Improving monitoring and management methods is of the utmost importance in countries at risk of invasion by the pinewood nematode

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Improving monitoring and management methods is of the utmost importance in countries at risk of invasion by the pinewood nematode

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Abstract

Key message The invasive pine wood nematode is a major threat to pine forests worldwide, causing extensive tree mortality. Although scientific knowledge and control measures are continuously improving, important gaps remain. We argue that some key questions, notably related to early detection and pest management, need to be urgently tackled in countries at risk of invasion such as France.

Keywords Pine wilt disease, *Bursaphelenchus xylophilus*, *Pinus*, Forest, *Monochamus*, Insect vector

1 Introduction

A major threat to pine forests worldwide is the pine wilt disease (PWD), which is caused by the pine wood nematode (PWN), *Bursaphelenchus xylophilus* (Mota and Vieira 2008; Zhao et al. 2008). This disease can lead to the death of the infested trees within a few weeks only (Webster and Mota 2008). The PWN is native from North America, and invaded large parts of Asia, namely Japan, China, and Korea (Mota and Vieira 2008). It was detected in Europe for the first time in Portugal in 1999 (Mota et al. 1999). It is always carried and transmitted by native longhorn beetles of the genus *Monochamus* spp. (Evans et al. 1996). In Europe, *Monochamus galloprovincialis* is the only known vector so far (Naves et al. 2016). In accordance with the EU regulation, control measures were immediately applied in Portugal but proved insufficient to contain the nematode (de la Fuente et al. 2018). The entire Portugal is now considered contaminated, and several isolated spots of infected trees have been observed in Spain to date, at less than 100 km from the Portuguese border (Sousa et al. 2021). Eradication and containment measures requested by the EU regulation involve clear cuts of host trees within 500 m from an infested tree and restrictions in the transportation of pine wood from infested areas. These measures have a major impact on the forestry and timber industries; they are very costly for both the national authorities and the

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private sector (Soliman et al. 2012; Zhao et al. 2020; Liu et al. 2023) and socially difficult to accept.

In South European PWN-free countries, the invasion risk is high with potentially huge impacts related to the PWD, particularly in France. Firstly, PWN is likely to arrive by accidental transportation of infested wood from contaminated countries (Robinet et al. 2011; Douma et al. 2017). From 2000 to 2019, 41 infested wood samples were intercepted in France (Mariette et al. 2023). Additionally, the PWN might arrive by dispersal of infested vectors. France is contiguous to the Iberian Peninsula (Portugal and Spain) but separated by the Pyrenean mountains. Although the insect vector is not likely able to fly across these mountains which culminate at around 3400-m asl, western and eastern hillsides represent important corridors for *M. galloprovincialis* populations (Haran et al. 2015). Since the closest infested spots in Spain is located at more than 400 km, this introduction scenario is unlikely at a short time horizon, at least. Secondly, the population level of *M. galloprovincialis* is currently high in potential recipient forests in south-western France, as shown by trap captures (Mariette et al. 2023), increasing the risk of rapid PWN propagation. Lastly, according to climate conditions, a large part of France is suitable for the development of pine wilting symptoms (Mariette et al. 2023). The economic impact of the PWN invasion is expected to be the highest in south-western France (Soliman et al. 2012) where the largest area of plantation forest is located, mainly composed of maritime pine, one of the most sensitive host species.

Since PWN is knocking at the door of France, economic and sociopolitical issues and stakes are jointly explored by scientists and stakeholders. Although scientific knowledge and control measures are continuously improving, we argue that there are still some important gaps to be filled. Hereafter, we identify and prioritize a list of research questions that should be addressed to better assess and manage the invasion risk of PWN. This list resulting from a transdisciplinary brainstorming is not exhaustive but aims to reflect the most important and challenging questions raised nowadays by the French researchers and stakeholders' community. Although mainly focused on the French situation, the same questioning may apply to other parts of the world where PWN is an important threat or already causing dramatic damage.

