Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 2024:67
Faculty of Forest Sciences

Forest *Phytophthora* – Ecology, Diversity and Management

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SLU
SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

DOCTORAL THESIS
Alnarp 2024

Acta Universitatis Agriculturae Sueciae
2024:67

Cover: Schematic representation of the microbiome in healthy versus declining oak trees. (Photo: Noelia López–García, with assistance by Dall E 3)

ISSN 1652-6880
ISBN (print version) 978-91-8046-358-4
ISBN (electronic version) 978-91-8046-394-2
DOI: https://doi.org/10.54612/a.4p1n97bp4k

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Print: SLU Grafisk service, Alnarp 2024

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Abstract

Invasive *Phytophthora* species significantly threaten the health and productivity of forest ecosystems. This thesis aims to explore the diversity and distribution of pathogenic forest *Phytophthora* species, as well as their interactions with microbial communities and human activities. We explore existing regulations and management strategies to prevent and control the spread of *Phytophthora* species across different production settings and ecosystems worldwide. *Phytophthora* species were isolated from different forest settings in southern-mid Sweden through both direct isolations and a Sanger sequencing approach. To understand the role of the soil microbiome in oak decline, we studied the fungal and bacterial communities in the rhizospheres of both declining and healthy pedunculate oak trees. We used metabarcoding to analyse microbial diversity and composition. We found that current regulations have largely been ineffective in controlling the issues caused by oomycete pathogens. The adaptability of these pathogens and their spread through human activities and international trade highlight the urgent need for exhaustive management approaches and robust legislative measures. Enhancements in testing, detection methods, and phytosanitary infrastructure, along with raised awareness among stakeholders and consumers, are key. Our study identified significant gaps in the practical implementation of existing research, which are attributed to the limited holistic understanding by practitioners of these processes over time and space. Furthermore, there are few or no field experiments, which are essential for validating new treatments and optimizing application methods. Advancements in technology and a better understanding of epidemiology and host resistance are crucial for enhancing surveillance and management tools, enabling more effective control measures. Metabarcoding analysis revealed significant differences in bacterial and fungal diversity between healthy and declining trees, suggesting a bidirectional dependence between tree health and microbial community composition. We isolated eight *Phytophthora* species, including some newly-identified species and first-time host associations, underscoring the intricate interactions among this pathogen, microbial communities, host trees, and human activities on *Phytophthora* distribution. Overall, our findings emphasise the need to integrate advanced detection methods, public engagement, and robust legislative measures to develop effective management strategies against *Phytophthora* diseases, ultimately aiming to protect forest ecosystems from this escalating threat.

Keywords: EU legislation and policies, oomycete dispersal pathways, management practices, biocontrol mechanisms, pesticides, metabarcoding, microbial community, *Phytophthora* damage, forest decline

Phytophthora i Skog – Ekologi, Mångfald, och Åtgärd

Abstract

Invasiva *Phytophthora*-arter utgör ett betydande hot mot hälsa och produktivitet i skogsekosystem. Denna avhandling syftar till att undersöka mångfalden och spridningen av patogena *Phytophthora*-arter hos skogsträd, samt deras interaktioner med mikrobiella samhällen och antropogena aktiviteter. Vi undersöker befintliga regleringar och förvaltningsstrategier för att förebygga och kontrollera spridningen av *Phytophthora*-arter i olika produktionsmiljöer och ekosystem världen över. *Phytophthora*-arter samlades in från olika skogsområden i södra mellersta Sverige genom direkt isolering och Sanger-sekvensering. För att förstå rollen som mikroorganismerna i rhizosfären spelar för ekens hälsa studerade vi svamp och bakteriesamhällena runt både sjuka och friska skogsekar. Metabarkodning användes för att analysera mikrobiell mångfald och sammansättning för svampar och bakterier. Vi fann att nuvarande regleringar till stor del har varit ineffektiva när det gäller att motverka problemen orsakade av algsvampar. Dessa patogeners anpassningsförmåga och deras spridning genom antropogena aktiviteter och internationell handel visar på det akuta behovet av omfattande kontrollmetoder och mer robust lagstiftning. Förbättringar i testning, detektionsmetoder och fytosanitära infrastrukturer, tillsammans med ökad medvetenhet bland intressenter och konsumenter, är avgörande. Vår studie identifierade betydande brister i den praktiska tillämpningen av befintlig forskning, vilket tillskrivs en begränsad holistisk förståelse hos praktiker av processerna över tid och rum. Dessutom saknas fältexperiment som är väsentliga för att validera nya behandlingar och optimera tillämpade metoder i praktiken. Framsteg inom teknik och bättre förståelse för epidemiologi och värdträds resistens är avgörande för att förbättra övervaknings- och hanteringsverktyg, vilka skulle möjliggöra mer effektiva kontrollåtgärder. Metabarcoding-analyser av mikrober i rhizosfären hos skogsek visade stora skillnader i bakterie- och svampmångfald mellan friska och sjuka träd. Detta tyder på att trädens hälsa och mikrobiella samhällen påverkar varandra. Vi isolerade åtta *Phytophthora*-arter, inklusive några nyligen identifierade på olika värdträd, i skogsmiljöer understryker den interaktion som sker mellan dessa *Phytophthora*-arter, mikrobiella samhällen, värdträd och mänskliga aktiviteter och vilken påverkan det har på spridningen av patogener. Avhandlingen betonar behovet av att integrera avancerade detektionsmetoder, engagemang av civilsamhället och robusta lagstiftande åtgärder för att utveckla effektiva strategier i hanteringen av *Phytophthora*-sjukdomar, och därigenom bättre skydda våra skogsekosystem.

Keywords: EU-lagstiftning och -policys, oomyceters spridningsvägar, åtgärd, biologiska kontrollmekanismer, bekämpningsmedel, metabarkodning, mikrobiellt samhälle, *Phytophthora*-skador, skogsnedgång

Dedication

To my family and friends. Thank you for your support and unconditional love.

A mi familia y amigos/as. Gracias por vuestro apoyo y amor incondicional.

"*The garden of the world has no limits, except in your mind*"

Rumi

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Clara Benavent–Celma; **Noelia López–García**; Tahmina Ruba; Magdalena E. Ściślak; David Street–Jones; Pieter van West, Stephen Woodward; Johanna Witzell* (2022). Current practices and emerging possibilities for reducing the spread of oomycete pathogens in terrestrial and aquatic production systems in the European Union. Fungal Biol. Rev. Vol. 40, pp. 19–36. https://doi.org/10.1016/j.fbr.2021.10.001

II. **Noelia López–García***; Carmen Romeralo; Jonas Rönnberg; Johanna Witzell (2024). Control and management of *Phytophthora* damage in forestry – A systematic mapping study. For. Pathol. 54 (4): e12878. http://doi.org/10.1111/efp.12878

III. **Noelia López–García***; Carmen Romeralo; Christian B. Andersen; Jonas Rönnberg; Laura J. Grenville–Briggs; Johanna Witzell (2024). Metabarcoding reveals rhizosphere microbiome shifts between healthy and declining *Quercus robur* trees. (manuscript)

IV. **Noelia López–García*;** Michelle Cleary; Mimmi Blomquist; Stephen Woodward; Laura J. Grenville–Briggs; Jonas Rönnberg (2024). Association of *Phytophthora* species with diseased trees in urban– and peri–urban forests in southern–mid Sweden. (manuscript)

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Additional publications that are not part of this thesis:

Iryna Matsiakh, **Noelia López–García**, Magdalena Kacprzyk, Michelle Cleary (2023). Susceptibility of silver birch and black alder to several *Phytophthora* species isolated from soils in declining broadleaf forests in western Ukraine. For. Pathol. 53 (4): e12817. https://doi.org/10.1111/efp.12817

The contribution of Noelia López–García to the papers included in this thesis was as follows:

I. C.B.C., **N.L.G.**, M.E.Ś., T.R., and D.S.J., developed the search stream, coordinated the searches, and jointly wrote the manuscript together with the co-authors; Authors contributed equally and formulated the original idea.

