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Fertile Soils Increase Susceptibility of *Pinus sylvestris* to *Cronartium pini*

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ABSTRACT

Cronartium pini, Scots pine blister rust, is a rust fungus that has caused severe damage in both old and young Scots pine (*P. sylvestris*) forest stands in northern Fennoscandia. To understand the many drivers of these outbreaks we examined putative factors and their explanatory power of *C. pini* incidence based on data collected in Lapland, northern Finland. Diseased stands were selected from the 10th Finnish National Forest Inventory (NFI) and control plots were randomly selected from the 11th NFI. A damage assessment was conducted in 2014, 4 years later in separate 10–15 sample plots within each stand. Stand and tree characteristics, including incidence of *C. pini*, were recorded. Site type (fertility) and age of trees significantly explained the incidence of *C. pini* in sample plots. Incidence of *C. pini* infection increased significantly in fertile sites, while the risk was non-significant in more arid sites. Risk of infection by *C. pini* was significantly reduced when the proportion of deciduous trees increased. There was an increased infection risk (up to over 50%) proportional to how well the trees grew for the last 5 years if *Melampyrum* spp. were present. Our results support previous observations that fertile sites are more susceptible to infection by *C. pini*. For the first time, we also demonstrate that an increase in the number of deciduous trees reduces the risk of *C. pini* infections. These results offer tools to improve forest management practices in reducing the risk of damage caused by *C. pini* in northern pine forests.

1 | Introduction

Scots pine (*Pinus sylvestris* L.) is the dominant tree species in the northern boreal forests of Lapland, northern Finland, where it covers 76% of a total of 4,998,000 ha forest land (Natural Resources Institute Finland 2019). A pathogen that causes serious damage on *P. sylvestris* in northern Finland is Scots pine blister rust (*Cronartium pini* (Willd.) Jørst). The rust consists of two life-cycle forms of which the autoecious form (parasitic organism that completes all stages of its life cycle on a single host species) spreads directly from pine to pine and the heteroecious form via alternate host plants (Kim et al. 2022).

The autoecious nature of the rust was first described by successful inoculations on pine in the early 1900s (Haack 1914). Since that the autoecious life-cycle form has been reported throughout Europe (Lagerberg 1912; Klebahn 1918, 1938; Jørstad 1928; Rennerfelt 1943; van der Kamp 1970; Gibbs et al. 1987; Greig 1987; Diamandis and de Kam 1986; Kaitera 2003; Kaitera and Nuorteva 2008). The heteroecious life-cycle form has been described on various alternate hosts plants in Europe (e.g., Liro 1908; Ragazzi 1983; Kaitera et al. 1999). The early literature of alternate host range of *C. pini* was summarized by Gäumann (1959) and updated by Kim et al. (2022). In northern boreal forests, species of Orobanchaceae are important, of which *Melampyrum sylvaticum* L. is the most important susceptible species (Kaitera and Hantula 1998). This species is frequent especially in most fertile nutrient-rich sites in Finland (Hämet-Ahti et al. 1984; Reinikainen et al. 2000). Besides on *M. sylvaticum*, *C. pini* has been found in natural forests on

Melampyrum pratense L. (Kaitera et al. 2024), *Euphrasia* sp. (Kaitera et al. 2018) and *Rhinanthus* sp. (Kaitera et al. 2018) in northern Finland. A high number of other plant species are, however, susceptible to *C. pini* (Kim et al. 2022). In a study in western Lapland, several plant species including *Veronica longifolia* L., *V. daurica* Steven, *Euphrasia stricta* L., *Castilleja miniata* Dougl. ex. Hook., *Myrica gale* L., *Impatiens balsamina* L. and *Vincetoxicum hirundinaria* Medicus were infected by *C. pini* under natural inoculum (Kaitera et al. 2015). Therefore, a high number of plant species are susceptible to the northern Finnish *C. pini*, which has also been shown by a series of inoculation experiments using Northern Finnish spores (e.g., Kim et al. 2022). Occurrence of *C. pini* on alternate hosts other than *Melampyrum* in natural forests is unknown in northern Finland, and therefore, also other plant species may spread *C. pini* in northern Finland.

None of the National Forest Inventories conducted in northern Finland include data of accurate determination of the specific life-cycle form of *C. pini*. According to the 7th National Forest Inventory (NFI7) in Kuusamo, Northern Ostrobothnia, 3.28% of the pine sample trees carried a stem lesion caused by *C. pini*. At the time, only a few percent of infected pines were < 50 years old, indicating that infected pine sapling stands were almost missing (Jalkanen 1989). According to Kaitera et al. (1994) *C. pini* caused significant growth and timber quality losses on *P. sylvestris* in the Kuusamo region. Similarly, *C. pini* was reported to cause losses in radial increment of pine trees in Sweden (Martinsson and Nilsson 1987). As comparison, Ylikojola and Nevalainen (2006) reported that the overall incidence of *C. pini* was 2%–3% based on the 8th NFI (National Forest Inventory) in Finland. In Lapland, the proportion of forest stands damaged by *C. pini* from all forest stands with pine increased from 2% to 3%, and the basal area with *C. pini* increased from 2% to 3.5% from 10th NFI to 13th NFI (Hantula et al. 2023). Recent calculations estimate that annual financial losses caused by *C. pini* are ca. 3.5 million euros in Finland (Hantula et al. 2023).