2 Questions to urgently tackle regarding the PWD

The PWD results from complex biotic interactions involving mainly the invasive PWN, its host trees, and its vectors (Fig. 1). In addition, it appears that the associated microbiotes (e.g., fungi, bacteria) and human activities should be considered as a part of the system, impacting and being impacted by the PWN. Hereafter, we suggest questions to urgently tackle for each main component of the biological interaction (nematodes, host trees, insect vectors) as well as for the PWD management and public policies. Although we do not explicitly refer to the effects of international and intra-EU trade, or the effects of climate change, these are also important drivers of the PWN invasion risk, and further studies should continue on these aspects as well.

2.1 Questions about the pine wood nematode and associated microbiotes

2.1.1 Effects of native nematode communities

A parasitic invasive species can establish in a novel environment only if local conditions at arrival are favorable, i.e., climate suitability and host tree availability, and if it can either occupy an empty niche in the ecosystem or outperform competitive indigenous species. Empirical evidence from areas where the PWN is already established suggests that the epidemic is not prevented by the occurrence of congeneric nematode species, but their possible influence (e.g., competitive exclusion) on invasion dynamics remains unknown. Under laboratory conditions, the closely related species *B. mucronatus* did not outcompete *B. xylophilus* (Vincent et al. 2008), but many other species may be considered (e.g., 12 *Bursaphelenchus* species detected in French pine forests; Mariette et al. 2023). Species displacement resulting from intrinsic factors (e.g., production of nematode pheromones, Meng et al. 2020; or sex ratio of competitive nematodes species, Zhou et al. 2023) could also play a role in the invasion of the PWN. As a whole, we note that the community ecology of the nematode remains largely unexplored and need careful consideration.

2.1.2 Evolutionary potential of the pine wood nematode

Involving a diversity of host trees and insect vectors, the invasive success of the PWN across continents suggests a high evolutionary potential and abilities to adapt to new environmental conditions. However, understanding of the underlying mechanisms is still largely missing. Deciphering the demogenetic processes affecting the evolution of this species (i.e., gene flow, genetic drift, and inbreeding) at different spatial scales could allow to predict their relative effects in the event of introduction of the PWN in a new area. In particular, we think that determining which traits and/or genes are involved in the pathogenicity of the PWN and how this compares with other, non-pathogenic species (e.g., *B. mucronatus*) is essential. In parallel, it is crucial to understand the variability of these traits and genes within *B. xylophilus* populations, which may drive or not the development of the PWD. Moreover, since hybridization between *B.*

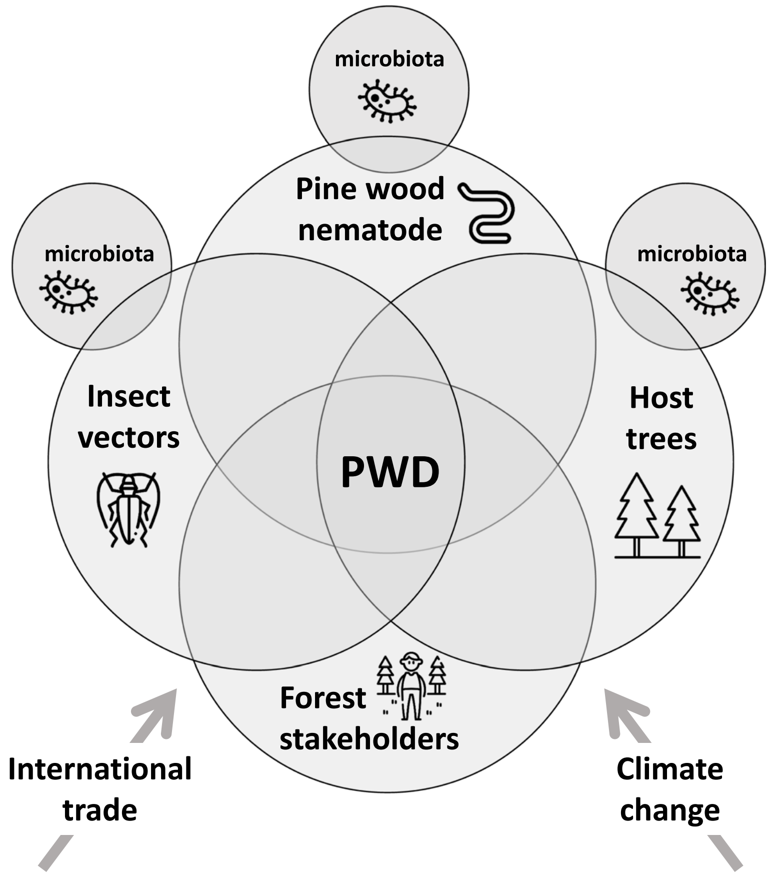

Fig. 1 Socio-ecosystem of the pine wilt disease (PWD)

