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Could Pine Wood Nematode (*Bursaphelenchus xylophilus*) Cause Pine Wilt Disease or Even Establish inside Healthy Trees in Finland Now—Or Ever?

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Abstract: Pine wilt disease (PWD) caused by the pine wood nematode (PWN, *Bursaphelenchus xylophilus*) can, in suitable conditions, lead to mass mortality of susceptible trees. In the European Union, PWN is a quarantine pest. To support PWN risk management in Finland, we assessed the suitability of the Finnish present and future climate for both PWD and PWN establishment inside susceptible healthy trees. The former was done using the mean summer temperature concept and the latter by relating annual growing degree days to the likelihoods of PWN extinction and establishment inside healthy trees. The likelihoods were derived from the previously published modelling of PWN population dynamics for 139 locations in Germany. Both assessments were conducted using 10 × 10 km resolution climate data from 2000–2019 and Finland-specific climate change projections for 2030–2080. The results indicate that the present Finnish climate is too cool for both PWD and PWN establishment inside healthy trees. Furthermore, even global warming does not appear to turn the Finnish climate suitable for PWD or PWN establishment inside healthy trees by 2080, except under the worst-case representative concentration pathway scenario (RCP8.5). Consequently, giving top priority to PWN when allocating resources for biosecurity activities in Finland might deserve reconsideration.

Keywords: pine wood nematode; pine wilt disease; invasive species; forest pest; quarantine pest; risk assessment; risk management; mean summer temperature; climate; climate change

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1. Introduction

Pine wood nematode (PWN, *Bursaphelenchus xylophilus*) is the causal agent of pine wilt disease (PWD) that can lead to mass mortality of susceptible trees (e.g., [1]). In the European Union (EU), PWN is a quarantine pest for which all EU countries must conduct annual surveys and, if detected, eradication measures shall be taken [2,3]. For the northernmost EU countries, some of the specific requirements set in the EU plant health legislation for the surveys and eradication measures may be overcautious since there, average summers are considered to be so cool that PWN is unlikely to cause PWD [4–6]. Therefore, to support the appropriate use of biosecurity risk management resources, a thorough assessment of the suitability of the present and future Finnish climate for PWN is needed.

PWN is thought to be native to North America and introduced in Asia, first in Japan and later in China, Taiwan and South Korea [7–10], and eventually in Europe, Portugal and Spain [11,12]. It can spread over long distances through the transport of wood and wood packaging material [4,13]. From tree to tree, PWN is spread by *Monochamus* beetles [14]. Feeding by an infested vector beetle transmits PWN to healthy trees, whereas by oviposition, it is transmitted only to weakened trees, recently felled logs or logging

waste (e.g., [15]). In conditions where PWD does not occur, PWN is very unlikely to spread further from trees infected by feeding of the beetles.

In Finland, two *Monochamus* species (*M. galloprovincialis* and *M. sutor*) are widely present [16,17], and of these, *M. galloprovincialis* is known to transmit PWN [18]. The most susceptible hosts to PWN are in the genus *Pinus,* but other conifers such as *Abies*, *Picea* and *Larix* can also be attacked (e.g., [19]). Scots pine (*Pinus sylvestris* L.), which is the most common tree species in Finland, is highly susceptible to PWN [20,21].

The occurrence of PWD is highly dependent on temperature. In laboratory and greenhouse experiments, PWD has been shown to occur at 23–32 °C but not at temperatures below 21 °C [20,22,23]. In forests in North America and Japan, PWD only occurs in areas where the summer temperatures are above 20 °C, although PWN is also present in cooler areas [24].

In cool areas, PWN can survive inside living trees for several years without necessarily causing PWD. Halik and Bergdahl [25] found nematodes could survive for at least six years inside susceptible hosts (*P. sylvestris*) in northern Vermont, USA, and at the end of the study period, 53% of the unharvested trees from which PWN had been detected were still alive.

The first assessments of the risk of PWD in Europe were done solely based on the observed relationship between temperature and wilt expression. Magnusson [26] estimated that the summers in Sweden were too cool for PWD. However, he noted that the possibility of PWD in the Nordic countries due to other environmental factors, such as water stress, could not be excluded. Similarly, Evans et al. [4,5] estimated that the climate in northern Europe is not suitable for PWD due to the cool summers.

The most recent assessments of the risk of PWD in Europe have been done with an evapotranspiration model (ETpN) that considers the effect of various environmental factors on the interaction between PWN and its host tree [6,27]. The ETpN model also predicted that the present climate in Northern Europe is unsuitable for PWD [6]. However, for Finland, the predictions were based on climate data for only three years and six locations, and therefore, they do not fully rule out the possibility of PWD in exceptionally warm summers in the warmest regions of the country.

The likelihood of PWD expression in the future climates has also been assessed for some European countries, such as Spain [28] and Germany [27], but the only assessments that cover the northernmost part of Europe are the global ones by Hirata et al. [29] and Ikegami and Jenkins [30]. For Finland, the results of these assessments are somewhat contradicting. For example, assuming the representative concentration pathway (RCP) [31] scenario with the highest greenhouse gas concentration (RCP8.5) [32], Hirata et al. [29] predicted that in the 2070s, only small areas in southern and south-eastern Finland might be moderately vulnerable to PWD. In contrast, Ikegami and Jenkins [30] predicted that, at that time, PWD might be possible in the entire southern half of the country.