Already in the early 1980s, *P. sylvestris* seedling stands severely damaged by *C. pini* were recorded in southern Lapland and northern Ostrobothnia (Jalkanen 2003). Later, it was discovered that both life-cycle forms of *C. pini* occur in sapling stands in these areas (Hantula et al. 1998; Kaitera 2000; Kaitera and Kokko 2023; Samils et al. 2021). Both life-cycle forms also occur in sapling stands in northern Sweden, and populations of different life-cycle forms do not differ between Finland and Sweden and between southern and northern *C. pini* populations (Samils et al. 2021). Earlier, the causal life-cycle form of *C. pini* causing the disease on pines was suggested to be of the autoecious one, but a discovery of *C. pini* on *M. sylvaticum* indicated that also the heteroecious life-cycle form occurs in northern areas (Kaitera and Hantula 1998; Kaitera et al. 2005, 2011). However, silvicultural studies in 7–15 years-old pine sapling stands showed that damage caused by *C. pini* occurred in only 0.1% of pine sapling stands in Lapland and Kuusamo area in Northern Ostrobothnia in 2001 (Hyppönen et al. 2003; Hallikainen et al. 2004). In these studies, incidence of *C. pini* was highest in single municipalities of the Tornionjoki river valley, next to the Swedish border (Penttinen et al. 2002; Jalkanen 2003). Wulff et al. (2012), on the other hand, estimated that one third of all young pine stands with mean height of 1–4 m (131,000 ha) were infected by *C. pini* in inventories of the two northernmost territories of Sweden in 2007–2008. There is no accurate information of exact areas of affected stands available from northern Finland.

The Swedish *C. pini*-incidence and factors affecting the incidence were reported by Wulff et al. (2012), Wulff and Hansson (2013) and Zhang and Svennerstam (2026). The Finnish rust incidences in young plantations were reported by Penttinen et al. (2002), Hyppönen et al. (2003), Jalkanen (2003) and Hallikainen et al. (2004). Populations of different life-cycle forms of *C. pini* do not differ genetically within life-cycle forms between either northern or southern Swedish and Finnish rust populations, but populations of different life-cycle forms differ genetically from one another (Samils et al. 2011, 2021). The pathogenic variation of the heteroecious life-cycle form on alternate hosts is low between Swedish and Finnish spore sources regardless of the geographic origin (Kaitera et al. 2012). The pathogenic variation among Finnish geographic spore sources of the autoecious life-cycle form on *P. sylvestris* is low as well (Kaitera and Nuorteva 2008).

Factors affecting susceptibility of pine to *C. pini* have been studied either at general level or in detail with specific life-cycle forms: susceptibility is highly dependent on both pine provenances and individuals (Haack 1914; Pawsey 1964; Pei and Brodie 1995; Raddi et al. 1979). Many artificial inoculations on pine have been negative, suggesting that pine is highly resistant to *C. pini* (van der Kamp 1970; Kaitera 2003; Kaitera and Nuorteva 2008). Therefore, other predisposing factors may be more important at tree and stand level (Pawsey 1964). High site nutritional level may increase pine susceptibility to *C. pini* (Wulff et al. 2012; Wulff and Hansson 2013). Wulff and Hansson (2013) pinpointed the role of weather factors in predisposing pine to successful infection. Moisture and temperature are known to affect strongly fruiting and dissemination of spores of the heteroecious life-cycle form of *C. pini* (Ragazzi 1983; Ragazzi et al. 1989).

Abundant numbers of sapling stands occur at suitable age on fertile sites susceptible to *C. pini*, and there is a lack of information on the occurrence of the rust in young pine forests in northern Finland. Therefore, we carried out an inventory of the damage caused by *C. pini* aiming to (1) clarify factors affecting the *C. pini* incidence in sapling stands based on the National Forest Inventory (NFI10 and NFI11) plots in Lapland. Another aim was to (2) support forest owners to control already diseased forests and to reduce damages caused by *C. pini* in their forests in the future. As a high number of plant species can act as alternate hosts for *C. pini*, we also aimed to (3) clarify the impact of *Melampyrum* spp. on *C. pini* incidence. Our hypothesis was that site fertility and growth rate predispose *P. sylvestris* to *C. pini*.

2 | Materials and Methods

2.1 | Sampling and Measurements

Based on the NFI10 inventory, we had preliminary information on forest stands with observations of damage caused by *C. pini* in one or more sample plots of the stand. Random forest

stands from the NFI11 inventory with no prior information on damage caused by the fungus *C. pini* were also included as control stands in the 2014 measurements and modelling. The sample frame consisted of 16 (NFI10) and 13 (NFI11) *P. sylvestris*-dominated sapling stands in Finnish Lapland in 2009–2013. Sapling stand is defined here as a stand including pines with median height of 0.2–12.2 m and age of 5–60 years. (Table 1). Block design and NFIs' protocols for measurements in northern Finland and estimation of the damage caused by *C. pini* and other variables are described in detail in a field guide of National Forest Inventory (Valtakunnan metsien 11. inventointi (VMI11) 2009).