mucronatus and *B. xylophilus* has been observed both in laboratory and *in natura*, it appears necessary to evaluate whether it could affect the fitness and pathogenicity of such interspecific hybrids (Tomalak and Filipiak 2021).

2.1.3 The roles of microbiotes

The PWD is mainly the result of a tripartite interaction between the PWN, the host tree, and the insect vector, but there is growing evidence about the role of microbial communities in this pathosystem, each of the main actors possibly carrying a large panel of microbes (bacteria, virus, archaea, protists, and fungi) which could potentially affect the fate of PWD epidemics (Espada et al. 2022). Fungi are necessary for feeding nematodes in the early stages of their development, but some fungal species can be harmful (e.g., nematode-trapping fungi) and thus represent promising biocontrol candidates (Zhang et al. 2022). The diversity of bacteria associated with the PWN in host trees is quite well documented, but we highlight that their roles in the interaction are not yet fully understood. Some species may be involved in nematode virulence, while others have shown nematicidal properties *in vitro*. However, the scientific community remains divided about the role of associated microorganisms in the PWD, and whether they have any strong consequence for the development of the disease is still under debate.

2.2 Questions about the host trees

2.2.1 Host tree status of conifer species

Here, we define as a host tree the species where both the PWN and its vector can complete their whole life cycles and thus potentially spread the PWD. The knowledge of host tree status is important to better predict PWN potential invasion and for better management since applying the European Decision 2012/535/EU involves clear cutting of all host trees around PWN-infested trees. However, we claim that this status is uncertain for some conifer species (e.g., *Pinus taeda*, *Pseudotsuga menziesii*, *Picea abies*) and should be further clarified.

Conifer species have been classified as resistant, susceptible, or intermediate (Evans et al. 1996). However, this classification was based on a large set of methods (e.g., laboratory inoculation of PWN in young tree seedlings) and sometimes with contrasting results. For example, *P. taeda* is considered so far as non-susceptible (ANSES 2019) because the vector cannot reproduce on this species, while this statement is questioned since *M. galloprovincialis* adults have been trapped in *P. taeda* plantations in France (Hervé Jactel, unpublished). It is thus urgent to clarify the host tree status of these coniferous species.

2.2.2 Identifying resistant tree populations and the mechanisms involved

While breeding forest trees is a long and complex process, identifying and deploying resistant trees combined with control methods could help to support productivity of the wood sector in case of PWN invasion. Breeding programs for pine resistance to PWN started in different countries on several *Pinus* species (Toda and Kurinobu 2002; Carrasquinho et al. 2018; Menéndez-Gutierrez et al. 2018; Kleinhentz et al. 2021). However, the intraspecific genetic variability of susceptibility to PWN in host tree species is still largely under-explored, for example, between and within *Pinus pinaster* populations. We assert that additional studies are needed to identify resistant trees that would provide a genetic base for the creation of resistant forest reproductive material (FRM).

In existing breeding programs, the selection methodology is based on inoculation tests on young seedlings or grafted trees in confined environments. This selection methodology and the choice of PWN populations for inoculation tests need to be optimized with regard to the possible evolution of the virulence of PWN populations and the risk of resistance breakdown. Furthermore, while breeding programs for PWD resistance have yet not reached (or only recently in Japan), the stage of resistant material deployment in the forest, a deployment strategy, and a sustainable resistance management based on resistant FRM distribution over time and space still need to be modelled.