While the likelihood of PWD, at present and in the future, has been addressed in several studies [4–6,26,29,30], the suitability of the climate for PWN establishment inside living trees has received very little attention, but see [6,33,34]. Still, information about PWN's ability to establish a population inside living trees would be highly relevant for risk management, e.g., when deciding where to target the PWN surveys required by the EU plant health legislation or which measures are needed to eradicate PWN outbreaks.

To facilitate risk management decisions related to PWN, easily usable methods for assessing the suitability of the climate for its establishment and symptom expression are needed. Using the ETpN model, Gruffudd et al. [6] showed that the suitability of conditions for PWD could be predicted by the average of mean daily temperatures over three summer months (mean summer temperature, MST). However, there is currently no similarly user-friendly method for assessing the suitability of the climate for the establishment of PWN populations inside living trees. The ETpN model contains an element that predicts PWN population dynamics inside living trees using PWN's developmental temperature thresholds [35–37], development and reproduction rates in different temperatures [38] and the level of tolerance that a tree has to PWN. Unfortunately, the ETpN model is not publicly

available and using its nematode element, as such, may be challenging for many users since it requires daily temperature data.

To support risk management related to PWN, we assessed the suitability of the Finnish present and future climate for PWD in susceptible but healthy host trees using the mean summer temperature (MST) concept presented by Gruffudd et al. [6]. In addition, we defined easily usable annual growing degree day (S_{DD}) intervals for predicting the likelihood of PWN extinction and establishment inside healthy trees and applied them to Finnish present and future climates. The intervals were determined using the results of the ETpN model for Germany [27]. Both assessments were done using high spatial resolution (10 × 10 km) climate data and climate change projections prepared specifically for Finland under three RCP scenarios [31].

2. Materials and Methods

2.1. Method to Assess the Suitability of Climate for PWD in Healthy Trees

We used the MST concept developed by Gruffudd et al. [6] to assess the suitability of the climate for PWD. However, while Gruffudd et al. [6] calculated MST as the average of the mean daily temperatures of June, July and August, we considered the warmest three-month period between May and September. In other words, we defined MST as the highest average of the mean daily temperatures of three consecutive months between May and September.

The MST concept is based on the results of the more detailed ETpN model [6]. According to Gruffudd et al. [6], the ETpN model did not predict wilt for any locations in which MST was below 19.31 °C. It predicted some wilt, under certain conditions, for 83% of locations with 19.31 ≤ MST < 20 °C, and wilt for 99% of locations with MST ≥ 20 °C. Considering these results, we defined the following thresholds for our assessment:

- MST 19.31 °C, threshold for potential PWD expression;
- MST 20 °C, threshold for certain PWD expression.

Gruffudd et al. [6] assumed that the trees were susceptible to PWD but that they were healthy and thus had some tolerance to PWD. Therefore, the assessments based on MST thresholds are valid only for healthy trees.

2.2. Method to Assess the Suitability of Climate for PWN Establishment inside Healthy Trees

We assessed the suitability of the climate for PWN establishment inside healthy trees by calculating annual growing degree days and relating them to the probabilities of PWN dying out vs. being able to establish a long-term population.

2.2.1. Calculating Annual Growing Degree Days from Monthly Temperature Data

We derived annual growing degree days from monthly temperature data. This is essential for the useability of the method since using daily data at high spatial resolution requires a lot of computational resources. Moreover, daily data are not available for the climate change scenarios.

First, we calculated monthly growing degree days (M_{DD}) applying the method presented by Hitchin [39] for calculating M_{DD} in relation to the heating requirements of buildings when monthly mean temperatures (t_m) drop below a base temperature (t_b). Since we were interested in temperature differences above, rather than below, a base temperature, the Hitchin [39] equation was modified by switching the places of t_m and t_b and thus obtaining:

$$M_{DD} = N \frac{t_m - t_b}{1 - exp\{-k(t_m - t_b)\}} \quad (1)$$

where N is the number of days in the month, and k is a constant determined from the data. The temperature threshold for the development of PWN is 9.5 °C [40], and thus this value was used for t_b. The value for k was estimated so that the actual growing degree days summed over a 12-month period (G_{DD}) were calculated from daily climate data for

Germany with the *pollen* package [41] in R [42], and a non-linear model was fitted to the data for G_{DD}, t_m and t_b. This process returned a value of 0.425 for k.

Annual growing degree days (S_{DD}) were obtained as the annual sum of the monthly growing degree days (M_{DD}):

$$S_{DD} = \sum_{i=1}^{12} M_{DD_i} \quad (2)$$

2.2.2. Relating Annual Growing Degree Days to the Probability of Extinction vs. Establishment

The probabilities of PWN dying out vs. establishing a long-term population inside healthy trees over a range of annual growing degree days were estimated based on existing ETpN model simulations that were done to assess the likelihood of PWD in Germany [27]. The results of the simulations in healthy trees, covering 139 locations across Germany, were grouped into three categories according to the predicted PWN population dynamics:

- Extinction. Following the infestation, the nematode numbers rapidly decrease. In most cases, the population collapses by the following summer, and in all cases, it completely disappears during the three years simulated.
- Decreasing population. Following the infestation, the nematode numbers decrease but do not become zero during the three years simulated. However, since the trend in nematode numbers is decreasing, in these conditions, the nematodes are likely to eventually disappear from the trees.
- Establishment. Following the infestation, the nematode numbers remain relatively stable throughout the three years simulated, suggesting that in such conditions, the PWN population can establish inside healthy trees.