II. **N.L.G.**, C.R., and J.W., developed the research design and methodology; **N.L.G.**, and J.W., developed the search stream, coordinated and conducted searches; **N.L.G.**, and C.R., conducted the classification of the literature; **N.L.G.**, managed data analyses, interpreted results and wrote the manuscript together with co–authors. J.W., formulated the original idea.

III. **N.L.G.**, C.R., and J.W., developed the research design and methodology; **N.L.G.**, collected soil samples in the field, coordinated and conducted lab work; **N.L.G.**, and C.B.A., built the bioinformatics pipeline; **N.L.G.**, performed statistical analyses, interpreted results and wrote the manuscript together with co–authors. L.J.G.B., and J.W., formulated the original idea.

IV. **N.L.G.**, contributed to data compilation, analysis, and writing the initial version of the manuscript. M.B., and M.C., collected samples in the field, coordinated and conducted lab work; M.C., L.J.G.B., J. R., and W.S., contributed to the data interpretation and manuscript writing, together with **N.L.G.**; M.C., formulated the original idea.

Abbreviations

ASV	Amplicon Sequence Variant
bp	base pair
EFSA	European Food Safety Authority
eNoses	electronic Noses
EU	European Union
GC-MS	Gas Chromatography-Mass Spectrometry
GIS	Geographic Information Systems
HTS	High Throughput Sequencing
IAS	Invasive Alien Species
IPM	Integrated Pest Management
ITS	Internal Transcribed Spacer
LAMP	Loop Mediated Isothermal Amplification
NGS	Next Generation Sequencing
NPPOs	National Plant Protection Organisations
NPs	Nanoparticles
PPPs	Plant Protection Products
Q. robur	*Quercus robur* L.
VOCs	Volatile Organic Compounds

Background

In the last 30 years, there has been a noticeable trend of living organisms extending beyond their native habitats (Fisher et al. 2012; Ricciardi et al. 2013; Hansen 2015; Hulbert et al. 2017; Jung et al. 2018). International trade and human mobility have played, arguably, the major role in introducing forest pathogens to new areas, leading to the emergence of novel ecological interactions (Brasier 2008; Santini et al. 2013; Jung et al. 2016; Hulbert et al. 2017; Benavent–Celma et al. 2022). Incidences of the introduction of plant–pathogenic *Phytophthora* species are being documented worldwide (Webber et al. 2010; Jung et al. 2016; Burgess et al. 2017; Chapman et al. 2017; Puertolas et al. 2021), representing a significant threat to both forest plantations and ecosystems, also triggering losses in plant nurseries. Particularly in forest environments, the evident lack of effective measures for the control and management of these pathogens emphasizes the urgency for research focused on understanding and addressing these invasions. The primary aim of the work described in this thesis was to explore the diversity and distribution of pathogenic *Phytophthora* species in forest ecosystems in Sweden.

1. Introduction

Sweden is predominantly covered by forestlands, encompassing 28 million hectares. Of this area, approximately 88% is classified as productive forest, while around two million hectares are designated for conservation purposes (Scb, 2020; SFA, 2020). This productive forest significantly contributes to the global market, providing ten percent of the world's sawn timber, pulp, and paper (SFIF, 2024). Consequently, forestry practices and forest management play crucial roles in determining forest biodiversity and productivity. Current forest management in Sweden mainly relies on clear–cutting and subsequent reforestation through seedling planting, leading to even–aged monocultures (Kuuluvainen et al. 2012). As a result, the historical exploitation of forests in southern Sweden has created a uniform forested landscape, contrasting with the natural forests, which were typically dominated by broadleaved or mixed coniferous–broadleaved species (Björse and Bradshaw, 1998; Lindbladh, 1999). Biodiversity in the nemoral zone (southernmost Sweden, dominated by broadleaved trees) and especially in the hemiboreal zone, a transition area between the nemoral and boreal forests (northern to south–central Sweden), is directly influenced by forest operations (Lariviere, 2023). The hemiboreal zone has the highest species richness for many organism groups, such as insects and fungi, due to climatic overlap and a greater variety of tree species, making it suitable for a higher diversity (Nilsson et al. 2001; Gustafsson et al. 2015). However, intensive forest management practices have reduced environmental diversity in Swedish forests, threatening biodiversity and ecosystem resilience (Felton et al., 2020).

The capacity of forests to provide essential ecosystem services is increasingly threatened by the rapidly changing climate and the pressures of a globalized world (Ghafoor et al. 2023; Pardi et al. 2023). To ensure continuity of these services, forests must remain functional, which means staying vital and healthy. However, both endemic and alien pests and pathogens continuously threaten forest health. Several organisms, including fungi, bacteria, oomycetes, phytoplasmas, parasitic plants, nematodes and

viruses, can trigger forest diseases (Tainter and Baker, 1996). Among these, fungi are predominantly the largest group responsible for diseases affecting forest trees (Sinclair and Lyon, 2005). Moreover, filamentous pathogens of the genus *Phytophthora*, are important pathogens causing several devastating tree diseases (Erwin and Ribeiro, 1996). The introduction, establishment, and spread of invasive alien species may pose a risk to trees and their associated biodiversity, potentially triggering cascading effects on ecosystems (Pautasso et al. 2015). Among the most economically and environmentally destructive diseases worldwide are those caused by *Phytophthora* species (Erwin and Ribeiro 1996; Hansen et al. 2012; Burgess et al. 2021). For example, in Australia, significant infestation of natural ecosystems by *Phytophthora cinnamomi* has led to irreversible biodiversity loss (Burgess et al. 2017, 2021). Climate change is an external factor that impacts trees and forest health, thereby disrupting ecosystem services (Pardi et al. 2023; Hof et al. 2023). Variations in temperature and humidity can also significantly influence microbial population dynamics (Lindner et al., 2010). Hence, the diverse and dynamic microbial communities associated with trees play a crucial role in helping trees respond to environmental changes and cope with abiotic and biotic stressors (Terhonen et al. 2019; Asiegbu 2021; Allsup et al. 2023).

Sweden aims to transition to a bio–based economy by the mid–21st century, shifting from fossil fuels to a resource–efficient economy based on sustainably produced renewable materials. The Swedish forest, as a key renewable natural resource, will play a vital role in this future economy. However, climate change and the introduction, establishment, and spread of invasive pathogens and pests threaten this goal. According to the latest forest damage report for 2023, significant damage was attributed to ungulate browsing pressure, bark beetle attacks, and the storm Hans (SFA, 2024). Spruce bark beetles attacked and killed *Pinus contorta* trees for the first time, while a *P. contorta* stand experienced a *Diplodia sapinea* attack, representing the northernmost and first confirmed occurrence in Sweden (SFA, 2024, 2022). In southern Sweden, *Heterobasidion annosum* remains the most serious pathogenic fungus, along with other threats such as *Hymenoscyphus fraxineus*, *Phytophthora* species and *Armillaria mellea* (SFA, 2024). Therefore, it would be wise to adapt forest management practices, regulate game populations, and optimize site conditions to effectively address invasions and mitigate damage in Swedish forests.

