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Long-Term Projections of the Natural Expansion of the Pine Wood Nematode in the Iberian Peninsula

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Abstract: The invasive pine wood nematode (PWN), *Bursaphelenchus xylophilus*, causal agent of pine wilt disease, was first reported in Europe, near Lisbon, in 1999, and has since then spread to most of Portugal. We here modelled the spatiotemporal patterns of future PNW natural spread in the Iberian Peninsula, as dispersed by the vector beetle *Monochamus galloprovincialis*, using a process-based and previously validated network model. We improved the accuracy, informative content, forecasted period and spatial drivers considered in previous modelling efforts for the PWN in Southern Europe. We considered the distribution and different susceptibility to the PWN of individual pine tree species and the effect of climate change projections on environmental suitability for PWN spread, as we modelled the PWN expansion dynamics over the long term (>100 years). We found that, in the absence of effective containment measures, the PWN will spread naturally to the entire Iberian Peninsula, including the Pyrenees, where it would find a gateway for spread into France. The PWN spread will be relatively gradual, with an average rate of 0.83% of the total current Iberian pine forest area infected yearly. Climate was not found to be an important limiting factor for long-term PWN spread, because (i) there is ample availability of alternative pathways for PWN dispersal through areas that are already suitable for the PWN in the current climatic conditions; and (ii) future temperatures will make most of the Iberian Peninsula suitable for the PWN before the end of this century. Unlike climate, the susceptibility of different pine tree species to the PWN was a strong determinant of PWN expansion through Spain. This finding highlights the importance of accounting for individual tree species data and of additional research on species-specific susceptibility for more accurate modelling of PWN spread and guidance of related containment efforts.

Keywords: pine wood nematode; pine wilt disease; forest pests; Iberian Peninsula; invasive alien species

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1. Introduction

In 1999, the invasive alien species pine wood nematode (PWN; *Bursaphelenchus xylophilus* Steiner & Buhrer, 1934 (Nickle, 1970)), causal agent of pine wilt disease (PWD), was first reported in Europe, on *Pinus pinaster* Ait. trees in the district of Setubal, in southwestern Portugal, near Lisbon [1]. Since then, it has quickly spread through Portugal, producing large-scale damage in Portuguese forests [2]. The area now affected by the PWN covers most of the Portuguese mainland territory (http://www.icnf.pt/portal/florestas/prag-doe/ag-bn/nmp/infgeo, accessed on 10 September 2019) and has reached Spain, with several and so-far isolated foci close to the border with Portugal [3–9].

Under suitable climatic conditions that trigger PWD, the PWN is able to rapidly kill susceptible pine trees [10]. Though this pest causes limited damage in its native range in North America, it has caused massive mortality in conifer forests elsewhere, most recently in Portugal but also in Eastern Asia since its accidental introduction in Japan and neighboring Asian countries at the beginning of the 20th century [11]. The mortality patterns caused by PWD are already gradually changing the structure and composition of pine stands in Portugal, rendering them less dense and with fewer mature and old trees [12].

As is typical for epidemic processes, early detection plays a vital role for the eradication and containment of the PWD. Knowing which areas are most likely to be infected at a particular point in time is essential to control the disease. The widely distributed cerambycid beetle *Monochamus galloprovincialis* Oliver is the only known PWN vector in the Iberian Peninsula [13]. Consequently, the natural spread of the PWN in Europe depends on the dispersal abilities of this vector beetle that can infect pine trees when feeding or breeding on them [14,15]. Understanding the behavior of *M. galloprovincialis* is therefore a key to predicting the dynamics of the PWN invasion front.

Coniferous forests cover almost 1 Mha in Portugal and about 8 Mha in Spain, or ca. 30% of the total forest area in these countries, reflecting their major ecological and economic importance in the Iberian Peninsula. Pine forests are ubiquitous on the Iberian Peninsula, with pine species ranging from the coastal areas (Aleppo pine *Pinus halepensis* M. and Stone pine *Pinus pinea* L.) to the upper areas of the mountain ranges (Scots pine *Pinus sylvestris* L. and Mountain pine *Pinus uncinata* Ram.). As *Pinus* species make up 95% of coniferous forests in Portugal and Spain, further spread of the PWN would have a strong impact on the forest-based economy [16–19], on biodiversity and on other important ecosystem services provided by coniferous forests inside and outside protected areas [20–22].

There is evidence that the resistance of pine species to the PWN may be related not only to the possibility of migration of the nematodes through the pine tissues after their entrance into the tree, but also to other specific intrinsic factors that repel, immobilize or disrupt the life cycle of nematodes, including their reproduction [23,24]. Although all European pine tree species appear susceptible to some degree to the nematode infection [25], inoculation tests in controlled conditions have shown that they differ in their susceptibility to PWD [26,27]. According to the results of the inoculation tests carried out by Menéndez-Gutierrez et al. [28], *Pinus sylvestris* and *Pinus pinaster* are the European native pine species most susceptible to the PWN, while *Pinus pinea* and *Pinus halepensis* appear to be less susceptible to the PWN. So far in Portugal, *Pinus pinea* trees seem not to be affected in areas where *Pinus pinaster* [1,12] and *Pinus nigra* Arn. [29] trees are killed by the PWN. This agrees with the results reported by Nunes da Silva et al. [26]. Among the non-native pine species that are planted for timber production in the northern part of the Iberian Peninsula, *Pinus radiata* showed considerable susceptibility to the PWN [28]. Thus far, however, the different susceptibility of the European pine species to the PWN has not been considered in PWN spread predictive modelling [30,31].

