/globalassets/mer-om-skog/skogsskotselserien/skogsskotselserien-12-skador-pa-skog-del-2-gamla-och-nya-epidemier-och-utbrott-pa-skog.pdf⟩)

SLU National Forest Inventory, 2023. Riksskogs Taxeringen. Officiell statistik om de svenska skogarna. ⟨https://skogsstatistik.slu.se/pxweb/sv/OffStat/⟩.

SMHI, 2023. Sveriges klimat har blivit varmare och blötare. SMHI. ⟨https://www.smhi.se/kunskapsbanken/klimat/sveriges-klimat/sveriges-klimat-har-blivit-varmare-och-blotare-1.21614⟩ (URL).

Strandberg, G., Andersson, B., Berlin, A., 2024. Plant pathogen infection risk and climate change in the Nordic and Baltic countries. Environ. Res Commun. 6, 031008. https://doi.org/10.1088/2515-7620/AD352A.

Svennerstam, H., 2023. Arbetsrapport 11782023 Törskateinventering i ungskog. ⟨https://www.skogforsk.se/contentassets/6b2136e7326d4bc18d18cdd7201e6285/arbetsrapport-1178-2023-torskateinventering-i-ungskog_231128.pdf⟩ (URL).

Thoma, D.P., Shanahan, E.K., Irvine, K.M., 2019. Climatic correlates of white pine blister rust infection in whitebark pine in the greater yellowstone ecosystem. Forests 10, 666. https://doi.org/10.3390/F10080666.

Tillberg, E., 2010. Resin top disease, *Cronartium flaccidum*, and occurrence of alternate hosts, *Melampyrum* spp. in young stands of *Pinus sylvestris* treated with prescribed burning and mechanical scarification. Master Thesis SLU. ⟨https://stud.epsilon.slu.se/1094/1/Tillberg_E_100423.pdf⟩.

van Arsdel, E.P., Geils, B.W., Zambino, P.J., 2006. Epidemiology for hazard rating of white pine blister rust. In: Guyon, J.C. comp. Proceedings of the 53rd Western International Forest Disease Work Conference; 2005 September 26–30; Jackson, WY. U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden UT.

van Der Kamp, B.J., 1970. *Peridermium pini* (Pers.) Lev. and the resin-top disease of Scots Pine: III. Infection and Lesion Development. Forestry 43, 73–88. https://doi.org/10.1093/FORESTRY/43.1.73.

van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. Clim. Change 109, 5. https://doi.org/10.1007/s10584-011-0148-z.

White, M.A., Brown, T.N., Host, G.E., 2002. Landscape analysis of risk factors for white pine blister rust in the mixed forest province of Minnesota, U.S.A. Can. J. For. Res. 32, 1639–1650. https://doi.org/10.1139/x02-078.

Wulff, S., Hansson, P., 2009. Riktad skogsskadeinventering Av. törskaterost 2008. Umeå, URL: https://res. slu. se/id/publ/128840.

Wulff, S., Hansson, P., 2013. Nation riktad skadeinventering (NRS) 2012. Arbetsrapport/Sver. Lantbr. Inst. F. öR. Skoglig Resur. ållning (386). URL. ⟨https://publications.slu.se/?file=publ/show&id=51717⟩ (URL).

Wulff, S., Walheim, M., Roberge, C., 2022. Inventering av skador på ungskog 2022 i Norrbotten, Västerbotten, Västernorrland och Jämtlans län. SLU Inst. F. öR. Skoglig Resur. ållning 20. ⟨https://internt.slu.se/globalassets/ew/org/inst/sresh/miljoanalys/nrs/wulff_walheim_roberge_2022.pdf⟩ (URL).

Zeglen, S., Diprose, R.S., 2021. Efficacy of delayed entry low branch sanitation pruning in preventing mortality of western white pine infected with white pine blister rust. Can. J. Plant Pathol. 43, S358–S369. https://doi.org/10.1080/07060661.2021.1916602.

Zhang, K., Kaitera, J., Samils, B., Olson, Å., 2022. Temporal and spatial dispersal of *Thekopsora areolata* basidiospores, aeciospores, and urediniospores. Plant Pathol. 71, 668–683. https://doi.org/10.1111/ppa.13510.

Zhang, K., Samils, B., 2024. Differences in population structure and zygosity between heteroecious and autoecious forms of *Cronartium pini* suggest selfing in the autoecious form. Fungal Biol. https://doi.org/10.1016/j.funbio.2024.09.007.