2. Importance of trees in Forest Ecosystems

Trees are crucial for forest ecosystems, maintaining biodiversity, providing food and habitat for several organisms, and supporting essential functions like carbon cycling and water regulation (Kozlowski and Song, 2022). Their relevance extends beyond food provision to environmental sustainability, biodiversity conservation, and ecosystem resilience. Trees interact with soil microbial communities, promoting soil organic matter decomposition and nutrient cycling, which are vital for ecosystem functioning (Gardner et al., 2023). Moreover, trees and forests provide essential ecosystem services that support human well–being and environmental sustainability, including oxygen production, clean air and water, carbon sequestration, climate regulation, and soil stabilization (Simpson 2022; Davis et al. 2022; Adelisardou et al. 2023). However, threats such as diseases, pests, and climate change impact forest health, making it essential to assess and implement effective disease management strategies to maintain a sustainable supply of ecosystem services.

2.1 The role of microbiome communities in plant health

Plants, including forest trees, are complex systems known as holobionts, comprising the plant cells, tissues, and the diverse community of microorganisms it hosts (Vandenkoornhuyse et al. 2015; Sánchez–Cañizares et al. 2017; Berg et al. 2020). These microorganisms, collectively referred to as the microbiota, engage in varied relationships with the plant, including pathogenic, mutualistic, endophytic, and commensal interactions (Terhonen et al., 2019). They play a crucial role in promoting plant growth and health, and enhance the ability of a plant to adapt to different environmental

conditions and forest biome variations (Bulgarelli et al., 2013; Gehring et al., 2017; Vandenkoornhuyse et al., 2015). Consequently, the plant–associated microbiome, referred as the second genome of the plant (Berendsen et al. 2012), is crucial for plant survival and resilience. However, further understanding of the diverse composition of the microbiome and its interactions within the host plant and surrounding environment is crucial to enable forest trees to cope with future environmental stressors arising from climate change and the increasing threat of both invasive and non-invasive pathogens (Trumbore et al. 2015; Lehmann et al. 2020).

2.2 Abiotic and biotic interactions in the rhizosphere

The plant microbiome, also known as the phytobiome, comprises all microbial genomes associated with the host plant phyllosphere, rhizosphere, and endosphere (Guttman et al. 2014). The rhizosphere, the root–soil interface, encompasses both endophytic (host plant internal) and epiphytic (external) microbial communities, predominantly bacteria and fungi associated with the root surface and surrounding soil layer (Mardanova et al., 2019; Terhonen et al., 2019). This zone, highly active due to root exudation and nutrient uptake, plays a pivotal role in ecosystem functioning including, regulation and mediation of litter decomposition (Wardle et al. 2004; Kuzyakov et al. 2007; Ribbons et al. 2022).

The diversity of the rhizosphere–associated microbiome is influenced by different abiotic factors, such as soil physicochemical properties, nutrient levels, management history, climate, and specific characteristics of the host plant like age, genetics, and physiological status (Berg et al. 2016; Dastogeer et al. 2020). However, the structure of surrounding soil microbial communities and environmental parameters, including soil type, climate, and management practices, have a more pronounced impact on shaping the rhizosphere–associated microbiome community compared to plant genotype or species (Schlaeppi et al., 2014; Vandenkoornhuyse et al., 2015). Therefore, studying the interaction between the microbiota and diverse plant backgrounds in both stressed and non–stressed environments could help bridge knowledge gaps in research on plant–microbiome interactions. This research may also support the potential development of new biocontrol strategies to combat diseases.

The balanced interaction between microbe communities and their plant hosts is crucial for maintaining host wellness (Guttman et al. 2014; Vandenkoornhuyse et al. 2015; Thompson et al. 2017; Asiegbu 2021). Imbalances due to abiotic and biotic interactions may lead to significant changes in microbial community structure, affecting both healthy and declining host tree species (Guttman et al. 2014; Vandenkoornhuyse et al. 2015; Kovalchuk et al. 2018; Asiegbu 2021). Soil microbial communities can adapt their activity and functional responses to enhance host health and defend against pathogen invasion (Desprez–Loustau et al. 2016; Raaijmakers and Mazzola 2016; Byers et al. 2020a, 2020b). Hence, the plant microbiome plays a significant role in disease resistance, with studies suggesting a correlation between host plant resistance to pathogens and the composition of their microbial communities (Ardanov et al., 2012; Martín et al., 2013; Terhonen et al., 2019). However, more research is required to comprehensively understand the molecular mechanisms underlying immune signalling pathways between plant genes and rhizosphere microbial communities.

2.3 Interaction of pests and pathogens with trees

Trees, as long–lived organisms, continuously face threats from pests and pathogens, enduring simultaneous infections and environmental changes throughout their lifespan. As a result, trees have developed a complex defence system that can be activated at different time scales, depending on the pathogen or pest, to overcome or defend against these attacks. The constitutive defences of trees comprise physical and chemical barriers in their tissues and cells to ward off attacks (Gilbert and Parker 2023; Wang et al. 2023). Physical barriers such as the plant cuticle and cell walls on the surface play a vital role in preventing pathogen entry (Warghat et al., 2023). Activation in response to specific signals, like pathogen attack, is a feature of inducible defence mechanisms (Wang et al., 2023; Warghat et al., 2023). The induced defence system may combat current infections through mechanisms such as the hypersensitive response and local resistance, and may also prepare the organism to resist future biotic stress (Bonello et al., 2006; Eyles et al., 2010). Plants can detect and quickly respond to the presence of pathogens or other harmful stimuli. These signals may involve specific molecules produced by the pathogen, surface patterns, or even

physical damage caused by the pathogen (Gilbert and Parker 2023; Wang et al. 2023; Warghat et al. 2023). Upon detection, plants trigger signalling pathways that initiate defence mechanisms, including producing antimicrobial compounds (terpenoids, phenolics, lignans, flavonoids, stilbenes), activating mechanisms that cause cell wall alterations (suberization, lignification), or other defensive actions (Wang et al., 2023; Warghat et al., 2023).

The discovery of microbiota–mediated plant defence has introduced new research avenues, enriching our understanding of plant–microbe interactions. Beneficial microbes associated with plants play a significant role in influencing plant immunity (Chakraborty, 2023). These microbes can protect plants from pathogens either by directly combating them or by stimulating the production of antifungal chemicals in plants, thereby providing microbiota–mediated plant protection (Chakraborty, 2023). Understanding how these mechanisms respond to specific pathogen attacks is essential for the development of new strategies to combat diseases and infections while also improving overall tree health.