PWN transmission to a host tree does not necessarily lead to PWD and tree decline. PWD expression depends on environmental factors [32], such as the role of water stress caused by seasonal drought and high temperature in disease development [33]. When an area is not climatically suitable for the development of the PWD, the lack of declining trees prevents further spread of the pest to other potentially susceptible trees or areas. According to Gruffudd et al. [34], the risk of conifer trees infected with PWN becoming symptomatic is low if the mean summer temperature (June–August) is below 19.31 °C, and high if it is above 20 °C. Locations between 19.31 °C and 20 °C are considered at some risk of PWD [34]. Therefore, the northern part of the Iberian Peninsula, and some high-altitude areas in certain Iberian mountain chains, are currently not climatically suitable for PWD expression [30,35]. However, climate warming may progressively change this [36,37]. Therefore, considering both current and future climate in the Iberian Peninsula is important for long-term projections of the potential PWN expansion.

In this study, we modelled the spatiotemporal patterns of future natural spread of the PWN in the Iberian Peninsula, as dispersed by the longhorn beetle *Monochamus galloprovincialis*. We improved the accuracy, informative content, forecasted period and number of factors considered in previous modelling efforts for the PWN in Southern Europe [30,31,38]. Unlike in previous studies, we jointly considered the distribution and different susceptibility of pine tree species, the effect of climate change projections on environmental suitability for PWN spread and the dynamics of PWN natural expansion toward the end of the century. We applied the spatio-temporal network model described in De la Fuente et al. [30], which was validated with actual PWN spread data in Portugal and was shown to have a high predictive accuracy [30]. We applied this model to predict the areas of the Iberian Peninsula through which the PWN is most likely to spread by natural means and in absence of dedicated containment measures, and the most likely year of infection in each location. We also evaluated the potential influence of climate warming on PWN spread and the effect of the susceptibility to the PWN of different pine tree species in the expected patterns and magnitude of spread. Our results can support management efforts by forecasting when areas are at greater risk of vector-mediated invasion. They also indicate how climate and tree species distribution may mediate the long-term patterns of PWN spread and inform the related pest containment and forest planning measures that may be applied in the Iberian Peninsula.

2. Materials and Methods

2.1. Study Area

In our analysis, we considered the entire Iberian Peninsula as study area, which has an extent of about 597,000 km^2. We described the study area using a grid of 1 km × 1 km cells (referred to as nodes in the modelling). This spatial resolution was considered sufficiently high given the extent of the study area and the >1 km dispersal range of the vector beetle *Monochamus galloprovincialis* [30].

2.2. Pine Tree Species Susceptibility to Pine Wood Nematode

We considered two different scenarios (A and H) regarding which pine species are susceptible to infection and which species can be a source of newly infected vector beetles that can further transmit the PWN to other pine trees:

- Scenario A: All pine tree species on the Iberian Peninsula are equally susceptible to the PWN. Under this scenario, the PWN spread modelling does not distinguish between pine species.
- Scenario H: Only pine species with high (*P. pinaster* and *P. radiata*) or very high (*P. sylvestris*) susceptibility to the PWN, following Menéndez-Gutiérrez et al. [28], can get infected and infect other pine trees. The other pine species were considered as neither targets nor sources of infection in the PWN spread modelling.

These two scenarios covered the range of plausible responses of different pine tree species to the PWN, according to the available studies [26–28], as well as the range of modelling scenarios within which the actual spread of the PWN in the Iberian Peninsula may be contained. They also allowed to evaluate the impact that not considering the different susceptibility to the PWN of pine tree species may have had on the results of previous modelling work on this invasive tree pest in Southern Europe.

2.3. Forest Tree Species Maps

For each cell i, we calculated the area covered by pine forest in the cell (a_i), either considering all pine tree species (Scenario A above) or only those pine tree species with high susceptibility to the PWN (Scenario H above). Pine forest area in the cell was calculated considering the area of pure pine forest ($a_{c,i}$) and of mixed pine–broadleaved ($a_{m,i}$) forest in the available maps (see below) as $a_i = a_{c,i} + F \times a_{m,i}$, where F indicates the fraction of pine tree cover in mixed stands, which was taken from the maps when available and otherwise set to 0.5.

For this purpose, we considered the spatial distribution of the different pine forest species as reported in the most detailed forest maps available in our study area: the Forest Map of Spain developed by the Spanish Ministry of Environment in coordination with the Third Spanish National Forest Inventory (scale 1:50,000, minimum mapping unit of 2.25 ha) and the 2007 land cover map of continental Portugal (COS2007) developed by the Portuguese Geographic Institute (1:25,000 scale, minimum mapping unit of 1 ha).

The Spanish Forest Map differentiates the distribution of each individual pine tree species. The Portuguese land cover map only differentiates *Pinus pinaster* (Maritime pine forests) and *Pinus pinea* (Stone pine forests), which are by far the pine species more widely distributed in Portugal. A total of 94.6% of the coniferous forest territory of continental Portugal is covered by these two species according to the results of the 6th National Forest Inventory of Portugal (http://www2.icnf.pt/portal/florestas/ifn/ifn6, accessed on 10 September 2019). Therefore, for Portugal, we used only the spatial distribution of Maritime pine forests when running Scenario H. For Scenario A, we used the distribution of the following three map categories: Stone pine forests, Maritime pine forests and forests of other coniferous species.