Several studies based on individuals or families identified as resistant in different pine species have highlighted mechanisms involved in resistance at anatomical, molecular, or metabolic levels, some of which are relatively shared between species (Modesto et al. 2021), but remain to be elucidated in their functioning. We highlight that future research should explore resistance mechanisms and study (tree) genotype × (PWN) genotype and (tree) genotype × (PWN) genotype × environment interactions to predict susceptibility or resistance at the individual level and provide elements for modelling disease evolution, as well as criteria for early selection. In addition, cascading effects of different biotic and particularly abiotic stresses on tree health are expected to impact the PWD dynamics.

2.3 Questions about the insect vector

2.3.1 Ecology of potential vectors

To assess the risk of PWN invasion and spread, it is crucial to know the spatial distribution, population level, and life traits (such as dispersal capability and growth rate) of insect vectors. So far, *M. galloprovincialis* is the only known vector of the PWN in Europe. Although largely distributed throughout Europe, its spatial distribution is not accurately known, and, except trap captures at several sites, its abundance is even less documented throughout its range. Regarding dispersal patterns, gene flow between populations revealed the effects of landscape and mountains on dispersal (Haran et al. 2015, 2017). Dispersal capability (flight distance) was also assessed using flight mill experiments and/or mark-release-recapture experiments in large pine forests (Robinet et al. 2019), and preliminary studies suggest that the dispersal behavior is modified in more heterogeneous landscapes (Nunes et al. 2021). We believe that it is crucial to better understand the effect of forest landscape composition and fragmentation on the flight capabilities and behavior of *M. galloprovincialis* in order to predict its spread but also to possibly modify forest management to curb it. In addition, another knowledge gap is the effects of the PWN load on the biology and ecology of its vector, in particular its dispersal capabilities. Furthermore, other insect species might carry and transmit the PWN. A known vector in Asia (*Monochamus saltuarius*) occurs in Europe. Although not carrying the PWN in Europe so far, it could likely carry the PWN here as well. Other species occurring in Europe might also carry and transmit the PWN such as *Monochamus sartor* and *Monochamus sutor* (Evans et al. 1996; EPPO 2022). We argue that our knowledge about potential vectors is surprisingly poor and their co-occurrence could permit the PWN to potentially shift on other host tree species. Better assessing the invasion risk requires to fill in this gap, namely to identify more clearly the potential vectors, their distribution, their abundance, and their life-history traits.

2.3.2 Regulating M. galloprovincialis populations

Since the PWN is transmitted by native *Monochamus* spp., and the increase of wilting trees offers more suitable breeding substrate to *Monochamus* females, both partners act in a synergetic way. While it is unethical to target eradicating the populations of native beetles and possibly disturb the associated biodiversity, we believe that maintaining *Monochamus* populations at a low level could contribute to manage successfully the PWN. At least three directions could be explored. Firstly, we need to identify and promote tree harvesting methods to avoid beetle oviposition and larval development, such as salvage cutting of declining trees, grinding of thinning, or logging residuals in areas at risk. The efficiency levels of the various shredding techniques still need to be assessed in order to identify management compromises. Secondly, early larval stages of *M. galloprovincialis* (L1 and L2) need pine bark for their development (Koutroumpa et al. 2008). Debarking immediately after felling would limit the development of *Monochamus* spp. during storage and make transport safer. The feasibility and effectiveness of debarking pine logs in controlling the *Monochamus* population levels should be determined. Lastly, forest diversification seems promising (Jactel et al. 2021). Indeed, maritime pine mixed with umbrella pine is less likely to be attacked by *M. galloprovincialis* (van Halder et al. 2022), and deciduous woodlands are forest habitats avoided by the insect as it disperses (Nunes et al. 2021). It would therefore be interesting to better assess the effect of forest species mixing on the population dynamics of the insect vector, at both stand and landscape levels. Nevertheless, the combination of these management efforts and their potential efficiency, as well as their effects on biodiversity, should be investigated.

2.4 Questions about the management of the pine wilt disease

2.4.1 Early detection of infested stands and infested trees

Because eradication success of invasive species is the highest when pests are detected at the early stage of their invasion (Pluess et al. 2012), managers need faster and more specific methods to detect PWD symptomatic trees. Here, two spatial scales should be considered. At the landscape scale, remote sensing has recently provided very valuable results to detect wilting trees in forests (Luo et al. 2023). However, this technique leads to the over-detection of wilting trees, not necessarily in relation with PWN infection. We assert that artificial intelligence should be used to identify wilting patterns which correlate with the presence of PWD. In addition, refining the status of tree species as susceptible or tolerant to the PWN and mapping these host trees on a landscape scale could enable surveillance to be focused on the most relevant areas.