3. The genus *Phytophthora*

3.1 Overview of the genus *Phytophthora*

The term "*Phytophthora*" originates from Greek, meaning "the plant–destroyer", (phytón = plant and phthorá = destruction), and was initially suggested by the mycologist Anton de Bary, who focused on the potato blight pathogen *Phytophthora infestans* (Mont.) de Bary, providing the first description of the genus *Phytophthora* (Ribeiro, 2013). The oomycete genus *Phytophthora* is the second-largest genus in the family Peronosporaceae, which belongs to the kingdom Stramenopila and is evolutionarily related to brown algae (Beakes et al. 2014; Thines and Choi 2016; Jung et al. 2018). The genus *Phytophthora* encompasses 192 formally described species and 33 informal taxa (Coomber et al. 2023; Abad et al. 2023), although authors have estimated that there may be as many as 500 species (Brasier 2008; O'Brien and Hardy 2014). *Phytophthora* species are classified into 12 phylogenetic clades comprising both saprophytic and plant pathogenic species, which are implicated in significant crop and tree diseases (Yang et al. 2017; Vannini and Morales–Rodriguez 2022). *Phytophthora* species can be soilborne and/or airborne. Under favourable conditions such as periods of rainfall and flooding, *Phytophthora* releases motile spores called "zoospores" that can be transported by water (e.g. runoff and rain splash). Zoospores swim in the water film of moist soils and are chemotactically attracted to plant roots. They then establish cysts on susceptible tree roots and bark near the root collar (Abad et al., 2022; Erwin and Ribeiro, 1996). In adverse conditions such as drought or when there is a lack of water, *Phytophthora* species produce resilient spores such as chlamydospores and their sexual spores, oospores, in infected roots, organic matter, and soil. These dormant spores can survive for many years, waiting for favourable conditions to return (Erwin and Ribeiro 1996; Crone et al. 2013; Jung et al.

2013; Vannini and Morales–Rodriguez 2022). Air–borne *Phytophthora* species release zoospores in high humidity, which disperse by water splash or wind (Erwin and Ribeiro 1996; Vannini et al. 2010). Some *Phytophthora* species have a natural life cycle in flowing water, which is their main dispersal pathway (Jung et al. 2011). Occasionally, natural hybridization may occur in water courses (Nagel et al. 2013; Burgess 2015). *Phytophthora* species may also be spread over long distances by animals or humans moving infested soil, which are common pathways of dispersal (Cushman and Meentemeyer, 2008). *Phytophthora* species can be introduced into nursery facilities through the use of water contaminated with *Phytophthora* in irrigation systems (Ghimire et al. 2011; Loyd et al. 2014; Marčiulynas et al. 2020). Further, numerous studies have recognized the international plant trade as a major pathway for the introduction of alien *Phytophthora* species (Brasier, 2008; Chapman et al., 2017; Pérez-Sierra et al., 2013; Puertolas et al., 2021; Santini et al., 2013).

Among the most damaging plant–pathogenic *Phytophthora* species, which are responsible for significant global losses in agriculture and forestry, are *P. cinnamomi*, *P. ramorum*, and *P. infestans. Phytophthora cinnamomi* is one of the most destructive plant pathogens globally, infecting over 5,000 plant species. It has caused extensive mortality on several *Eucalyptus* spp. and many other plant species in Western Australia (Burgess et al. 2017; Hardham and Blackman 2018). *Phytophthora ramorum*, the causal agent of "sudden oak death" and "ramorum blight," affects a wide range of hosts. It has caused extensive mortality of *Larix* species in Ireland (McCracken, 2013), the UK (Webber et al. 2010; Brasier and Webber 2010) and France (Beltran et al., 2024), as well as tanoak trees in California and Oregon (Garbelotto et al. 2001; Goheen et al. 2002; Rizzo and Garbelotto 2003). Since the mid–1800s, *P. infestans* has caused significant damage to potato and other solanaceous crops globally (Erwin and Ribeiro, 1996). In Europe, the *P.* × *alni* complex has significantly decreased the population of alder trees (*Alnus* spp.) in riverbank habitats (Brasier et al. 1995; Jung and Blaschke 2004; Aguayo et al. 2014; Marçais 2018).

3.2 Current approaches to analyse *Phytophthora* communities

Given the significant impacts on agriculture and forestry attributed to several *Phytophthora* species, coupled with advancements in detection and diagnosis methods, recent years have seen a surge in research focusing on community species (Sims et al. 2015; Dunstan et al. 2016; Burgess et al. 2017; Jung et al. 2019). This emphasis arises from the recognition that *Phytophthora*–induced tree diseases commonly encompass the involvement of multiple species, as demonstrated by different community–based studies (Bose et al., 2018; Corcobado et al., 2020; Pérez-Sierra et al., 2013; Scanu et al., 2015). Traditionally, researchers have investigated *Phytophthora* communities by isolating them from specific substrates like plants, soil, or river water (Jung and Blaschke 2004; Jung et al. 2019). However, these isolation methods are often labour–intensive and may introduce biases. For example, *P. cinnamomi* is rarely isolated from streams (O'Brien and Hardy 2014; Dunstan et al. 2016; Burgess et al. 2017), increasing the likelihood of false negative results. Recent advances in high–throughput sequencing (HTS) technologies, such as metagenomics and metatranscriptomics, along with bioinformatics tools, have greatly improved our ability to study *Phytophthora* communities (Sapkota and Nicolaisen 2015; Burgess 2015; Burgess et al. 2017). Nevertheless, HTS still faces limitations in taxonomic classification. According to Paloi et al. (2021), accurate species identification through HTS relies on the careful selection of consensus sequences to effectively manage high intragenomic variation. Early studies employing genetic Internal Transcribed Spacer (ITS) primers identified a limited number of oomycetes (Choi et al., 2015; Coince et al., 2013). In contrast, research utilizing *Phytophthora*–specific primers developed by Scibetta et al. (2012) has identified multiple species across different environments (Català et al., 2017; Riddell et al., 2019), thus advancing our understanding of oomycete biology and ecology. These studies offered foundational data (Burgess et al. 2017) and more detailed insights into environmental filtering processes (Redondo et al., 2018a). However, Burgess et al. (2022) recommended using technical replicates, internal controls, and a phylogenetic approach when using these primers, as oomycete–targeting primers underestimated *Phytophthora* compared to *Phytophthora*–specific primers. Research aimed at enhancing current HTS methods is necessary to achieve higher resolution in species identification.

4. Navigating the complexities in *Phytophthora* Management

The lifecycle and genetics of *Phytophthora* species presents significant challenges for their control and management. Their motile zoospores enable rapid infection of new host plants, while dormant structures such as chlamydospores, hyphal aggregations, and oospores allow them to survive unfavourable conditions for extended periods (Erwin and Ribeiro 1996; Judelson and Blanco 2005; McCarren et al. 2005; Jung et al. 2018). Therefore, completely eradicating the inoculum from forests is extremely difficult. Moreover, as oomycetes, *Phytophthora* species exhibit resistance to fungicides, particularly those that target fungal physiology and affect cell structures. This resistance arises from fundamental physiological and biochemical differences between oomycetes and fungi (Hu et al. 2008; Olson and Benson 2013; Adomako et al. 2017), complicating their management in plant production systems. Management options for *Phytophthora* species include silvicultural practices, biological or bio–based methods, chemical treatments, and the use of genetic resistance or resistance breeding.