This resulted, for Scenario A, in a network of 210,338 nodes (1 km^2 cells) describing the distribution of all pine forests on the Iberian Peninsula (Scenario A). For Scenario H, we obtained a network of 121,200 nodes describing the spatial distribution of the three most susceptible pine species (*P. pinaster*, *P. sylvestris* and *P. radiata*) on the Iberian Peninsula.

2.4. Climatic Suitability to Pine Wilt Expression

We considered the climatic suitability of different areas in Spain and Portugal for the development of PWD in PWN-infected areas in current and future climates. The current climate data for Spain and Portugal were obtained from Ninyerola et al. [39]. For future climates, we examined the climate change projections provided by the ENSEMBLES project (http://ensembles-eu.metoffice.com/, accessed on 5 March 2020), considering the IPCC A1B scenario. These projections indicate that by 2100 all the areas with pine forests in the Iberian Peninsula will be climatically suitable for the PWN, except some isolated locations around a few mountain peaks that cover less than 1% of the pine forest distribution in the Iberian Peninsula. Therefore, we modelled PWN spread under the following two climate scenarios:

- Current climate (Scenario C): Only 1 km^2 cells in which the current mean summer temperature is above 19.31 °C are considered climatically suitable for wilt expression [31]. Excluded from the climatically suitable areas was 23% of the total pine forest extent in the Iberian Peninsula when considering all pine tree species (Scenario A) or 38% of the area covered in the Iberian Peninsula by the pine tree species that are highly susceptible to the PWN (Scenario H). In Scenario C, we simulated PWN spread assuming no dispersal of infected beetles from the areas where the disease does not express due to climate constraints.
- Future climate (Scenario F): All the Iberian Peninsula, except the isolated locations mentioned above, is climatically suitable for the expression of PWD. All 1 km^2 cells can act as spreaders of the PWN once they are invaded by the disease.

These two scenarios covered, therefore, the most climatically restrictive scenario (C) and the least restrictive scenario (F) that can be considered for the PWN expansion modelling.

2.5. PWN Spread Model

We simulated the PWN expansion using the process-based network model presented in De la Fuente et al. [30], which predicts the natural spread of the PWN through the dispersal of the vector beetle *Monochamus galloprovincialis*. This model was validated with data on the past PWN expansion patterns in Portugal and showed a high predictive accuracy [30].

In this model, nodes represent locations with pine forest (here 1 km^2 cells), and links (edges) reflect the probability of disease spread between two nodes. The model predictions are calculated based on two main analytical steps. First, the model calculates the weight of the links in the network as the probability that a sufficient number of vector beetles is able to disperse between two nodes during the yearly flight period so as to transmit the disease to the destination node (if the source node was infected). Second, using the distribution of infected and non-infected nodes in a given year and the link weights, it calculates, each year, the probability that individual nodes actually become infected, considering the contribution of all possible infection source nodes and dispersal pathways. Each of the nodes could be, in any year, in an infected or non-infected state: for the purpose of this study, we considered a cell infected when the infection probability is higher than 0.9 and non-infected when the infection probability is lower than 0.1. Intermediate probability values (between 0.1 and 0.9) were considered separately but represent a considerably small number of cells given that the infection probabilities predicted by the model are almost binary, i.e., very close to 0 or 1 [30].

The model has the following five parameters:

- d, the mean dispersal distance of the vector beetle, *Monochamus galloprovincialis*.
- N, the number of infected beetles emerging from each infected tree and thus available for dispersal.
- k, the number of infected beetles that need to reach an uninfected pine tree to actually transmit the disease to that tree.
- β, a coefficient determining the tail fatness (kurtosis) of the vector beetle dispersal kernel.
- c, the number of infected trees per hectare of pine forest in newly infected areas. This parameter was used to convert the pine forest area in a cell i (a_i) to the number of pine trees expected to be infected in that cell when PWN transmission occurs.

Based on available empirical and modelling studies on the PWN (see De la Fuente et al. [30]), we set d = 1500 m, N = 9, k = 2, β = 1 and c = 0.5, which were the best supported and validated parameter values and hence those used in all the predictions presented in this study. Further model details and equations are provided in De la Fuente et al. [30].

2.6. PWN Spread Modelling Scenarios

We predicted future patterns of natural PWN spread through the Iberian Peninsula at yearly intervals up to year 2150 in the absence of effective containment measures, starting the model runs from the PWN distribution observed in Portugal in June 2018 (http://www.icnf.pt/portal/florestas/prag-doe/ag-bn/nmp/infgeo, accessed on 10 September 2019). Model runs were conducted in the four scenarios combining those on pine tree species susceptibility to the PWN and those related to climate described above:

- Scenario AC: all pine tree species (Scenario A) and current climate (Scenario C) considered.
- Scenario AF: all pine tree species (Scenario A) and future climate (Scenario F) considered.
- Scenario HC: only highly susceptible tree pine species (Scenario H) and current climate (Scenario C) considered.
- Scenario HF: only highly susceptible tree species (Scenario H) and future climate (Scenario F) considered.

Of these scenarios, AF has the greatest potential for higher rates of PWN spread, because any pine forest stand of any pine tree species and in any location in the Iberian Peninsula can be infected by the nematode and thus be a source of PWD. Conversely, HC is the most restrictive scenario for the modelled spread.

The models were implemented and run in the R programming language [40], as were all related analyses.