The continuous variables used at stand level in the plots in NFI10 and NFI11 were average temperature sum in 1961–90, altitude and Ca-concentration in soil. Average temperature sum in 1961–90 was calculated by plot coordinates using models described in Ojansuu and Henttonen (1983). Altitude was counted also by plot coordinates from a national model that covers whole Finland (https://asiointi.maanmittauslaitos.fi/karttapaikka/tiedostopalvelu/korkeusmalli?lang=fi). Ca-concentration in site was picked up also by plot coordinates from a geographic database in northern Finland (Salminen 2005; De Vos and Tarvainen 2006).

All together 29 sapling stands were specifically surveyed for stand and tree characteristics in 2014. Plots in these stands were located within the NFI sample stands but outside the original NFI plots. Each sample stand was surveyed by using 10 (in case the stand area < 5 ha) or 15 (≥ 5 ha) sample plots (size 50 m^2, $r = 3.99$ m). Distance between the sample plots was fixed within each stand but it varied between stands. Plots were located in either of the cardinal points of the compass. The variables measured or estimated in these sample plots that were used in the calculations later were site type fertility classes from the most fertile to the least fertile: ('moist', 'sub-dry', 'dry'), age, height and 5-year growth of median *P. sylvestris*, total number of various tree species (*P. sylvestris*, *P. abies*, deciduous trees), proportion of deciduous trees, presence of *Melampyrum* spp. and pines with branch damage symptoms caused by *C. pini*. Moist site is occupied mainly by *P. abies*, *P. sylvestris*, *B. pendula* and *Vaccinium myrtillus* L., sub-dry site by *P. sylvestris* and *Vaccinium vitis-idaea* L., and dry sites by *P. sylvestris* and *Calluna vulgaris* (L.) Hull (Lehto and Leikola 1987). In addition, time between the NFI10 and NFI11 inventory and the sampling inventory in 2014 was recorded (Table 1). Presence of *Melampyrum* spp. were recorded in the sample plots or next to them by classes of '*M. sylvaticum* occurs', '*M. pratense* occurs', 'both *Melampyrum* spp. occur', 'Unidentified *Melampyrum* occur', or '*Melampyrum* spp. are lacking'. However, in statistical analysis these observations were combined in two classes, '*Melampyrum* occurs' or '*Melampyrum* is lacking'.

TABLE 1 | Description of forest stands and sample plots.

	Damage caused by *C. pini* in the stand										
	C	D	C	D	C	D	C	D	C	D	
Stand and plot variables	**Minimum**		**Maximum**		**Mean**		**SD**		**Median**		***p***
Continuous variables at stand level											
Average temperature sum in 1961–1990, d.d.	698	663	940	967	787	789	70	103	790	756	0.861
Altitude, m a.s.l.	84	53	290	311	229	206	59	75	247	228	0.273
Calcium-concentration in site, ppm	1730	1500	6010	4780	2765	2706	1229	890	2190	2610	0.776
Continuous variables at sample-plot level											
C. pini-damaged pines, no. of sample plots	0	0	2	5	0.1	0.5	0.3	1.1	0	0	0.127
Pines with branch-symptoms, no. of sample plots	0	0	1	4	0.0	0.3	0.2	0.8	0	0	0.203
Age of pines, years (only plots with pine)	5	5	60	47	19.5	17.1	10.1	10.9	19	12	0.514
Height of pines, dm (only plots with pine)	2	2	103	122	39.4	35.4	23.3	33.0	40	13	0.668
5-year height growth of pines, dm (only plots with pine)	2	2	31	30	14.9	11.1	6.8	7.3	16	9	0.335
Total no. of trees per sample plot	1	1	33	27	8.7	9.9	4.5	4.7	8	9	0.215
No. of pines per sample plot	0	0	33	27	7.0	7.7	4.8	5.2	6.0	6.0	0.480
No. of spruces per sample plot	0	0	6	7	0.5	0.9	1.0	1.4	0	0	0.358
No. of birches per sample plot	0	0	10	10	1.1	1.1	1.8	2.1	0	0	0.729

Note: Modelled *p*-value for continuous variables is presented to test the difference between the groups based on the damage caused by *C. pini* (C = 'Control', D = 'Diseased') in the National Forest Inventories (NFI10 and NFI11). Modelled denotes mixed-effects zero-inflated negative binomial, mixed effects binomial (*Melampyrum* sp.) or log-transformed linear mixed effects model.
Abbreviations: a.s.l., above sea level; d.d., Degree days.