To estimate the probabilities for each category over a range of annual growing degree days (S_{DD}), first, S_{DD} for each of the 139 locations were calculated using mean monthly climate data. The results are summarized in Figure 1. Then, an ordinal logistic regression model was fitted to the data using the *polr* (proportional odds linear regression) function from the *MASS* package [43] in R. The proportional odds model is used to model categorical response data when the categories have a natural ordering. The model assumes proportional odds (or parallel regression), which means that the relationship between each pair of outcome groups is the same. This assumption was tested using the *brant* package [44] in R, and it was found to hold. Finally, a new dataset was generated over the range of values obtained for S_{DD}, and the model was used to obtain predicted probabilities for each category (Figure 2).

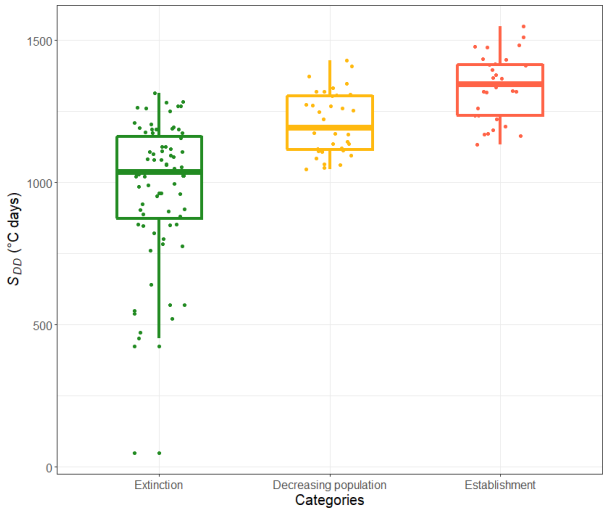

Figure 1. The annual growing degree days above 9.5 °C (S_{DD}) in the 139 locations considered in the German pest risk assessment [27] divided into the categories extinction, declining population and establishment.

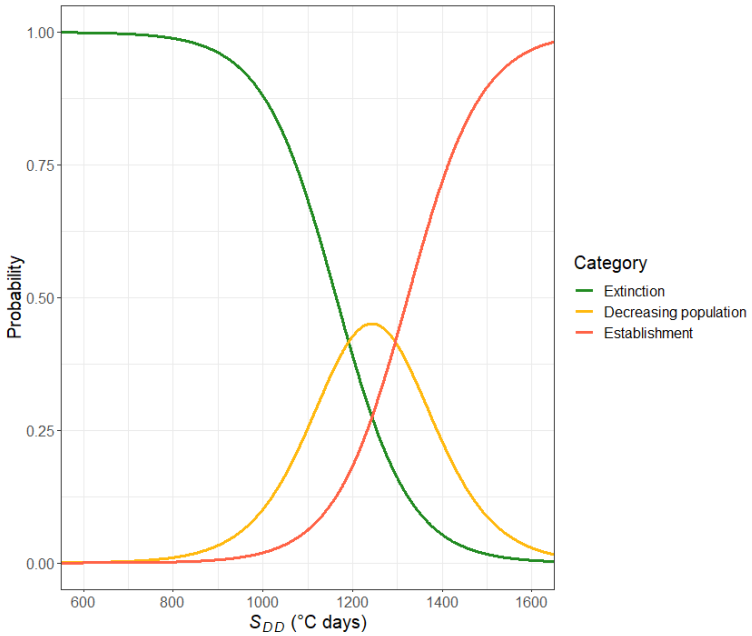

Figure 2. Predicted probabilities of the categories extinction, declining population and establishment over the considered range of annual growing degree days above 9.5 °C (S_{DD}).

2.2.3. S_{DD} Intervals for Estimating the Likelihood of PWN Extinction vs. Establishment inside Healthy Trees

To clarify communication of the results and to allow for wider use of the approach, verbal descriptions were defined for the following probability intervals of the extinction and establishment categories. If the probability of a category was ≥0.95, the category was considered almost certain, while if the probability was ≥0.75 but <0.95, the category was considered likely. The S_{DD} values corresponding to these probabilities were:

- $S_{DD} < 923$, almost certain extinction;
- $923 \leq S_{DD} < 1074$, likely extinction;
- $1413 < S_{DD} \leq 1565$, likely establishment;
- $S_{DD} > 1565$, almost certain establishment.

For the decreasing population category, respective descriptions were not defined since the probability of that category was below 0.75 for all S_{DD} values (Figure 2).

If the above-defined probability intervals are used, underestimating the suitability of climate is unlikely (Figure 1). This is because within the interval of almost certain extinction, the probability of the category establishment is at maximum 0.007, and within the interval of likely extinction, it is at maximum 0.045. Furthermore, predicting establishment to areas where the population would actually quickly go extinct is unlikely since, within the interval of likely establishment, the probability of the category extinction is at maximum 0.045. However, predicting likely establishment in areas where the population would be declining, and thus eventually disappear from the trees, is possible. This is because, within the interval of likely establishment, the probability of a declining population is up to 0.2.

Although the pest risk analysis for Germany [27] also covered stressed, already weakened trees, we used only the results for healthy trees to relate annual growing degree days to the probability of PWN extinction vs. establishment. Therefore, the S_{DD} intervals defined above are valid only for healthy trees.