3. Results

3.1. PWN Spread in Scenario AF: All Pine Forests and Future Climate

In Scenario AF, which is the least restrictive scenario for the PWN expansion (all pine forests considered and no climatic restrictions), the PWN spread from Portugal into Spain is predicted to occur uninterrupted through the expansive tracts of host vegetation (Figure 1). The spread in scenario AF is faster than in the other three scenarios (Figures 1 and 2). Modelling results indicate that by 2050 the PWN will be present throughout the region of Galicia, entering the north of the region of Asturias through the coastal area and the south of Asturias through the Cantabrian Range (Figure 1). By 2050, the disease will have reached the pine forests of the Central Plateau of the region of Castilla y León through Sierra de la Culebra, in the province of Zamora. Through the pathway of the Central Range, the infection will have reached by 2050 the central part of Spain up to the border of the region of Madrid (Figure 1). In the south of Spain, the mountains of Sierra Morena are predicted to start to be affected by the PWN by 2050, and through the coast the PWN will have reached the pine forests on the Guadalquivir Valley by that date (Figure 1).

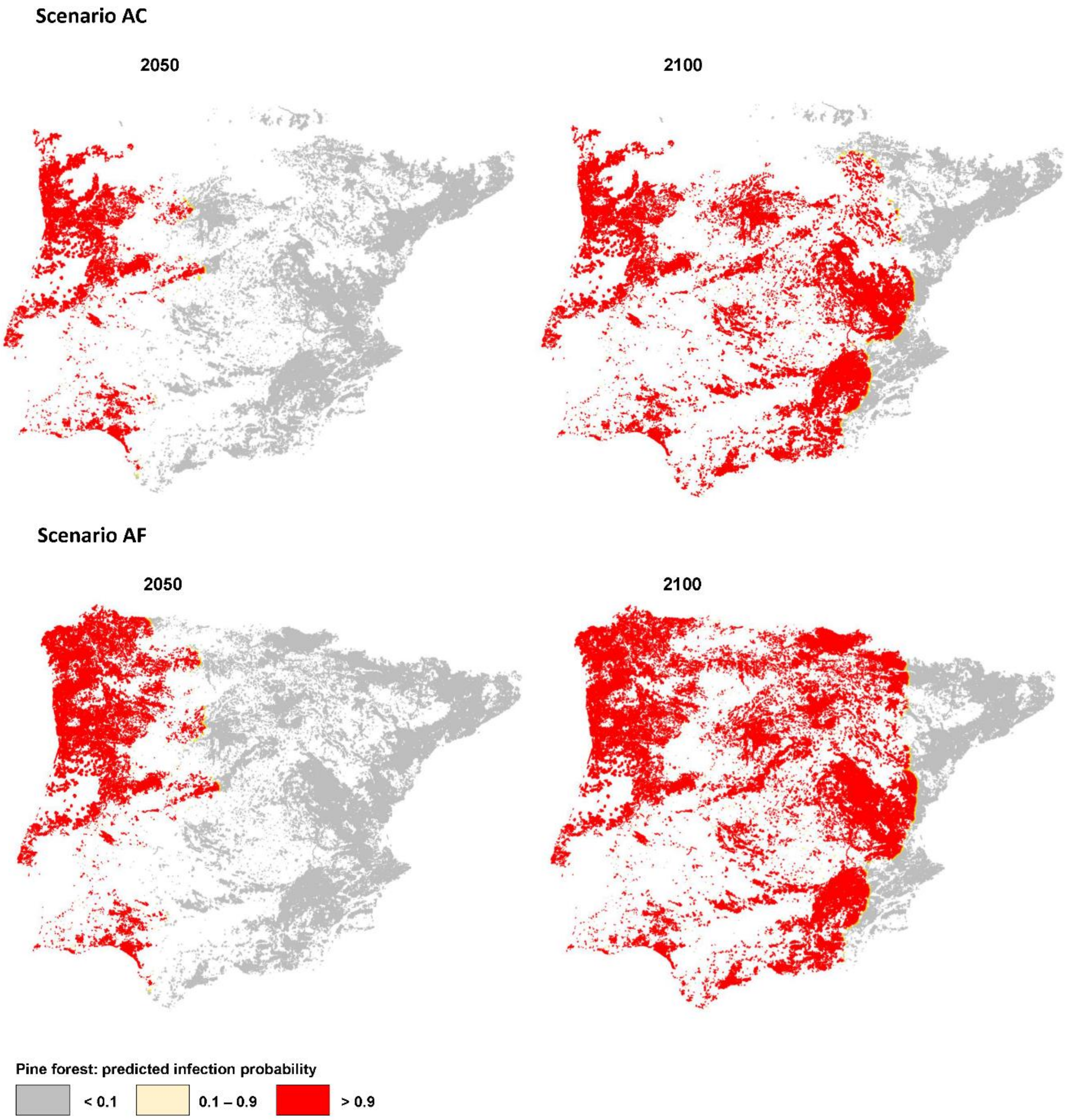

Figure 1. PWN spread in the Iberian Peninsula for the years 2050 and 2100, considering all pine tree species as susceptible of being infected. Both the current climate (Scenario AC) and future climate (Scenario AF) are considered.