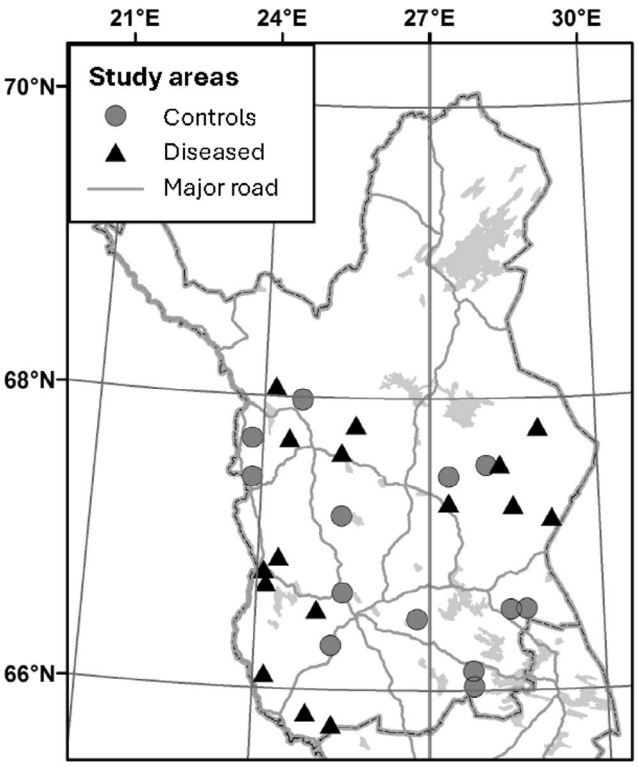

FIGURE 1 | The locations of the stands surveyed in 2014. The stands were classified either as 'Controls' or 'Diseased'.

The diseased and control stands (i.e., sub-samples) were named as 'Diseased' and 'Control' stands (Figure 1). The data with the tested variables (Table 1) was hierarchical. The binary response variable (a tree or several trees inside a sample plot) was either 'Diseased' or 'Control', and the potential explanatory variables (predictors) were measured at sample-plot level within each stand. In addition, some of the explanatory variables were measured at stand level.

2.2 | Statistical Analyses and Modelling

2.2.1 | Distributions of 'Diseased' and 'Control' Stands and Sample Plots

Due to a considerable over-dispersion and highly different sampling rates, the count data in the comparison between the sub-samples ('Diseased', 'Control') were modelled separately using negative binomial distribution assumption. The NB2 parameterization (Bolker 2015) of the variance was used. The NB2 variance can be expressed as $\text{variance} = \mu + \left(1 + \frac{\mu}{k}\right)$, where μ denotes expected value (mean) and k denotes a clumping parameter, also called as theta.

The differences in the stand characteristics of the two sub-samples were tested using log-transformed linear mixed effects models using stand as a random factor to avoid pseudo-replication and biased standard errors for the variables tested at sample-plot level. If the response variable consisted of counts (e.g., total number of trees), the negative binomial model using the stand as a random factor was used in testing the difference between the 'Diseased' and 'Control' sample plots. If the response variable was binary at the sample-plot level (the presence of *Melampyrum* spp. in a sample plot), the differences between the sub-samples were tested using binomial mixed models, stand being the random factor. The sample ('Diseased', 'Control') was the only explanatory variable in these models. Differences of the categorical variables between the sub-samples at stand level were tested using chi-squared test (Table 1). Further, it was tested whether the sub-samples differed in their characteristics at stand or sample-plot level (Table 1).

2.2.2 | Sample-Plot Disease Model

To study the effects enhancing the spread of disease caused by *C. pini*, binomial mixed models were computed separately for both sub-samples instead of weighting the sub-samples or including them in the same model. This made it possible to obtain a deeper interpretation of the effects of stand characteristics on disease caused by *C. pini* with a clearer comparison of the results.

The response variable in the models was considered Bernoulli-distributed. In the inventory, each sample plot was classified as 'Diseased' (1) or 'Control' (0). A 'Diseased' plot denoted that the disease caused by *C. pini* was recorded at least in one branch or stem of *P. sylvestris*. A stand was 'Diseased' if at least one plot carried trees with symptoms of *C. pini*. The model consisted of a fixed part (fixed factors and covariates) and the random factor of a stand. A log-link function was used between the response and linear predictors. A scale parameter in the binomial model was estimated rather than fixed as 1.

The binomial mixed model to predict the probability of an infected sample plot was described as follows:

$$y_{ij} \sim \text{binomial}\left(n_{ij}, p_{ij}\right)$$

$$\log_{it}\left(\pi_{ij}\right) = \ln\left(\frac{p_{ij}}{1 - p_{ij}}\right) = f\left(X_{ij}, \beta\right) + \mu_i,$$

where y denotes the probability of the event, that is, the sample plot with at least one infected *P. sylvestris*. Binomial (n,p) denotes the binomial distribution with parameters (n_{ij} describes binomial sample size, in our case the number of sample plots, and p is describing the proportion or probability of events, the occurrence of the infected sample plot). $\ln(p_{ij}/(1-p_{ij}))$ is a logit-link function and f(.) describes the linear function, the fixed predictors and their coefficients. Term μ_i denotes the random between-stands effect. The dispersion parameter of the logistic model was estimated.

The explanatory variables for the model were selected among the candidate variables (Table 1) using the data of the 'Diseased' stands. Then the significant variables and interactions in the model for the 'Diseased' stands were tested in the sub-sample of the 'Control' stands. The significances of the variables in the model for 'Control' stands were presented despite their significance to compare the two sub-samples.

Because the response in the explanatory (predictive) models was binary, the total number of trees was included in the models despite its significance at 5% risk level. It was assumed that the risk increases with increasing number of pines. When the number

of trees and the proportions of the tree species were included in the model, the predictions could be computed for the number of trees on a sample plot. The proportions of tree species [*P. sylvestris*, *P. abies* and deciduous trees (mainly *Betula* spp.)] in the sample plots (Figure 2) were tested and included in the models if they were statistically significant.