At the tree scale, detection need to be improved as well (Li et al. 2022). Wood sampling is commonly done at human breast height, whereas the PWN first invades tree branches and can take several days or weeks to reach the tree stem. Sampling in tree canopy with new operational tools could improve the effectiveness of PWN detection and reduce damage to tree trunk. Besides, molecular identification of the PWN is now available with LAMP methods (loop-mediated isothermal amplification) but still needs to be more operational in the field (Kikuchi et al. 2009; Wang et al. 2022). Lastly, new innovative methods avoiding the drawbacks of wood sampling could be explored, such as the sensor characterization of specific volatile organic compounds emitted by infested trees.

2.4.2 Efficiency of field treatments and alternative wood treatments

Many direct control methods of PWN (e.g., chemicals, natural enemies, competitors…) have been tested in vitro or on young seedlings in laboratory in controlled conditions. However, their efficiency in the field (where their effects could be very different), and their cost-effectiveness have yet to be assessed.

Moreover, the International Standard for Phytosanitary Measures (ISPM15) requires the application of an approved treatment to wood packaging materials. In the context of reduction or ban of phytosanitary chemicals in some countries, the methyl bromide treatment is being disregarded, while heat is the main approved treatment currently used. However, in view of the difficulty in applying such a treatment and the increase in energy costs, we believe that the effectiveness of potential alternative methods should be studied.

2.4.3 Toward integrated pest management?

Since there is no silver bullet against the PWD, we conclude that an integrated pest management (IPM) strategy combining a set of measures would be the most promising. First, it is crucial to reinforce surveillance in areas at risk of invasion. Some directions have been discussed in this paper (e.g., remote sensing). However, because infested trees do not always show wilting symptoms, it is important to consider detection methods independently of the presence of symptoms. In addition to random wood sampling, checking the absence of the PWN on *M. galloprovincialis* individuals is a complementary method commonly used. Pheromone traps have an attraction distance of about 100 m (Jactel et al. 2019) and can only capture a very low proportion of *M. galloprovincialis* (Robinet et al. 2019). Optimizing the trapping network over France, based on the latest knowledge (notably on *M. galloprovincialis* dispersal behavior), is strategic for surveillance and early detection. Beyond such surveillance methods, an integrated control strategy including the plantation of resistant pine tree genotypes, the mixing of host trees species with non-host tree species, and the removal of the vector breeding substrate in the forest could be implemented.

2.5 Legitimacy and support of public policy actions

2.5.1 How risk perception impacts policy governance?

Given the increasing number of biological invasions worldwide, one can wonder why the PWN would be more frightening than other invasions. We need to know in depth which factors influence stakeholders' perceptions of PWN and guide their decision-making. For a given social group, risk perceptions of PWN may be influenced by previous experiences about similar biotic risks, available information, trust in informants, and existence of a contingency plan. Furthermore, since transdisciplinary research involves stakeholders, it could serve the interests of the most influential and powerful groups, who could use scientific arguments selectively for a specific purpose. Some of them may question the wisdom of spending a lot of money on monitoring and managing the PWN or wonder whether the impact of management on the forestry sector is worse than the damage caused by the PWN itself. To convince people of the legitimacy of public policy actions to manage the risks associated with the PWN, we believe it is important to continue exploring the hypothetical "what if nothing was done" scenario.

2.5.2 Stakeholders preparation and support: how to accompany the most vulnerable?

Once it arrives, the PWN will undoubtedly have a considerable impact on the pine forest ecosystem and the timber industry. Those involved in the field need to be aware of the problem and be prepared. More research should be done to identify the most vulnerable actors of the forest and wood sector, their level of preparedness, their self-capacity to cope with the crisis, and, if not, their needs for specific support (public subsidies, actors' coordination, wood marker regulations) in a short and midterm. It will be also useful to identify hard-to-reach areas where management in PWN will be very difficult.