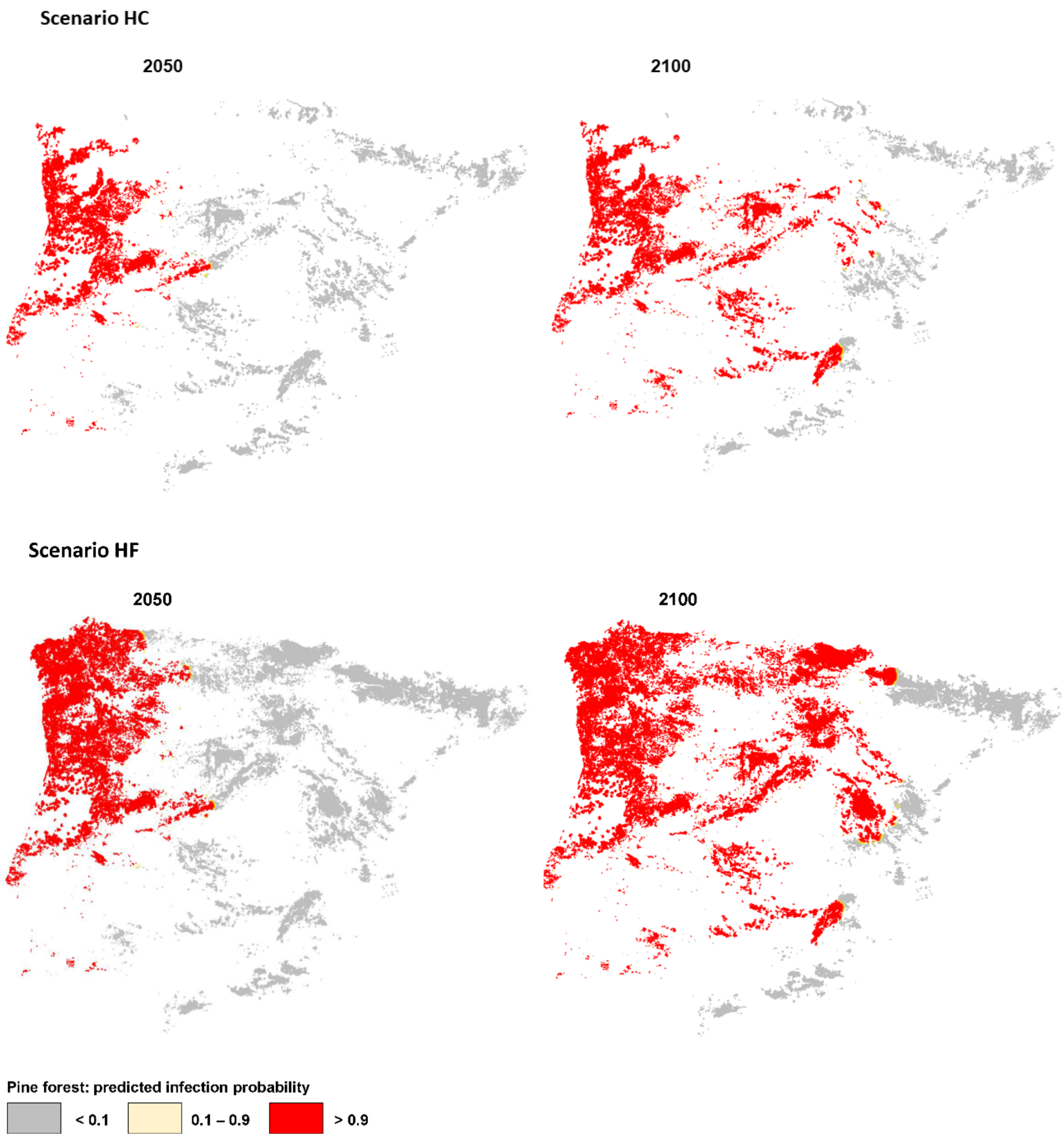

Figure 2. PWN spread in the Iberian Peninsula for the years 2050 and 2100, considering only the forests composed by pine tree species with high susceptibility to infection. Both the current climate (Scenario HC) and future climate (Scenario HF) are considered.

The rate of PWN spread is predicted to considerably increase after 2050 in Scenario AF (Figure 3). The average rate of infection increases from 43,763 ha per year in the period 2020–2050 to 68,038 ha per year in the period 2050–2100 (Figure 3), which is due to the higher continuity of host pine trees in the eastern half of the Iberian Peninsula (Figure 1).