Receiver operating characteristics (ROC) curves were computed to determine the classification efficiency of the logistic models. If the value under the ROC curve approaches 1, the logistic model predicts events correctly (coded as 1 in the binomial response variable). The ROC curve was computed using the R software package ROCR (Sing et al. 2005). The linear mixed models for testing the differences between the 'Diseased' and 'Control' stands were estimated using the R package nlme (Pinheiro et al. 2013). The negative binomial models were computed using the R package glmm ADMB (Fournier et al. 2012). The binomial model was estimated using the R package MASS and its function glmm PQL (Venables and Ripley 2002). The fit of the binomial model was checked using the ROC curve. The predictions with the approximate confidence intervals were calculated using the R package effects (Fox 2003; Fox and Weisberg 2018, 2019). All modellings were carried out in the R statistical environment (R Core Team 2013).

3 | Results

3.1 | Comparison of the Variables Between the 'Diseased' and 'Control' Sub-Samples

The differences in stand characteristics between the sample plots and stands in both sub-samples were small and non-significant (Table 1). The number of *P. sylvestris* was 700–800 ha^{-1}, and the average number of diseased pines varied from 10 to 50 ha^{-1} in the 'Control' and 'Diseased' sub-samples, respectively (Table 1).

About 70% of all stands had been regenerated artificially using clearcutting, planting or direct seeding of pine. The proportion of natural regeneration using the seed-tree method was about one fifth in the stands. In the 'Diseased' sub-sample, the proportion of both direct seeding and planting of pine was about 40% (Table 2). On the other hand, about 60% of the stands in the 'Control' sub-sample had been planted.

Due to difficulties in identifying *Melampyrum* spp. by species in the field, a positive case of *Melampyrum* sp. was recorded if a single plant individual was present in the plot. However, the presence of *Melampyrum* sp. in the plot did not differ statistically significantly between the sub-samples (Table 3).

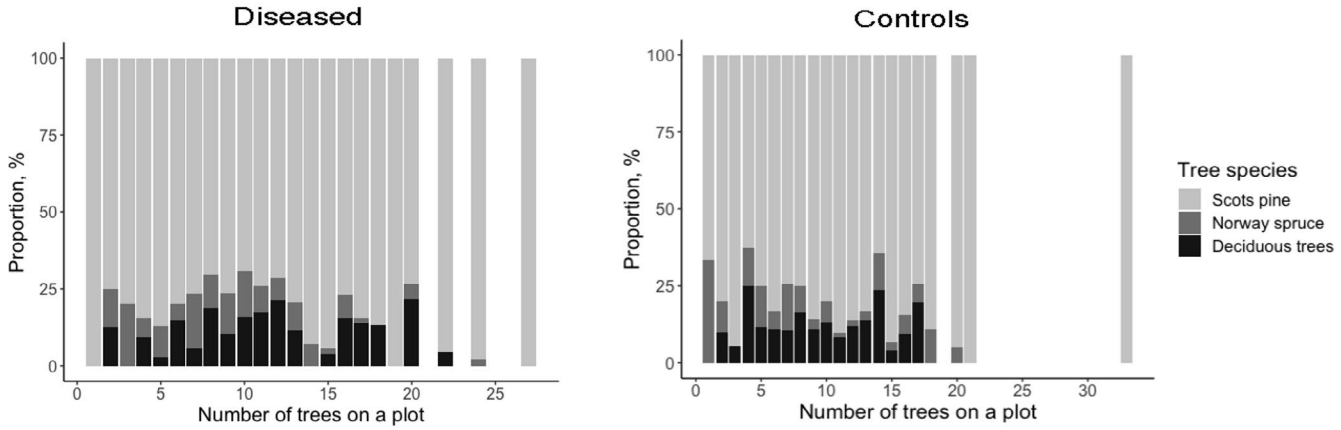

FIGURE 2 | The proportions of tree species in the sample plots. The stands were classified either as 'Controls' or 'Diseased'.

TABLE 2 | Distributions of categorical variables at stand level in percent and counts, and *p*-value of chi-squared test testing the counts.

Original tree species	***P. sylvestris***	***P. abies***	**Mixed**	***p***
'Control' (13 stands)	54 (7)	31 (4)	15 (2)	0.059
'Diseased' (16 stands)	69 (11)	0 (0)	31 (5)	
Cutting	**Clear-cutting**	**Seed-tree cutting**	**Something else**	
'Control' (13 stands)	77 (10)	15 (2)	8 (1)	0.296
'Diseased' (16 stands)	63 (10)	37 (6)	0 (0)	
Regeneration method	**Direct seeding**	**Planting**	**Natural regeneration**	
'Control' (13 stands)	23 (3)	62 (8)	15 (2)	0.494
'Diseased' (16 stands)	38 (6)	37 (6)	25 (4)	

TABLE 3 | Parameter estimates of the logistic mixed model.