3 Conclusions: priority questions

In this opinion paper, we highlight important questions that should be urgently tackled. For each question, each author provided the following: (1) a priority score which was then averaged and (2) the categorization, and the most frequent category was then considered to build Fig. 2. In particular, we conclude that improving the PWN surveillance and management is of the utmost importance in countries exposed to the risk of invasion, such as in France (Fig. 2).

More precisely, it is very urgent to optimize early detection, to develop an adequate integrated pest management, and to determine the best field and wood treatments. Although top priority questions are more related to the PWN management, another very high priority question for both management and academic

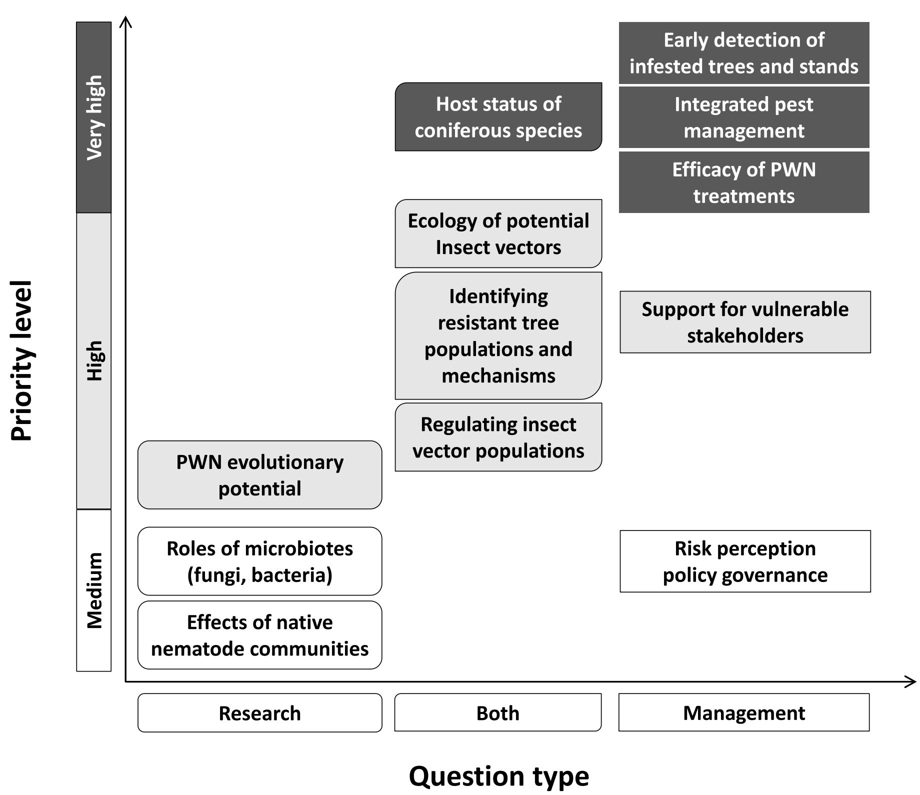

Fig. 2 Ranking of priority questions as a function of its category (research, management, or both)

researches is to clarify the host status of some coniferous tree species.

Priority questions coming just after mainly involve both management and research issues. Better understanding the ecology of vectors, identifying resistant tree populations and understanding resistance mechanisms, and regulating vector populations are highly important questions from our point of view (Fig. 2). Supporting the most vulnerable forest and wood actors and understanding the PWN pathogenicity are high priority questions for management and research respectively.

Then, roles of microbiotes and native nematode community in the invasion success also deserve to be addressed — although at a lower priority — to better assess the risk of PWN invasion. In terms of management, a more secondary issue deals with how the PWN invasion risk perception impact public policies.

We provide this prioritization ranking at the current time, based on a set of various expertises covered by the authors. Of course, this ranking may not reflect priority questions in the future or in another context. Anyway, for most of these questions, it is necessary to shift from experimental results to more operational and efficient management options in the field. Intensifying international collaboration with countries already infested by the PWN would be very helpful for that purpose. Finally, in addition to identifying key questions together, we would like to emphasize that close interaction between scientists and forestry sector players remains essential to answer them in the field, and that a research-action approach is therefore necessary to gain speed and efficiency.

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