Silvicultural practices include containment measures to limit forest access and establish quarantine areas (Valachovic et al. 2017; Goheen et al. 2017; Daniels et al. 2022). These strategies involve demarcating infested areas and implementing eradication treatments such as herbicide application, uprooting, clear–cutting, and burning (Goheen et al. 2017; Swiecki and Bernhardt 2017). Additionally, establishing buffer zones beyond the disease front and removing and burning host plants within 100 meters of known outbreaks are recommended (Valachovic et al., 2017; Goheen et al., 2017; O'Hanlon et al., 2018). Continuous monitoring using baiting techniques, high–resolution digital aerial imagery for early detection, and ongoing research are crucial components of these management strategies (Kanaskie et al., 2011; Goheen et al., 2017; Valachovic et al., 2017; O'Hanlon et al., 2018).

Integrated pest management (IPM) is an effective and environmentally sustainable strategy for controlling pests that combines practical methods to manage pest damage cost-effectively while minimizing risks to people and the environment (Scheff and Phillips, 2022). Recent research on biological and bio–based approaches aims to develop new treatments for IPM strategies. These studies explore using bacteria like *Bacillus* spp. and fungi like *Trichoderma* spp. as biocontrol agents against different *Phytophthora* species (Oszako et al. 2019; Ruiz–Gómez and Miguel–Rojas 2021), employing methods such as inducing plant defences, competition, and antibiosis. However, applying these biological control agents in forests is still limited, requiring additional studies to elucidate the mechanisms involved and to understand how microbial biocontrol agents interact with their hosts and other microbes at the cellular and molecular levels. This research will help in identifying effective and eco–friendly bioagents (Siah et al. 2018; Zehra et al. 2021; Giachero et al. 2022).

Chemical treatments with systemic fungicides like the old synthetic chemical metalaxyl and fosetyl–Al, or the low-risk plant protection products (PPPs) such as potassium phosphite are commonly used to treat *Phytophthora* diseases. They are applied either through aerial foliar sprays over large areas (Hardy et al. 2001; Dalio et al. 2014; Solla et al. 2021), or through trunk injections (Horner and Hough 2013; Horner et al. 2015; Solla et al. 2021; Brandano et al. 2023). While phosphite treatments have proven efficacy in mitigating *Phytophthora* infections in forestry, their use is often challenged by regulations (EU, 2023, 2019), prompting efforts to innovate and adapt the chemical treatments to the current legislation (Singh et al. 2010; Serrano et al. 2011; Agbeniyi et al. 2014). Consequently, the effectiveness of new low-risk PPPs fungicides like ethaboxam, fluopicolide, mandipropamid, and oxathiapiprolin in reducing root rot and crown/trunk cankers on tree crops represents a significant advancement towards more environmentally sustainable approaches (Belisle et al. 2019; Adaskaveg et al. 2024).

The introduction of more resistant tree genotypes is a promising approach to controlling *Phytophthora* diseases in planted forests. Therefore, recent research has focused on screening plants by inoculation to identify and select resistant individuals within susceptible taxa. For example, seedling progeny resistant to *P. lateralis* in the conifer species *Chamaecyparis lawsoniana* (Port–Orford–cedar) have been successfully used for restoration and reforestation in the Pacific Northwest of the USA (Sniezko et al., 2020;

Sniezko and Nelson, 2022). However, some technical limitations must be overcome, such as the long time required to select tolerant and resistant tree families. Additionally, the genetic variation and high adaptability in pathogen populations complicates the selection of resistant host families (Eikemo et al., 2004).

5. Objectives

This thesis aims to address the increasing threat posed by invasive *Phytophthora* species to the vitality and productivity of forest ecosystems, particularly focusing on their relation to microbial communities and anthropogenic activities in forest environments. The specific objectives of the work leading to this thesis were:

I. To assess the current state of knowledge on existing legislation and measures aimed at preventing and controlling the spread of oomycetes via trade and transport networks (Paper I);

II. To evaluate and suggest potential directions for future research, fostering a comprehensive understanding of *Phytophthora* diseases and the formulation of effective strategies for their control and management in forests (Paper II);

III. To investigate the role of the rhizosphere microbiome, including evaluation of its microbial diversity and taxonomic composition in trees exhibiting visible signs of dieback compared to those appearing healthy (Paper III);

IV. To investigate the diversity and distribution of pathogenic *Phytophthora* species in different forest settings in Svealand and Götaland (Papers III and IV);

By achieving these objectives, the thesis seeks to enhance our understanding of the complex interactions between plant–pathogenic *Phytophthora* species, forest ecosystems, and anthropogenic influences, ultimately contributing valuable information for both regional pest risk assessments and management control strategies.

6. Methods

This section provides an overview of the methodology used in each Paper within the thesis. More detailed information is available in the corresponding Papers (Papers I–IV).

6.1 Analysis of current management strategies and regulations for controlling *Phytophthora* species

Two studies were conducted using both quantitative and qualitative methods aimed at fulfilling objectives I and II of the thesis (Papers I and II).

6.1.1 Information sources, literature searches and analysis

In Paper I, aiming to summarize existing knowledge on established management strategies and legislation for controlling the spread of pathogenic oomycetes in both terrestrial and aquatic production systems, a qualitative study was conducted. Databases including Web of Science, Scopus and Google Scholar were utilized for reference searches. Furthermore, articles were identified through reference lists of published papers; the selection of references was subjective, based on their quality and relevance to the review. For further details, refer to the individual articles in the thesis (Paper I).

In Paper II, a systematic mapping approach was used to compile evidence on the management of forest *Phytophthora* across different production settings and ecosystems globally. The Collaboration for Environmental Evidence guidelines (Pullin and Gardner, 2013) and Standards for Evidence Synthesis in Environmental Management (Version 5.1) (Pullin et al. 2023) were followed in this study (Paper II). Employing the PICO framework, criteria

were established, focusing on key elements: Problem or Population, Intervention, Comparison, and Outcomes. General questions were formulated for the systematic map report. Nine different databases were utilised, with the search limited to studies between January 2010 and December 2022. This 12–year period included recent and relevant studies, prioritizing up–to–date studies. This strategic approach aimed for efficiency and accuracy, and was in line with guidance documents (Cooper et al., 2018; Helbach et al., 2022).

The search strategy was developed to ensure comprehensiveness by including terms related to environments (forest settings), pathogens (*Phytophthora*), measures (chemical, biological, breeding/genetics, silvicultural), and outcomes (symptoms, disease damage, susceptibility, resistance).

Descriptive analyses were conducted to summarize study characteristics, including geographic distribution, type of management or control measures, study settings, facilities and target *Phytophthora* species. These analyses, performed in R studio v. 4.3.1 (R Core Team, 2023), grouped studies by outcome categories and examined the key characteristics mentioned above. Data were visualised using the *ggplot2* package v. 3.4.1 (Wickham et al., 2023).

6.2 Sampling sites and sample collection

At all study locations, samples of rhizosphere and tissues were collected from healthy trees and trees exhibiting disease symptoms such as chlorosis, crown thinning, dieback, and/or bleeding stem cankers (Papers III and IV).

6.2.1 Field sites and soil sampling

A 70–years–old pedunculate oak (*Quercus robur*) production forest in Skåne, Southern Sweden (55°30’ 16.3” N and 13°25’ 26.9” E) of approximately 15 hectares, was selected for study based on previous reports of general tree decline (Paper III). The health status of the stand was evaluated using a vitality scale that assessed crown defoliation, branch damage, wilting leaves, and the presence of epicormic branches (Müller and Stierlin, 1990). Oak trees were categorized into four vitality classes: Vitality 1 (V1) for healthy trees, Vitality 2 (V2) for trees in intermediate condition,

Vitality 3 (V3) for declining trees, and Vitality 4 (V4) for dying trees (Paper III). Tree sampling locations were chosen using a selective random approach (Paper III).