Observed *C. pini*-damage in 2014	Diseased					Control				
Fixed effects	**Est.**	**Std.**	**df**	***t*-value**	***p***	**Est.**	**Std.**	**df**	***t*-value**	***p***
Intercept	−1.687	1.622	181	−1.040	0.300	−2.663	1.800	153	−1.479	0.141
Site type/fertility (ref. sub-dry or dry)	−3.562	0.709	181	−5.022	< 0.001	−2.004	0.705	153	−2.844	0.005
The age of *P. sylvestris*, years	0.168	0.036	181	4.658	< 0.001	0.027	0.032	153	0.830	0.408
Number of trees	−0.012	0.056	181	−0.211	0.833	0.007	0.075	153	0.091	0.927
Proportion of deciduous trees, %	−0.044	0.012	181	−3.541	0.001	−0.013	0.016	153	−0.821	0.413
Height growth of *P. sylvestris*, dm	−0.137	0.098	181	−1.401	0.163	0.090	0.075	153	1.196	0.234
Presence of *Melampyrum* sp. (ref. No)	−1.918	1.481	181	−1.259	0.197	0.174	1.876	153	0.093	0.926
Presence of *Melampyrum* sp. * Growth of *P. sylvestris*	0.261	0.102	181	2.563	0.011	−0.058	0.101	153	−0.572	0.568
Random effects										
Random forest stand variance	1.027					0.116				
Dispersion parameter	0.420					0.771				
Fit of the model										
ROC marginal	95.86%					79.75%				
ROC conditional	97.41%					81.90%				

Note: The response variable: Yes = at least one or No = no pines damaged by *C. pini* in the sample plot or in the stand of the survey of 2014. ROC marginal denotes the area under ROC curve (classification efficiency of the model) using the fixed part of the model only, and ROC conditional the area under ROC curve using both the fixed and random part of the model.
Abbreviations: df, degrees of freedom; Est., parameter estimate in the logit scale; *p*, the significance of the parameter; Std., its standard error.

Damage caused by *C. pini* was not detected in all the stands estimated earlier as diseased ones in NFI10. In the present study in 2014, damage caused by *C. pini* was recorded in 26.3% and 8.3% of the sample plots in the 'Diseased' and 'Control' sub-samples. These differences were statistically non-significant at 5% risk level at sample-plot level (Table 1). The small difference in the proportions at stand level showed that disease caused by *C. pini* was sporadic within the stands, and it was absent at sample-plot level in some stands despite the positive earlier disease estimation in NFI10.

In general, *P. sylvestris* dominated in the sample plots in both sub-samples, while the proportions of *Picea abies* (L.) Karst and of deciduous trees were < 25%. However, a mixture of tree species occurred regardless of the total number of trees in the plots (Figure 2).

3.2 | Modelling Disease Caused by *C. pini*

Stand characteristics affecting disease incidence of *C. pini* were more evident in diseased than control stands (Table 3, Figure 3a–e). Forest site type that described site fertility explained best the probability of *C. pini*-damaged pines in the sample plots (Table 3, Figure 3a). It was the only variable that significantly explained the risk of *C. pini damage* in both sub-samples. The predicted probabilities for moist or more fertile sites with the highest fertility were about 20% and 45% in the 'Control' and 'Diseased' sub-samples, respectively. The probabilities of the infection in the least fertile sub-dry or dry sites were nearly zero in both sub-samples (Table 3, Figure 3a).

The number of trees (similar to the number of pines) did not affect the damage risk caused by *C. pini* significantly at the 5% risk level (Table 3, Figure 3b). During the modelling process, the number of trees per tree species (*P. sylvestris*, *P. abies* or deciduous trees) was tested in the models. Only the number and proportion of deciduous trees were negatively significant.

Age of *P. sylvestris* trees increased considerably the probability of damage caused by *C. pini* in the diseased forest stands. In < 5-years-old seedlings the disease was very rare (not shown), but the probability of damage caused by *C. pini* increased rapidly with increasing age of *P. sylvestris*. The infection risk increased slightly but non-significantly also in the originally 'Control' sub-sample (Table 3, Figure 3c).

The results showed that the increase in proportion of deciduous trees in the pine-dominated sapling stands reduced the risk to damage caused by *C. pini* especially in the 'Diseased' sub-sample (Table 3, Figure 3d).

The risk for damage caused by *C. pini* increased to ca. 50% probability with increasing height growth from 1 to 30 cm during the last 5 years, when *Melampyrum* sp. was present in a *C. pini*-damaged sample plot in the 2014 survey (Table 3, Figure 3e). If *Melampyrum* spp. were absent in the sample plots or the plots