2.3. Climate Data

To assess the suitability of the current Finnish climate for PWD and PWN, we used monthly mean temperatures for the period 2000–2019 [45]. This data has been derived from the national climate station observations in Finland and interpolated over the whole

country at a 10 × 10 km resolution using the Kriging interpolation method that accounts for topography and water bodies.

To assess the suitability of the future Finnish climate for PWD and PWN, we used climate change projections tailored for Finland under the RCP2.6, 4.5 and 8.5 scenarios for consecutive overlapping 30-year periods centred around the years 2030, 2040, 2050, 2060, 2070 and 2080 [46]. These projections were derived from the simulations of 28 Coupled Model Intercomparison Project Phase 5 (CMIP5) global climate models. Monthly temperature increases corresponding to the 28-model mean were added to observational mean temperatures of the period 1981–2010; this approach is termed a delta-change method. In the projections, monthly mean temperatures are running 30-year means and are represented on the same 10 × 10 km grid as the above-discussed observational analyses.

For both the recent past and future climate data, the grid cells of which more than two-thirds is covered by water bodies according to Finnish Corine Land Cover 2018 data [47] were excluded.

2.4. Assessment of the Suitability of Climate for PWD and PWN Establishment

The values of MST and S_{DD} were calculated for each cell of the 10 × 10 km grid over Finland separately for all years between 2000 and 2019, and for 2030, 2040, 2050, 2060, 2070 and 2080. S_{DD} was calculated using the same parameter values as for the German data, i.e., 9.5 °C for t_b and 0.425 for k.

To study if the present Finnish climate is suitable for PWD or PWN establishment, the average MST and S_{DD} for 2000–2019 were used. Although pest risks are typically predicted using climate normals (i.e., three-decade averages), we used two-decade averages to ensure that the data reflects the present, instead of historical climate.

To assess whether even the warmest summers of the present Finnish climate are suitable for PWD, we examined the highest MST of each cell between 2000 and 2019. For the climate change projections, such annual data were not available.

3. Results

3.1. PWD in Healthy Trees in the Present Climate

According to the two-decade average MST, the present climate in Finland is far too cool for PWD in healthy trees (Figures 3 and 4). Even in the warmest location, the average MST (16.9 °C) was about 3.1 °C below the threshold for certain PWD expression and about 2.4 °C below the threshold for potential PWD expression. In most of the country, the average MST was much lower.

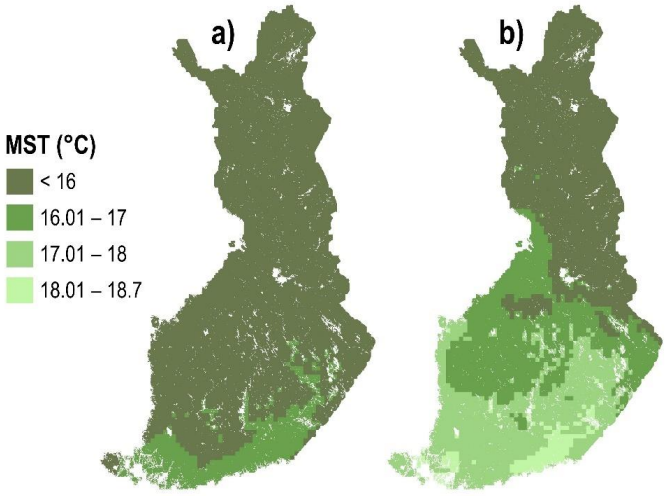

Figure 3. The average (**a**) and highest (**b**) annual MST in 2000–2019. All MST values are below the threshold for potential PWD expression.

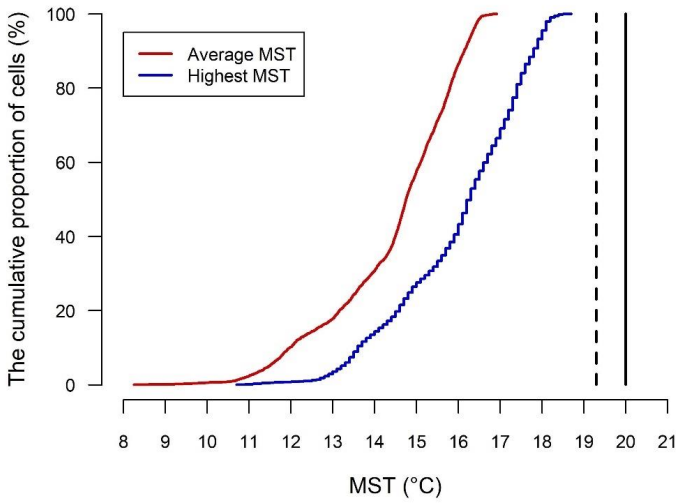

Figure 4. Cumulative distributions, over the 10 × 10 km cells, of the average and the highest MST values in 2000–2019. The black dashed line indicates the threshold for potential PWD expression, and the black solid line the threshold for certain PWD expression.

Furthermore, even the warmest Finnish summers appear to be, at present, too cool for PWD expression in healthy trees (Figures 3 and 4). The highest MST in 2000–2019 was 18.7 °C, which was recorded in one cell in south-eastern Finland by the lake Saimaa in 2010. This is still 1.3 °C below the threshold for certain PWD expression and 0.51 °C below the threshold for potential PWD expression. In most of the country, the highest values of MST in 2000–2019 were far lower.