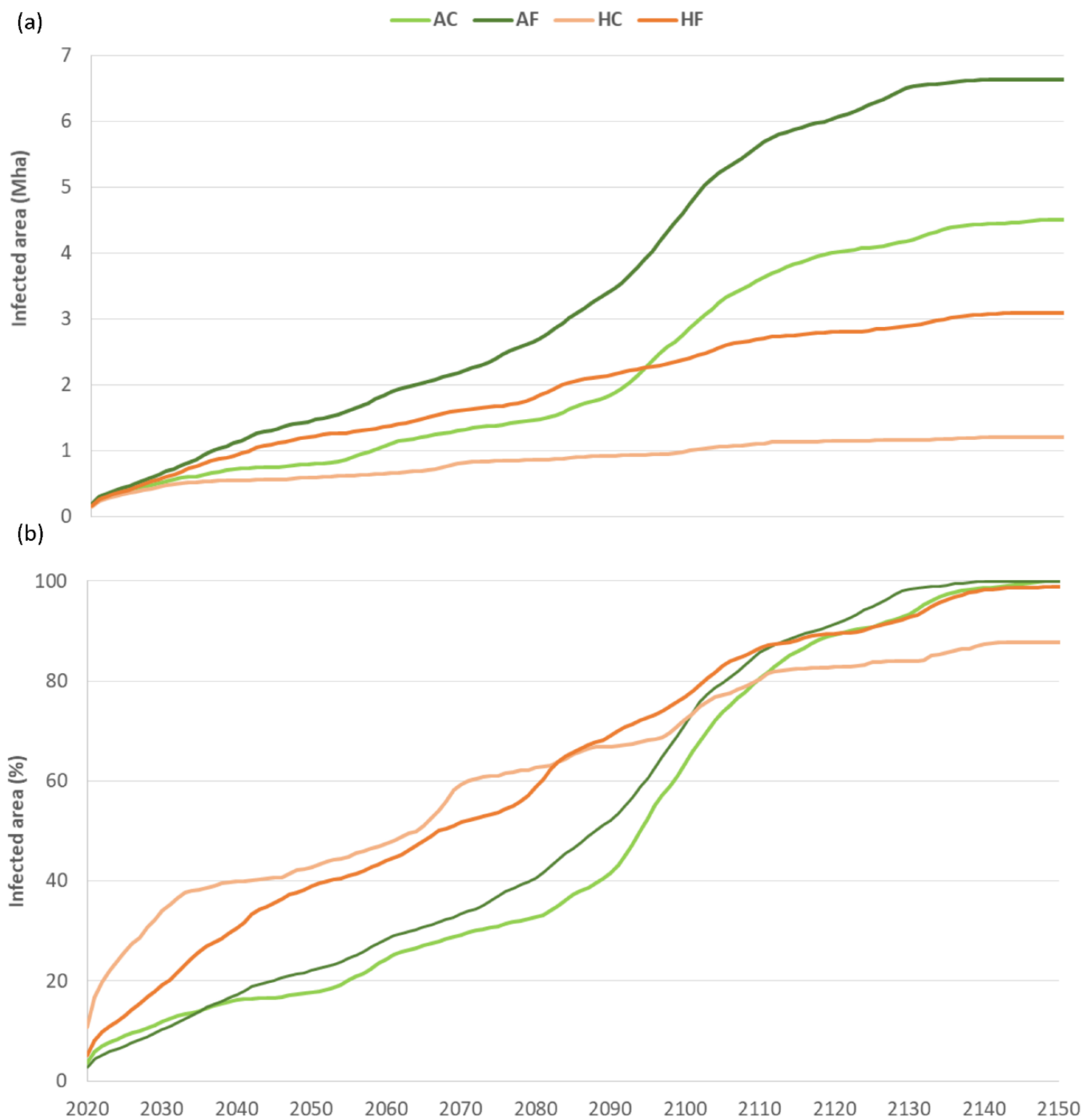

Figure 3. Infected area projections in the Iberian Peninsula for the four considered scenarios (AC, AF, HC and HF) up to the year 2150. Results are expressed in (**a**) as the forest area infected (Mha) and in (**b**) as the percent of the total forest area in the Iberian Peninsula that is infected. Projections consider all pine tree forest for Scenarios AC and AF (under current and future climate, respectively) and only the pine forest composed of highly susceptible species for Scenarios HC and HF (under current and future climate, respectively). Infected area corresponds to the cells with a probability of infection higher than 0.9 for a given year in the spread modelling. The asymptotes reached by the projections extend indefinitely beyond 2150 (all values remain constant up to 300 years of model runs).

In 2100, most of the Iberian Peninsula will be invaded by the PWN. Only the regions of Cataluña, Valencia and Murcia are predicted to be mostly free of infection by that year (Figure 1). All pine forests in the Iberian Peninsula are predicted to be infected by 2130 in Scenario AF (Figure 3).

3.2. *PWN Spread in Scenario AC: All Pine Forests and Current Climate*

When considering the current climate (Scenario AC), large tracts of forest in the northern part of the Iberian Peninsula, and particularly in the western half of this northern part, are not suitable to be infected or to transmit the disease (Figure 1). This results in less area that can be infected in any year compared to Scenario AF (Figure 3) and in a smaller portion of infected forest in the northeastern part of the Iberian Peninsula by year 2100 compared to Scenario AF, due to the lower continuity of susceptible forest in the north

(Figure 1). This delay in the PWN expansion due to the lower forest continuity in the north does not occur, however, in the invasion front through the central and southern parts of Spain (Figure 1), with patterns of spread that show similarities to those described above for Scenario AF (Figure 1). Finally, the PWN is able to spread, in the AC scenario, to all the pine forest in the Iberian Peninsula, even if a few years later than in Scenario AF (Figure 3).

The climatic constraints to PWN expression affect mostly the northwestern part of Spain, which is the one closer to the PWN sources in Portugal, and there is also a higher continuity of host pine trees in the eastern half of the Iberian Peninsula (Figure 1). For these reasons, the speed of PWN spread is considerably lower in the period 2020–2050 than in the period 2050–2100, with average rates of infection of 21,365 ha/year and of 43,146 ha/year, respectively (Figure 3).

3.3. PWN Spread in Scenario HF: Highly Susceptible Pine Forests and Future Climate

When only the pine tree species with high or very high susceptibility to the PWN (*P. pinaster*, *P. radiata* and *P. sylvestris*) are considered, the host vegetation distribution is considerably less continuous (Figure 2). In addition, the distribution of host vegetation (highly susceptible pine trees) is concentrated towards the western half of the Iberian Peninsula in this scenario (compare Figures 1 and 2).