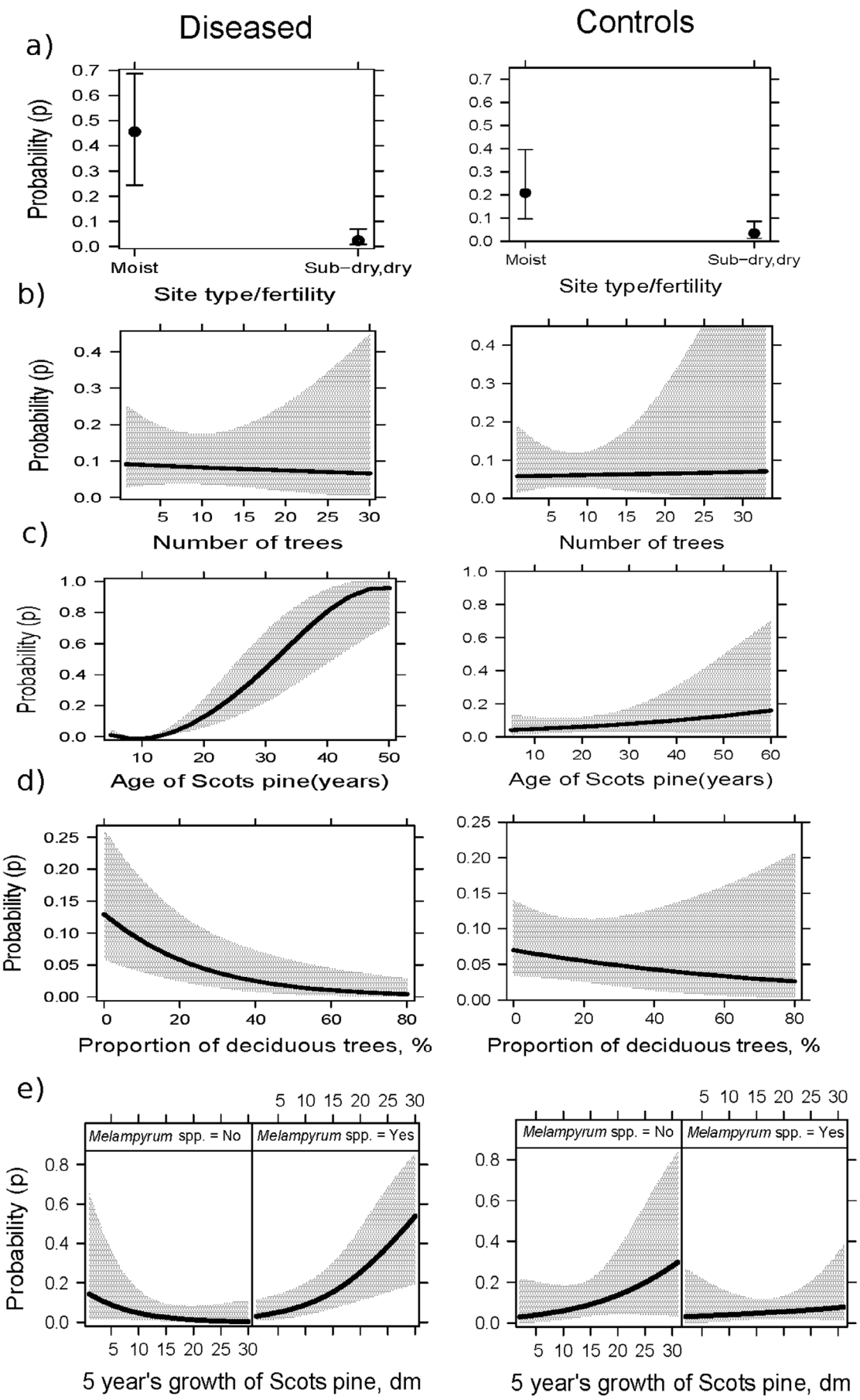

FIGURE 3 | Legend on next page.

FIGURE 3 | The predictions of the logistic mixed models for the probabilities of damage caused by *C. pini* by the explanatory variables (a–e) and their interactions. The stands were classified either as 'Diseased' or 'Controls'. a = site type/fertility, b = number of trees, c = age of Scots pines (years), d = proportion of deciduous trees (%) and e = 5 year's growth of Scots pines (dm).

were healthy, the growth did not affect the risk for damage caused by *C. pini* significantly at the 5% risk level.

Height growth of the last 5 years correlated strongly with the Ca-concentration in forest soil (data not shown). Thus, the height growth could be replaced with Ca-concentration in an alternative model for the 'Diseased' sub-sample (not shown). However, the interaction between Ca-concentration and the presence of *Melampyrum* sp. was non-significant ($t = -0.154$, df = 181, $p = 0.878$; data not shown). On the other hand, if the interaction between Ca-concentration and the presence of *Melampyrum* were removed from the model, and the Ca-concentration instead of 5 years' height growth (main effects model, not shown) was included in the model, the Ca-concentration was a significant explanatory variable ($t = 3.050$, df = 182, $p = 0.003$; data not shown).

The fit of logistic models measured by the classification efficiency in the data was considerably good. The ROC-curve analysis suggested that the proportion of correctly classified sample plots varied from 80% to 97% depending on the model (Table 3).

4 | Discussion

Site fertility explained significantly disease incidence of *C. pini* in the damaged sample plots, and the disease increased along site fertility. This is in good agreement with the reported high frequency of *C. pini* in nutrient-rich sites in young pine plantations in northern Sweden during severe rust epidemics in the 2000s' (Wulff et al. 2012). High *C. pini* incidence has been reported in individual moist nutrient-rich sites also in northern Finland (Kaitera 2000). This can be explained by the occurrence of a highly susceptible alternate host of *C. pini* in fertile moist sites. *Melampyrum sylvaticum* and *M. pratense* are common species in northern forests of which *M. sylvaticum* is frequent in moist sites and *M. pratense* in poor sites (Hämet-Ahti et al. 1984; Reinikainen et al. 2000). Among *Melampyrum*, *M. sylvaticum* is highly susceptible, while *M. pratense* is almost resistant to *C. pini* (Kaitera et al. 1999; Kaitera 1999). In natural northern forests, *C. pini* is more frequent on *M. sylvaticum* than on *M. pratense* (Kaitera et al. 2005, 2011). Also, other *C. pini*-susceptible hemiparasites of Orobanchaceae like *Euphrasia* spp. and *Rhinanthus* spp. have been reported to support sporulation of *C. pini* in nutrient-rich sites in northern areas (Kaitera et al. 2018, 2021), which may add spore load to *P. sylvestris* in corresponding sites. The results of this study revealed also that there was no significant difference in susceptibility to *C. pini* between healthy and diseased plots on poor sites, which can be explained by the occurrence of the highly *C. pini*-resistant *M. pratense* or total lacking of *Melampyrum* spp. in those plots. *Melampyrum pratense* is, however, not fully resistant to *C. pini* as has been shown earlier (Kaitera 1999; Kaitera et al. 2005, 2011). Recently, *C. pini* was shown to fruit and sporulate on *M. pratense* sporadically also on poor sites in northern Finland (Kaitera et al. 2024).