3.2. PWN Establishment inside Healthy Trees in the Present Climate

According to the two-decade average S_{DD}, the present climate in Finland is too cool for the establishment of PWN inside healthy trees (Figures 5 and 6). Extinction was almost certain in about 91% of the cells, and in the rest of the cells, it was likely. Even in the warmest cell, the two-decade average S_{DD} (1018 °C days) was 396 °C days below the lower threshold for likely establishment and 548 °C days below the threshold for almost certain establishment. Moreover, in most of the country, the average S_{DD} was much lower.

Figure 5. The suitability of the present Finnish climate for PWN establishment inside susceptible but healthy trees measured by the average annual growing degree days above 9.5 °C (S_{DD}) in 2000–2019.

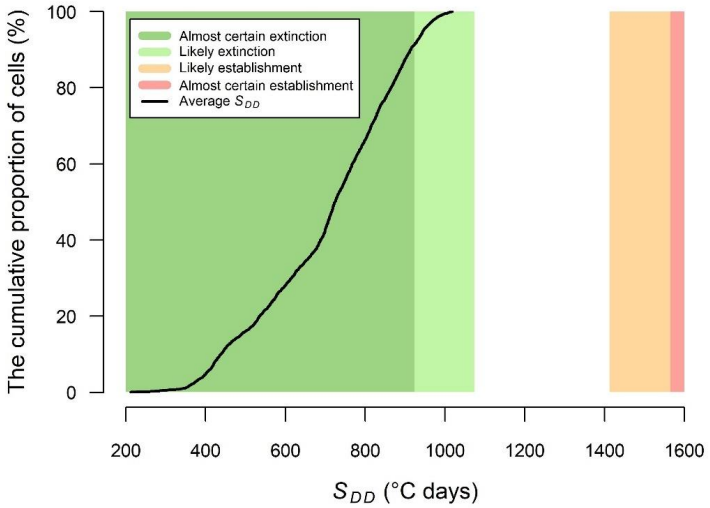

Figure 6. Cumulative distribution, over the 10 × 10 km cells, of the average annual growing degree days above 9.5 °C (S_{DD}) in 2000–2019.

3.3. PWD in Healthy Trees in the Future Climate

Under the RCP scenarios with the lowest and intermediate greenhouse gas concentration (RCP2.6 and 4.5), the climate was not projected to become suitable for PWD in healthy trees by 2080 anywhere in Finland (Figure 7). Assuming these scenarios, MST in all years and cells was below the threshold for potential PWD expression.

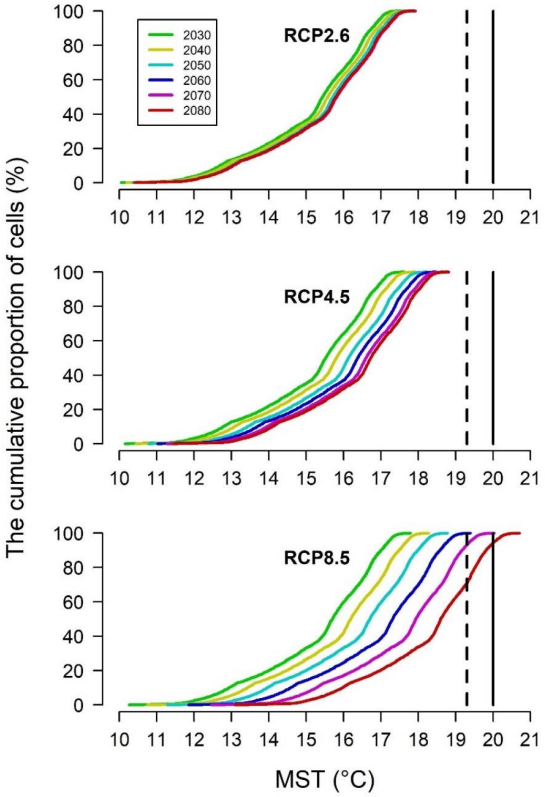

Figure 7. Cumulative distributions over the 10 × 10 km cells of the three-decade average MST values under the RCP scenarios 2.6, 4.5 and 8.5 in 2030–2080. The black dashed line indicates the threshold for potential PWD expression, and the black solid line the threshold for certain PWD expression.

Under the high-emission scenario (RCP8.5), the climate in parts of southern Finland was projected to become suitable for PWD by 2080 (Figures 7 and 8). In the 2070 projection,

MST was above the threshold for certain PWD expression in one cell, and above the threshold for potential PWD expression in 7% of the cells. In the 2080 projection, MST was above the threshold for certain PWD expression in 6% of cells, and above the threshold for potential PWD expression in 29% of cells. The highest MST was 20.7 °C, and it was recorded in the 2080 projection from a cell in south-eastern Finland by the lake Saimaa.

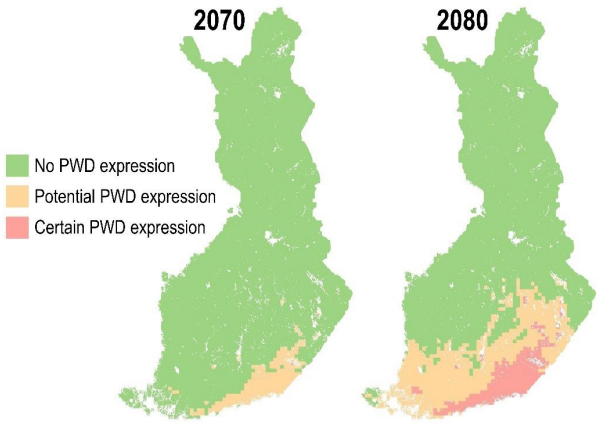

Figure 8. The suitability of the Finnish climate for PWD in susceptible but healthy trees under the RCP8.5 scenario in 2070 and 2080 based on the three-decade average MST values.