Rhizosphere soil samples were collected in July 2020 from V1 and V3 trees, encompassing three directions around each tree (3 samples per tree). The samples were taken using a shovel from a distance between 50 to 150 cm from the base of the tree stem to a depth of 15 to 35 cm, and following established protocols (Paper III). The samples were processed within 24 h from collection (Paper III).

Between 2016 and 2018, symptomatic broadleaved trees displaying *Phytophthora*–related symptoms were sampled from 23 sites across Svealand and Götaland. The sites, detailed in Table 1 (Paper IV), included a diverse range of environments such as city parks, peri–urban recreation forests, national parks, nature reserves, botanical gardens, churchyards, community gardens, and other urban areas. These locations were identified through reports from practitioners, the public, and a citizen science platform.

When feasible, the "Pocket Diagnostic *Phytophthora* test kit" (Foresite Diagnostics Ltd in York, UK), was employed to verify the potential presence of *Phytophthora* species on symptomatic trees. However, additional measures such as collecting tissue and/or soil samples were taken to confirm the identity of *Phytophthora* species (Paper IV). Tissue samples were collected from bleeding lesions on symptomatic tree stems using a chisel sterilized with 70% ethanol. These samples, containing both healthy and necrotic tissue, were placed in labelled bottles filled with deionized water and transported to the laboratory. To counteract inhibitory effects of phenolic compounds, water in the bottles was replaced at least four times within 24 hours. Soil samples, collected using a 2–cm diameter soil core from up to four locations around symptomatic trees, were blended in a zip–lock plastic bag and transported to the laboratory, where samples were processed within 24 h from collection (Paper IV).

6.3 Detection and identification methods

Two detection methods were used to isolate *Phytophthora* species in the laboratory. The first method, baiting, involves submerging soil samples in distilled water and floating pieces of bait (fresh leaves) on the water surface (Paper III). The second method, culture–based, entails plating the collected tissues under sterile conditions onto specific media in 9 cm Petri dishes (Papers III and IV).

6.3.1 Baiting and isolation of *Phytophthora* spp.

In the laboratory, soil samples from the rhizosphere were put into plastic containers (30 × 30 × 20 cm) and flooded with 1.5 L of distilled water. The soil surface and the water line were kept at a distance of 3–4 cm. After removing any floating debris, young, sterilised leaves of *Rhododendron* species (Papers III and IV) and Japanese camellia (Paper IV) were floated on the water surface in the containers and incubated at room temperature (20–21°C). After 3–4 days, leaves with dark lesions were cut into pieces of 3 × 3 mm size, and plated on PARP(H)+B V8 agar. The cultures were then examined at 24–hour intervals for the emergence of hyphae. Growing mycelia were transferred to potato dextrose agar (PDA) to obtain pure cultures. Isolates were categorized based on morphological traits, and representative samples selected for subsequent molecular analyses (Papers III and IV).

6.3.2 Isolation of *Phytophthora* spp. from plant tissue

Tissue samples were placed in distilled water and refreshed 3–4 times daily for 1–3 days (Paper IV) to remove excess polyphenols that might hinder *Phytophthora* growth on artificial media (Drenth and Sendall, 2001). To minimize bacterial contamination, the bark tissue samples were briefly surface sterilized in 70% EtOH (Paper IV). Using a sterile scalpel, clean surfaces were created on the tissue samples at lesion margins, which were then cut into pieces of approximately 3 × 3 × 5 mm size (Paper IV). These pieces were plated under sterile conditions onto PARP(H)+B V8 agar in 9 cm Petri dishes. After monitoring for mycelial outgrowth at room temperature, colonies appearing within 3–7 days were transferred to PDA (Merck KGaA, Darmstadt, Germany) and further subcultured by transferring

hyphal tips, as needed. The process followed guidelines outlined by Drenth and Sendall (2001) (Paper IV).

6.3.3 DNA extractions and Sanger sequencing from baits

The preselected isolates, each with pure hyphal cultures, were grown in malt extract broth (MEB) (Oxoid, UK) for two weeks at room temperature in the dark. Mycelium was harvested and lyophilized for 2–3 days and homogenized into a fine powder using a Rescht MM400 ball mill. DNA extracts were processed using the E.Z.N.A. SP Plant DNA Kit (Omega Bio–Tek, Inc., Norcross, USA) according to the manufacturer's protocol. The fungal internal transcribed (ITS) region was amplified by PCR using the ITS4 (forward) and ITS6 (reverse) primers (White et al. 1990; Cooke et al. 2000). PCR products were purified and quantified before being sent for Sanger sequencing (Paper III and IV).

6.3.4 Rhizosphere DNA extractions and amplicon sequencing

A sub-sample of 25 g from each rhizosphere soil sample were transferred to 50 ml Falcon tubes and total DNA was extracted using the Qiagen DNeasy Powermax® Soil kit (Qiagen, Germany). DNA purification was performed with the Dneasy Powerlyzer Power Soil kit (Qiagen, Germany). Both purified and unpurified rhizosphere soil samples in 25 ml centrifuge tubes were sent for amplicon sequencing, using a metabarcoding approach (Paper III). PCR assays were prepared with sterilized materials, with negative controls of nuclease–free water. The entire fungal ITS1 and bacterial 16S rRNA gene V4 regions were amplified using WineSeq® primers (Patent No.: WO2017096385; Becares and Fernández 2017). After quality control via gel electrophoresis, the 16S rRNA and ITS libraries were pooled in equimolar concentration and sequenced using pairs of sequences of the 2 × 300bp (base pairs) MiSeq® Reagent Kit v3 kit (Illumina, San Diego, CA, USA) on the Illumina MiSeq® platform, following the Biome Makers proprietary protocol (Paper III).

6.4 Data analysis

6.4.1 Analysis of Sanger sequencing data

Sequences were checked manually, aligned, and edited using the Lasergene software package *SeqMan* (version 5.07, DNAStar, Madison, WI, USA) (Paper IV). Comparison with known reference sequences was performed using the Basic Local Alignment Search Tool (BLAST) in GenBank (National Center for Biotechnology Information, NCBI), *Phytophthora*–ID (Grünwald et al., 2011), (Paper III and IV) and UNITE (Abarenkov et al. 2010; Nilsson et al. 2019) (Paper IV). Isolates were categorized at the species level if they demonstrated over 98.5% sequence similarity and at the genus level if they exhibited over 96% sequence similarity (Paper III and IV).

In Paper III sequences were checked manually, aligned, and edited using Geneious Prime Software Version 2021.0.3. Known reference sequence comparisons were conducted using the databases mentioned above, and The Barcode of Life Data System (BOLD) (Ratnasingham and Hebert, 2007). Once a species was confirmed, the sequence was assigned an accession number and deposited in GenBank.