In this study, age of trees increased significantly the risk to *C. pini*-damage in the plots, while the disease incidence was low in < 5-years-old planted stands. Disease symptoms of *C. pini* have been recorded frequently especially in old pine trees earlier (e.g., van der Kamp 1970; Greig 1987; Kaitera et al. 1994), which agrees with the present results. However, no specific old studies have included identification of the causal life-cycle form of the rust from old pines. In Finland, the autoecious life-cycle form was more frequent than the heteroecious life-cycle form in a population genetic study in old trees (Hantula et al. 1998). The lack of *C. pini* in very young seedlings is reasonable, whereas aecial sporulation, which is among the first observable disease symptoms on pine, starts 2 years after initial infection in case of the autoecious life-cycle form (Kaitera 2003; Kaitera and Nuorteva 2008) and after 3 years in case of the heteroecious life-cycle form on *P. sylvestris* (Kaitera and Nuorteva 2008). Therefore, disease symptoms appear slowly on pines. Duration of sporulation may also last for years in case of the autoecious life-cycle form, while the rust has been reported to sporulate for 8 years in the same lesion (Kaitera 2003). Lack of *C. pini* in very young seedlings has been reported also earlier (van der Kamp 1970; Greig 1987).

Although the age of trees increased the probability of damage caused by *C. pini*, this probability cannot increase endlessly due to closure of the canopy of the trees, which probably decreases spore dispersal within the stand. Canopy closure may also hinder long-distance aeciospore dispersal over the stand. Basidiospore dispersal within the stand from plants in the ground may also be reduced by the reduction of the number of *Melampyrum* spp. in the plots, which require open areas for growth (Hämet-Ahti et al. 1984; Reinikainen et al. 2000).

Mixture of deciduous trees was shown to significantly reduce the risk of *C. pini*-damage in pine-dominated plots. To our knowledge this is the first study when this effect is clearly shown. This may be due to the physical barrier of deciduous trees for spore dispersal next to pine trees both in old stands and especially in young plantations. Physical barrier may reduce infection via basidiospores from alternate hosts on the ground to pines as well as aeciospore infection from pines to other pines or to alternate hosts. Ragazzi et al. (1998) have shown that *C. pini*-infections on *Vincetoxicum hirundinaria* Medicus decrease by 90% when the distance from pine trees increases from 10 to 1000 m. Therefore, significant sporulation occurs close to pine trees. Deciduous trees may also affect moisture on the ground and thus reduce spore dissemination from alternate hosts to pines.

High 5-year-growth of pines did not increase risk for *C. pini*-damage in healthy plots or in plots that lacked *Melampyrum*. However, risk for *C. pini*-damage increased significantly when *Melampyrum* was present in the plot. This suggests that high growth potential predisposes pine to damage caused by the heteroecious life-cycle form of *C. pini*. This is probably linked to the

presence of *M. sylvaticum* in nutrient-rich sites which species has been shown to be highly *C. pini*-susceptible (e.g., Kaitera 1999; Kaitera et al. 1999). *Melampyrum sylvaticum* is known to dominate in nutrient-rich sites among *Melampyrum* species in Finland (Hämet-Ahti et al. 1984; Reinikainen et al. 2000). Unfortunately *Melampyrum* spp. could not be identified by species in this study to confirm linkeage between *M. sylvaticum* and high growth rate of pine. In old literature, higher susceptibility of pines with great growth rate compared to low growth rate to *C. pini*-damage has been suggested (van der Kamp 1970; Martinsson and Nilsson 1987).

In conclusion, the model indicated certain factors affecting damage caused by *C. pini*. The selected field survey approach increased understanding of the ecological factors enhancing damage risk caused by *C. pini* on *P. sylvestris* in northern forests. The results can be utilized in updating silvicultural forest management practices by increasing deciduous trees as a mixture in pine stands and to avoid fertile sites for pine cultivation to reduce *C. pini* risk.

Author Contributions

Juha Kaitera, Ville Hallikainen, Mikko Hyppönen, Risto Jalkanen, Marja-Leena Päätalo and Pasi Rautio participated actively in writing the text. Ville Hallikainen carried out the sampling and performed the statistical modelling. Ville Hallikainen, Mikko Hyppönen and Risto Jalkanen planned the study, proposed methodology and validated the initial objectives of the project.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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