3.4. PWN Establishment inside Healthy Trees in the Future Climate

Under the low-emission scenario (RCP2.6), the climate was not projected to become suitable for PWN establishment inside healthy trees by 2080 anywhere in Finland (Figures 9 and 10). S_{DD} values were far below the lower threshold for likely establishment everywhere in the country throughout the considered period. Furthermore, even in the last year, the considered extinction was almost certain or likely in 95% of the cells.

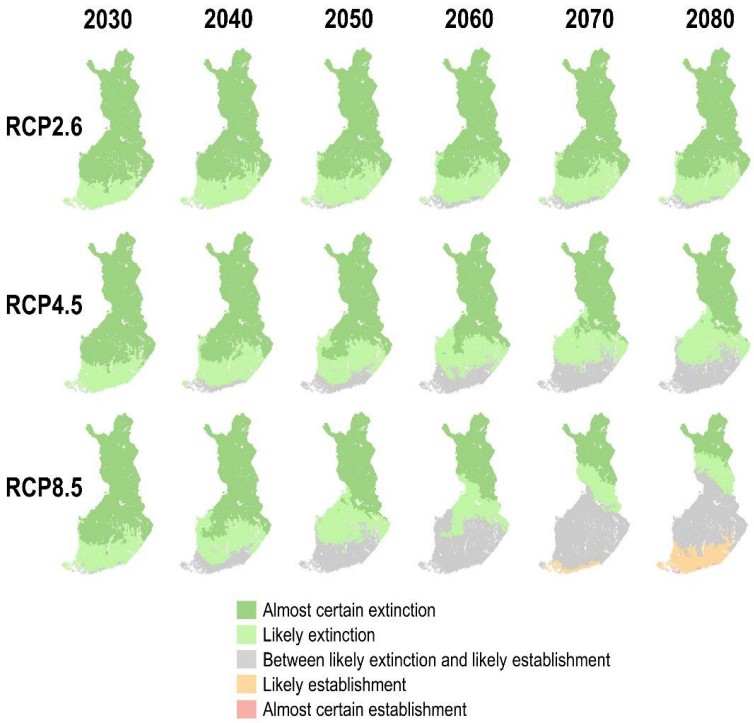

Figure 9. The suitability of the future Finnish climate for PWN establishment inside susceptible but healthy trees measured by the three-decade average annual growing degree days above 9.5 °C (S_{DD}) under the RCP scenarios 2.6, 4.5 and 8.5 in 2030–2080.

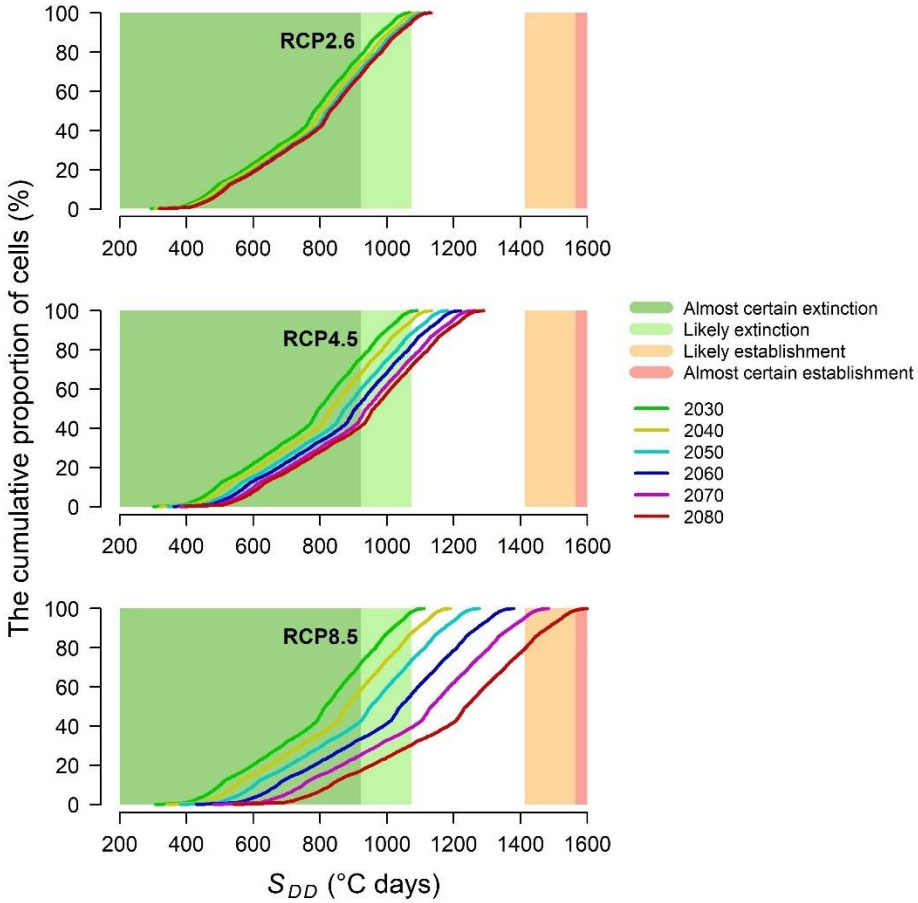

Figure 10. Cumulative distributions over the 10 × 10 km cells of the three-decade average annual growing degree days above 9.5 °C (S_{DD}) under the RCP scenarios 2.6, 4.5 and 8.5 in 2030–2080.