This different distribution gives much less host forest area that can be infected on the Iberian Peninsula in Scenario HF compared to Scenarios AF and AC (Figure 3). The rate of spread (quantified as the increase in the percent of total forest area that is infected), however, is faster in the first two decades (2020–2040) in Scenario HF than in Scenarios AF or AC (Figure 3) because a larger proportion of the considered forest is distributed closer to the infection sources in Portugal (Figure 2). However, in later decades this rate of spread does not exceed that of scenarios AF and AC, as the invasion front moves towards the eastern half of the Iberian Peninsula, where the distribution of highly susceptible pine forest is sparser (Figures 2 and 3).

In Scenario HF, there is only one small patch of highly susceptible pine forest that is predicted to remain free from infection even in the long run: Serranía de Ronda in the Sistema Bético (south of Spain), which represents only about 0.2% of the total area of highly susceptible pine forest on the Iberian Peninsula. All the other highly susceptible pine forests on the Iberian Peninsula are predicted to get infected by the PWN eventually, although it takes longer than in Scenario AF (Figure 3).

3.4. PWN Spread in Scenario HC: Highly Susceptible Pine Forests and Current Climate

Scenario HC, which considers only highly susceptible pine tree species together with the unsuitable areas for pine wilt expression in the current climatic conditions, is the most restrictive one for PWN expansion. Scenario HC has the lowest amount of pine forest in the Iberian Peninsula of the four scenarios, has the lowest proportion of the Iberian Peninsula infected by 2100 of all four scenarios and is the only scenario in which a significant proportion of the considered forest area never gets infected, even in the long run. Our model predicts that 12.2% of the forest area will never be reached by the PWN in the HC scenario (Figure 3). These non-infected areas in the long run include the entire Pyrenees, some northern coastal areas, the coastal mountain ranges in Catalonia (Cordillera Costero Catalana) and, as in Scenario HF, Serranía de Ronda (south of Spain).

The speed of spread in Scenario HF considerably decreases with time (Figure 3), with a rate of infection of 14,946 ha/year up to 2050 and of 8280 ha/year from 2050 to 2100.

4. Discussion

4.1. The Large Spread Potential of the PWN in the Iberian Peninsula

Our results indicate that, in the absence of effective containment measures, the PWN will naturally invade, through the dispersal flights of the vector beetle *Monochamus galloprovincialis*, all the pine forests of the Iberian Peninsula. This will not be, however, a fast invasion process. Our model predicts that the natural PWN spread to the entire Iberian

Peninsula will take a century or longer, progressing at an average rate (average for all the four considered scenarios) of 0.83% of the total pine forest area per year over the next century, which increases to 0.90% per year if considering only the scenarios under future climate (AF and HF).

Our findings stress the high capacity of the PWN to spread through the rest of Portugal and through Spain via the dispersal flights of the vector beetle. Even large spatial discontinuities in the distribution of suitable areas for the PWN, caused by the lack of susceptible host vegetation or by climatic restrictions (Figures 1 and 2), do not generally block the spread of the PWN to other regions of the Iberian Peninsula, and at best delay to some extent the PWN expansion (with the only relative exception of Scenario HC discussed in the next section). These discontinuities are either circumvented through other available pathways or simply jumped over thanks to the considerable capacity of the PWN natural spread associated with the dispersal flights of the vector beetle populations. These vector populations are large in the Iberian pine forests, and only a few individuals that succeed in long-distance dispersal events are needed to further spread the disease to relatively distant areas [30].

4.2. The Impact of Current and Future Climate on PWN Spread

Of the four considered scenarios, only Scenario HC (high susceptibility pine tree species and current climate) gives some significant percentage of total forest area free from PWN invasion in the long run (about 12% of the total pine forest area considered in this scenario). Importantly, the areas excluded from PWN reach under this scenario include the entire Pyrenees, which would hence halt the natural spread of the PWN from Spain to France and the rest of Europe, naturally containing the PWN spread to the Iberian Peninsula only.

The inability of the PWN to spread to the Pyrenees under Scenario HC is because of two reasons. First, the coastal mountain ranges in Catalonia, running parallel to the Mediterranean Sea, are dominated by *P. halepensis*, a non-highly susceptible species, which makes these ranges lack sufficient density and continuity of host vegetation to provide a corridor for PWN spread towards the Pyrenees. Second, the potential west-to-east PWN dispersal to the Pyrenees through the north of Spain is impeded by the natural discontinuity due to the climatically unsuitable areas there in current conditions. The first reason is a structural one that will remain in the long run, impeding the PWN spread through that coastal pathway. The second reason, however, is unlikely to last: climate warming makes increasing portions of the currently climatically unsuitable areas adequate for pine wilt expression, making Scenario HC not representative of the longer-term PWN distribution and spread potential. Climate change will therefore pave the way for PWN spread through this northern corridor even when considering only the highly susceptible pine tree species as hosts (Scenario HF).