6.4.2 Metabarcoding, sequencing and bioinformatics

The bioinformatics analysis of both the bacterial and fungal raw reads from the sequencing facility were analysed using the DADA2 pipeline (Callahan et al., 2016) in R studio version 4.3.2 (R Core Team, 2023). Default settings were used for filtering and trimming of reads. Identical sequencing reads were combined using the dereplication function. Further steps included merging paired–end reads, removing chimeras, building a reference database of amplicon sequence variants (ASVs) table using manually curated taxonomies from SILVA 138.1 (Glöckner et al., 2017) for 16S sequences and the UNITE 8.3 database (Nilsson et al. 2019) for ITS sequences. DADA2 data outputs were combined into a phyloseq object using the *phyloseq*–package (McMurdie and Holmes, 2013), and the phyloseq object was converted into a MicroEco–object using the *microeco*–package (Liu et al. 2021) for post–processing data analysis (Paper III).

6.4.3 Microbiome data visualisation and statistical analysis

The comprehensive microbiome data analysis and visualization integrated the *phyloseq*–package (McMurdie and Holmes, 2013) and the *microeco*–package (Liu et al. 2021). In Paper III, the statistical analyses and data visualization were conducted using R studio version 4.3.2 (R Core Team, 2023). The *rstatix* package (Kassambara, 2023) was employed for statistical tests, including the Wilcoxon test, t–test, ANOVA, and correlation analyses, with a significance level set at $P<0.05$. Boxplots illustrating data distributions were generated using the *ggplot2* package (Wickham et al., 2023). Community composition differences between healthy (V1) and declining (V3) trees were assessed through PERMANOVA analysis with 999 permutations (Anderson, 2001), utilizing the adonis2 function from the *microeco* package (Liu et al. 2021). Multivariate analysis of variance (MANOVA) was applied to evaluate ASV diversity differences and relative abundance between tree vitalities (V1 and V3) for fungi and bacteria. Beta diversity was analysed using Non–metric Multidimensional Scaling (NMDS) on Bray–Curtis dissimilarity matrices. Rarefaction and extrapolation curves (Chao et al., 2014; Colwell et al., 2012) were generated based on species abundance values using the *iNEXT* package (Hsieh et al., 2023), (Paper III).

7. Results and discussion

7.1 Management approaches and current regulations for controlling the spread of *Phytophthora* species (Papers I and II)

In Paper I, the primary objective was to explore the existing strategies and regulations, with a focus on the European Union (EU), designed to prevent and control the spread of oomycetes, which pose a global threat to forestry, agriculture and aquaculture production systems.

Results from this study highlight the challenging task of reducing the spread of oomycetes due to their complex life cycles, which include dormant resting structures (oospores, chlamydospores, or hyphal aggregations) that allow them to survive for years under unfavourable environmental conditions (Erwin and Ribeiro 1996; Jung et al. 2018). Our findings emphasize the wide range of natural and human-assisted pathways that make controlling oomycete pathogens extremely challenging. Among the main natural dispersal pathways, *Phytophthora* species can spread over long distances through flowing water, moist soil, wind, and animals. In terms of anthropogenic pathways, numerous studies have identified global trade in live plants (horticulture, agriculture, forestry) and live fish (food, ornamental) as the most significant pathways for the introduction of invasive oomycetes (Brasier 2008; Pérez-Sierra et al. 2013; Santini et al. 2013; Jung et al. 2016; Chapman et al. 2017; Puertolas et al. 2021). Moreover, highly populated areas are particularly susceptible to pathogen introduction through commodities, soil transported by vehicles, and even footwear (Hayden et al. 2013). Likewise, the frequent planting of asymptomatic yet infected ornamental plants exacerbates this issue (Alonso chavez et al. 2016).

Despite substantial investments by the European Union in controlling these pathogens, current management strategies and legislation have not effectively limited the spread of oomycete pathogens in terrestrial and aquatic production systems. Strategies to prevent and control oomycete diseases follow the general principles of disease management defined by Whetzel (1929), which include avoidance, exclusion, eradication, protection, resistance, and therapy. These principles align with the phases of biological invasion management described by Catford et al. (2012): prevention (avoidance and exclusion), containment (eradication), and long-term management (protection, resistance, and therapy). Our results emphasised the importance of prevention as the most cost-efficient strategy to reduce the spread of oomycete pathogens, given the difficulty of eradicating or managing species in the oomycete genus *Phytophthora* once they become established in an area (Jung et al. 2018). In terms of legislation, our study underscores key challenges in phytosanitary regulations and protocols that need to be addressed, including the inefficiency and high cost of border inspections, which often cover only a small percentage of imported plant stock (Brasier 2008; Jung et al. 2018). In addition, existing protocols and regulations predominantly focus on known pests, leaving significant gaps for new, invasive species that can cause considerable damage before being identified (Brasier 2008; Jung et al. 2016; 2018). The EU recognizes invasive alien species (IAS) as a major threat to biodiversity, economy and health (Genovesi et al. 2004). Our results highlight that while the IAS regulation aims to prevent spread in general, a more targeted and coordinated approach is needed specifically for managing oomycete and other pathogen invasions across the EU. Further, the recent establishment of the European Network of Plant Health Information Systems (EUROPHYT), an online database that compiles outbreak data on harmful organisms, has proven helpful for global disease monitoring by enabling National Plant Protection Organisations (NPPOs) to input pest interception data, providing quick alerts and linking member state authorities with the European Food Safety Authority (EFSA). However, no such web-based reporting system exists for aquaculture pathogens. It may be wise to establish a similar database for aquaculture pathogens to enhance global disease monitoring.

Early detection methods are crucial for containing the spread of *Phytophthora* infections. Recent advancements have shown promise in rapid on-site detection and monitoring, supporting management efforts. These

include portable DNA/RNA sequencing devices for identifying pathogens in the lab and directly at sampling sites (Chalupowicz et al., 2019), and field-based isothermal amplification methods like loop-mediated isothermal amplification (LAMP) (Aglietti et al., 2019). Techniques such as gas chromatography-mass spectrometry (GC-MS) and electronic noses (eNoses) can profile volatile organic compounds (VOCs) to detect diseases (Karakaya et al., 2020). While less sensitive than molecular methods, eNoses can still assist in diagnostics (Cellini et al., 2017). Trained dogs have also successfully identified *Phytophthora* VOC signatures, distinguishing infected from healthy plants and soil (Swiecki et al. 2018). Nanotechnology could improve disease and pathogen identification (Worrall et al., 2018). Nanoparticles (NPs) like silver and zinc oxide have demonstrated inhibitory effects against oomycete pathogens such as *Aphanomyces invadans* in aquaculture. However, challenges such as nanoparticle toxicity and high costs currently limit their broader adoption. Similarly, while field-deployable diagnostics show promise for improving early warning systems and IPM strategies against oomycete diseases, they still face challenges such as high costs, sequencing errors, and the requirement for technical expertise. Further development is needed to overcome these obstacles.

Controlling the spread of oomycetes requires continuous monitoring along with an exhaustive understanding of pathogen characteristics and epidemiology (Kozanitas et al., 2022). Qualified professionals must use appropriate tools and technologies for detecting, diagnosing, and mapping new and re-emerging oomycete pathogens, using both existing databases and newly collected information (Bonants et al. 2013). Effective protocols should include open access to real-time, updated epidemiological databases integrated with Geographic Information Systems (GIS) software. These GIS databases, combined with vegetation and climatic data, allow for the rapid development of predictive models for the invasion pathways of alien pathogens (Cunniffe et al., 2016). In addition, websites, social media, and citizen science platforms are increasingly important for real-time reporting, raising awareness, and enabling collaborative, rapid responses to combat oomycete disease outbreaks (Hulbert et al., 2023). This study highlights the complexity and challenges of managing oomycete pathogens and underscores the need for improved regulatory frameworks and innovative strategies to mitigate their impact on both terrestrial and aquatic production systems.