Assuming the RCP scenario with intermediate greenhouse gas concentration (RCP4.5), the summers in Finland were also not projected to warm up enough to enable PWN establishment inside healthy trees by 2080 (Figures 9 and 10). Even in 2080, S_{DD} values were below the lower threshold for likely establishment everywhere in the country, and extinction was almost certain or likely in 72% of the cells.

Under the high-emission scenario (RCP8.5), the climate in southern Finland was projected to become suitable for the establishment of PWN inside healthy trees by 2070 (Figures 9 and 10). In the 2070 projection, establishment was likely in 5% of cells, and in the 2080 projection, it was likely in 20% of cells and almost certain in 1% of the cells.

4. Discussion

4.1. The Suitability of the Finnish Climate for PWD and PWN Establishment

Our results suggest that, at present, even the warmest summers in the warmest parts of Finland are too cool for PWD in healthy trees. Moreover, the present Finnish climate appears to be too cool even for the long-term establishment of PWN populations inside healthy trees.

For the future, the results suggest that average summers in Finland are unlikely to become suitable for PWD in healthy trees by 2080, unless the worst-case RCP scenario (RCP8.5) is realized. The same holds for the suitability of average years for the long-term establishment of PWN populations inside healthy trees.

The suitability of exceptionally warm summers for PWD in the other RCP scenarios (RCP2.6 and RCP4.5) cannot be ruled out based on our analysis. However, it is not clear if a single warm summer would induce PWD if the average climate is unsuitable. Furthermore, the unsuitability of average years for PWN establishment inside healthy trees would slow

down the cumulation of the number of infested trees and thus decrease the severity of the epidemics possibly triggered by exceptionally warm summers.

Evidently, the Finnish climate appears unlikely to become suitable for PWD or PWN establishment inside healthy trees even after 2080, unless the scenario with the highest greenhouse gas concentrations (RCP8.5) is realized. This is because, in the other scenarios, warming is projected to slow down (RCP4.5) or cease (RCP2.6) in the second half of the 21st century [46]. In the high-emission scenario (RCP8.5), the favorable area would continue to extend towards the north, since under that scenario, warming is projected to continue unabatedly in the late-21st century [46]. However, if the targets of the current climate policy are pursued, such a pessimistic scenario is very unlikely.

It should be noted that our assessments do not cover stressed or otherwise weakened trees since both the MST concept and the intervals that we defined for assessing the suitability of the climate for PWN establishment inside trees assume that the trees are healthy. However, at least in the present Finnish climate, PWD seems unlikely even in stressed or weakened trees. This is because the ETpN model, which also accounts for the vigor of the trees, predicts PWD in stressed or weakened trees only for a few locations in Germany, where summers are clearly warmer than in Finland [27].

4.2. Comparison with Previous Studies

Our assessment of the suitability of the present Finnish climate for PWD is in line with previous Europe-wide [4–6] and global [30] studies that suggest a low risk of PWD for Finland.

The results of previous assessments of the suitability of future climates for PWD are somewhat contrary for Finland [29,30]. Our results agree with the global assessment by Hirata et al. [29] that projected moderate vulnerability to PWD for a small area in southern Finland in 2070 under the RCP8.5 scenario, and low vulnerability for the whole country under the other RCP scenarios. However, in Ikegami and Jenkins [30], the suitability of the future climate in Finland was projected to be higher than in our assessment. For example, for the RCP8.5 scenario in 2070, they projected possible wilt expression in half of the country, whereas our assessment projected wilt expression only for about 7% of the country.

We found two potential explanations for the differences between our results and those of Ikegami and Jenkins [30]. Firstly, the temperature threshold for PWD expression used by Ikegami and Jenkins [30] (19 °C) was somewhat lower than ours (19.31 °C). Secondly, Ikegami and Jenkins [30] derived their temperature projections from a sub-ensemble of 14 CMIP5 models, while in our analysis, 28 models were utilised. When we compared the multi-model mean temperature responses to RCP8.5 for both sub-ensembles, we found that the sub-ensemble of Ikegami and Jenkins [30] produced an approximately 0.5 °C higher summertime warming for Finland than the larger ensemble used in the present work. Given the rather modest spatial variations in summer mean temperatures in southern and central Finland, these factors may explain the differences between our predictions and those of Ikegami and Jenkins [30].

The suitability of the climate for PWN populations inside living trees has been addressed in only a few previous studies [6,33,34]. In the current climate in Llanwddyn in Wales, and in Sunne and Junsele in Sweden, the nematodes were predicted to go extinct inside living trees within 12 months of infestation [6,33,34]. Similarly, extinction during the first year was predicted at Junsele, assuming a climate change scenario aiming to limit global warming to less than 2 °C relative to pre-industrial levels (E1) [34]. Assuming a medium-high emission scenario (A1B), extinction was predicted at Junsele in the third year [34]. Our predictions are in line with these results, which is not surprising since they have all utilised the same nematode component of the ETpN model by Gruffudd et al. [6].