Current climatic constraints mean that an important portion of the Iberian Peninsula is not suitable for pine wilt expression and hence for the PWN spread: this happens in about 23% of the total pine forest area and 38% of the highly susceptible pine forest area, mainly in the north of Spain. These climatically unsuitable areas for the PWN will, however, progressively vanish with time, and all the pine forest area will be able to host and further transmit the wilt disease to other pine forest patches not later than by the end of the century, as predicted by the considered climate change models. Although we here base our climate forecasts on the IPCC A1B scenario, this may be in fact a relatively conservative or intermediate scenario that may underestimate the actual progression of climate warming [41], which would hence in any case result in the abovementioned significant lack of climatically suitable areas for PWN transmission by or before the end of the century. This will make, in summary, the natural spread of the PWN to the Pyrenees being delayed but not prevented in practice, in this or other realistic climate change scenarios. The expected climatic conditions do not offer, therefore, a significant limitation or barrier for the long-term spread and for the total pine forest area that can be invaded by the PWN in the Iberian Peninsula. Our results are consistent with the results obtained by Haran et al. [35] on the southern side of the Pyrenean chain, where they found that western and eastern hillsides may represent corridors favoring natural spread of the nematode from the Iberian Peninsula to France, and that temperature rise due to climate change may significantly reduce the extent of the barrier formed by the highest elevations.

4.3. The Importance of Pine Tree Species Susceptibility to the PWN

Unlike climate, the different susceptibility of pine tree species to the PWN is a structural and major long-term determinant of the invasion potential of the PWN; i.e., of the total pine forest area that can be invaded by the PWN in the Iberian Peninsula. The pine forest area that will be potentially affected by the PWN is less than half when considering only the highly susceptible pine tree species as PWN targets than when considering all pine tree species (compare Scenarios HF and AF in Figure 3). While several studies have examined and estimated the susceptibility of different pine tree species to PWD [26–28], this is probably the area of PWN research in which more additional efforts and studies are needed. More solid and detailed estimates of the responses of individual species to the PWN would considerably improve our ability to accurately predict the short-term and long-term spatiotemporal patterns of PWN spread, given the crucial role that tree species susceptibility plays in the modelling outcomes, as examined and determined for the first time in this study. A related and important avenue of further research is to understand and eventually quantify the potential adaptability of the genetic diversity of the domestic PWN populations and of the host tree species, which may alter the PWN capacity to infect and damage different pine forests in the Iberian Peninsula.

4.4. Measures to Contain PWN Spread

If no effective containment measures are taken, the PWN will invade all the pine forests in Portugal and Spain, resulting in large-scale ecological and economic impacts throughout the Iberian Peninsula. These impacts include, among others, wood and wood production losses [17–19]; changes in soil properties and pine forest communities; altered forest succession and regeneration; loss of the oldest and biggest pines [20,42], which frequently have a higher conservation and biodiversity value; and potential disruption of protected area networks [22].

Avoiding this damage to Iberian pine forests requires the combined application of several measures for PWN containment. These measures mainly consist of reducing the vector beetle population through mass trapping during the flight period (spring–summer) and the intensive surveillance of pine forests to allow the early detection and removal of infected trees before the PWN-infected beetles emerge and spread the disease to other pine trees or patches [30,43–47]. However, the effectiveness of this early detection and removal measure in containing the PWN spread may be compromised to some extent by the role of asymptomatic tree infections in the expansion patterns [48]. Other longer-term measures that could promote the capacity of the pine forests to resist or cope with the PWN infection include forest management treatments, such as thinning, that increase tree vigor or tree species diversity [49–51], or establishing pine half-sib families with higher genetic tolerance to the PWN [28,52].

It needs to be emphasized that our model and PWN spread projections only consider the natural spread of the PWN by its vector beetle. Human-mediated dispersal is not considered in our analysis and may, in case of uncontrolled transport of infected wood, drastically increase the speed and modify the spatiotemporal patterns of the PWN spread throughout the Iberian Peninsula and the rest of Europe. Therefore, our PWN expansion projections will only be valid, and the potential management measures outlined above will only be effective, under a rigorous application of the regulations and restrictions on timber treatment and transport. The control of the origin and sanitation of pine wood for transportation is essential to avoid larger-scale and uncontrolled human-mediated dispersal through the Iberian Peninsula [12,53]. Modelling anthropogenic PWN dispersal is complex, involving a considerable stochastic component, and is out of the scope of this study; however, it could be further explored in the future, by incorporating in our modelling framework some of the methods and ideas by Robinet et al. [54], Pukkala et al. [38] and Hudgins et al. [55].

5. Conclusions

Our modelling approach and the results for the set of considered scenarios allow us to reach the following four main conclusions:

- In the absence of effective containment measures, the PWN will spread naturally, through the dispersal of its vector beetle, to the entire Iberian Peninsula, including the Pyrenees, which would provide a gateway for further PWN expansion into France and the rest of Europe.
- The natural spread of the PWN will be relatively gradual, with an average rate of 0.83% of the total Iberian forest area infected yearly, so that it will take a century or longer for all the susceptible pine forests in Spain to be invaded by the PWN.
- Climate is not an important limiting factor for long-term spread of the PWN, because (i) there is ample availability of alternative pathways for PWN dispersal through the areas that are already suitable for the PWN in the current climatic conditions; and (ii) climate change projections, even conservative ones, indicate that future temperatures will make the whole Iberian Peninsula suitable for PWN transmission by or before the end of this century, except for some isolated mountain peaks.
- Unlike climatic conditions, the susceptibility of different pine tree species to PWN is by far the main determinant of PWN spread rates and of the extent of forest area affected by the wilt disease. Our findings highlight the need and importance of integrating data on individual pine tree species into predictive models on the spread and magnitude of damage caused by the PWN. Additional research that can refine our knowledge on tree species susceptibility is hence of particular importance for more accurate modelling of the PWN spread and for better guiding related containment efforts.

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