4.3. Strengths and Weaknesses of the Present Assessments

We used only MST to predict the suitability of the climate for PWD. However, other factors, such as the infestation date, initial nematode load and tree tolerance, may also

influence wilt expression [6,27]. The ETpN model [6] considers all these factors and, hence, is a more sophisticated model for analysing the likelihood of wilt expression. However, according to Gruffudd et al. [6], MST is a very good indicator of the likelihood of wilt expression, and therefore, we considered it to be sufficient for our purpose.

We assessed the suitability of the present climate for PWD by exploring the average and highest MST values in 2000–2019. Using average MST over several decades for this purpose has been validated, but the applicability of the annual MST has not. However, this does not compromise the conclusions of our assessment since the MST values in Finland were not high enough for PWD, even in the warmest summers of the present climate.

We defined the annual growing degree day (S_{DD}) intervals to assess the suitability of climate for PWN establishment inside healthy trees. Moreover, we employed a method developed by Hitchin [39] to derive monthly degree days from mean monthly temperatures. Together, these two methods make the assessment of the suitability of climate for PWN establishment inside healthy trees possible without special expertise or software.

The annual growing degree day intervals that we used to assess the suitability of climate for PWN establishment inside healthy trees were such that underestimating the suitability of climate is unlikely. This is because when S_{DD} is within the interval of almost certain or likely extinction, the probability of establishment of a long-term population is low. Hence, the intervals are suitable for guiding risk-averse decision making.

A notable weakness of the S_{DD} intervals for assessing the likelihood of PWN extinction and establishment inside living trees is the lack of validation. Although the equations that we used for defining the intervals (i.e., the nematode element of the ETpN model) are based on empirical results on the development, reproduction, life cycle and life span of PWN at different temperatures [35–37,48–51], and were in good agreement with results of field studies [52,53], they have not been validated to predict PWN population dynamics inside living trees. However, the ETpN model has been shown to predict PWD reliably, which also provides some support for the assumption that its nematode element works correctly. To validate the proposed S_{DD} intervals, data on PWN population dynamics inside living trees in different climatic conditions would be needed. Unfortunately, such data are currently not available.

To study the suitability of future climates, we used Finland-specific climate change projections, which evidently provide more accurate estimates of the future Finnish climates than the projections performed at a global scale. In the Finland-specific projections, it is anticipated that temperature increases will be more prominent in winter than summer [46], and as wilt expression depends mainly on summer temperatures [6,24,30], accounting for such seasonal contrast in warming when predicting the likelihood of PWD expression is essential.

4.4. Implications for Risk Management

All EU countries are required, by legislation, to carry out annual PWN surveys to ensure, as far as possible, its timely detection, with a high degree of confidence [3,54]. In addition to PWN, regular surveys must be conducted for all other quarantine pests. Consequently, plant health authorities may have to prioritize pests in order to allocate their limited survey resources effectively. Our results suggest that in Finland, giving top priority to PWN surveys might not be optimal.

If PWN is detected in an EU country, measures must be taken to eradicate it [2]. The measures shall include felling and destruction of all susceptible plants, including healthy trees, within a 500-m radius from infested plants. Our results suggest that in Finland, the destruction of healthy trees may be overcautious. This is because, according to our assessment, in Finland, PWN is likely to go extinct inside healthy trees within 1–2 years after infestation.

In the Finnish PWN surveys, samples are currently collected only from *Monochamus* vectors, weakened trees and dead wood material, not from healthy trees [55]. The present analysis suggests that this sampling strategy is the only appropriate option. This is because

if PWN rapidly goes extinct inside healthy trees, the likelihood of finding it in healthy trees is very low, even several years after an invasion.

The timely detection of PWN outbreaks required by the EU legislation [3,54] could become more achievable if the surveys could be targeted to areas with elevated probability of PWN presence, based on, e.g., the suitability of the climate for PWN establishment. However, our results provide only indirect support here since the long-term establishment of PWN populations inside healthy trees is not predicted anywhere in Finland. In this situation, the targeting of surveys could be based on the suitability of climate for establishment inside weakened trees or dead wood material, yet unfortunately, the conditions in which PWN can establish in such material have not been studied.

5. Conclusions

It appears that PWN could not cause PWD in healthy trees in Finland in, at least, the next 40 years, and even after that, PWD in healthy trees would be likely only in the worst-case climate change scenario (RCP8.5). Furthermore, the present analysis indicates that even PWN establishment inside healthy trees would not be possible at present or in the future, unless the worst-case climate change scenario (RCP8.5) is realized.

These results imply that when dividing the limited resources available for biosecurity activities in Finland, giving top priority to PWN might deserve reconsideration. Moreover, the results considering PWN establishment inside healthy trees suggest that in Finland, destruction of healthy trees when eradicating outbreaks might be overcautious, at least, in the present climate.

Of the two sets of results in this study, those relating MST to the likelihood of PWN causing PWD are more reliable than those relating S_{DD} to the likelihood of PWN establishment inside host trees. A major weakness of the latter is the lack of validation of the used S_{DD} intervals. Although the intervals are derived from solid empirical results, they have not been validated to predict the extinction vs. survival of PWN populations inside living trees. However, we hope that these intervals would inspire research that would eventually enable the development of a properly validated model for predicting the suitability of the climate for PWN establishment inside living trees. Given the considerable cost of PWN surveys and eradication measures, such a model would be valuable, not only for Finland but also for the other areas where PWD is not expected, including most of northern Europe.

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