In Paper II, the main objective was to gather evidence on the control and management of forest *Phytophthora* in different production settings and ecosystems globally, while identifying knowledge gaps and highlighting potential future research priorities. Results from the systematic review indicated that the most studied management measures between 2010 and 2022 were biological or bio-based methods (32.5%), genetics or breeding programmes (27.8%), chemical control (27%), and silvicultural approaches (5.5%). Only a few studies (7.2%) combined multiple approaches, such as biological or chemical methods with silviculture. Geographically, most studies were conducted in Europe (38.9%), followed by the Americas (26.19%), Australia and New Zealand (19.04%), Asia (12.7%), and Africa (3.17%) (Fig. 4). The selected studies were carried out in different environments such as laboratories (31 articles), greenhouses (14 articles), forest nurseries (9 articles), and the field (19 articles). Moreover, 53 experiments used a combination of these settings, such as laboratory and greenhouse, or laboratory, greenhouse, and field. The publications covered 32 *Phytophthora* species, where *P. cinnamomi* (44.4%) was the most studied, followed by *P. ramorum* (13.5%), *P. palmivora* (7.9%), and *P. cactorum* (7.9%). Fewer than 6% of studies included other species.

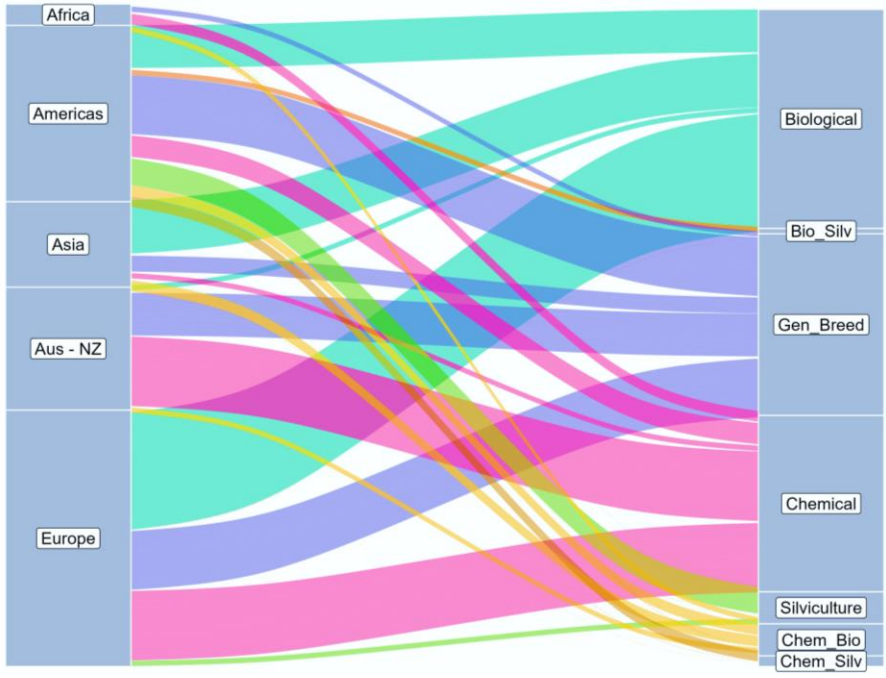

Figure 1. The most studied methods by geographic distribution. Aus – NZ = Australia & New Zealand; Bio_Silv = Biological and Silvicultural; Gen_Breed = Genetics & Breeding; Chem_Bio = Chemical and Biological; Chem_Silv = Chemical and Silvicultural.

Biological or bio-based measures included studies using bacteria and fungi as biocontrol agents, such as *Bacillus* spp. and *Trichoderma* spp., which show promise for future IPM strategies (Lefort et al., 2013; Oszako et al., 2019; Ruiz-Gómez and Miguel-Rojas, 2021). However, the research on beneficial microorganism interactions with host species is insufficient, particularly for evaluating the effectiveness of biological control in forest settings. Most studies were conducted in laboratories and greenhouses, with few in field conditions. Hence, more research is required to transfer these methods to the forest industry.

Genetic research has focused significantly on resistance breeding, with efforts to develop resistant tree genotypes for species (e.g., *Quercus* spp., *Castanea* spp., *Eucalyptus* spp., *Banksia* spp., *Fagus* spp., *Notholithocarpus* spp., *Agathis australis*, *Pinus* spp., *Picea abies*, *Abies fraseri*). For example,

Chamaecyparis lawsoniana (Port-Orford-cedar) seedlings resistant to *P. lateralis* have been successfully introduced for restoration and reforestation in the Pacific Northwest of the United States (Sniezko et al., 2020; Sniezko and Nelson, 2022). Yet, there are technical challenges that need to be addressed, such as the extended duration required for selecting tolerant and resistant tree families. Moreover, the genetic diversity within pathogen populations can complicate the process of identifying resistant host families (Eikemo et al., 2004).

Chemical treatments, particularly the use of synthetic pesticides and potassium phosphite, have been extensively studied for controlling *Phytophthora* infections. However, regulations complicate the use of synthetic fungicides (EU, 2023, 2019), and there are concerns about phytotoxicity and ecological impact, since most fungicides can have persistent environmental effects (Horner et al. 2015; Manghi et al. 2021). New fungicides and green pesticides are being explored for their effectiveness and sustainability (Belisle et al., 2019; Khdiar et al., 2023; Lacey et al., 2021). Therefore, future research strategies must prioritize the development of effective, sustainable organic products that combat *Phytophthora* diseases while preserving biodiversity and safeguarding public health.

Silvicultural management approaches represented the lower percentage in the systematic review, possibly due to their long-term nature and high costs. (Goheen et al., 2017; Hoover and Bates, 2012). It is also feasible that the limited representation of silvicultural approaches in our analysis might be due to the exclusion of grey literature sources such as Best Management Practices Handbooks. Studies have shown that these methods can be effective at reducing the inoculum (O'Hanlon et al. 2018; Hansen et al. 2019; Daniels et al. 2022). However, more research is required to understand their long-term effects (Roberts et al. 2020; Daniels et al. 2022) and to develop feasible, scalable approaches that integrate silvicultural practices with other management strategies, such as biological controls, genetic resistance, and chemical treatments. Exploring the synergies between these approaches could contribute to the development of more holistic and effective control measures.

The majority of the research reviewed was concentrated to Europe, North America, Australia and New Zealand, reflecting substantial investments in addressing challenging issues posed by specific *Phytophthora* species. These include sudden oak death caused by *P. ramorum* (Rizzo and Garbelotto, 2003), holm oak decline attributed to *P. cinnamomi* (Brasier et al. 1993; Camilo-Alves et al. 2013; Frisullo et al. 2018), red needle cast caused by *P. pluvialis* (Dick et al., 2014) and kauri dieback driven by *P. agathidicida* (Bradshaw et al., 2020). Our research also underscores the lack of investigation into the effectiveness of control methods for *Phytophthora* species in Africa and, to a lesser extent, in Asia.

The fact that most studies have focused on *P. cinnamomi* and *P. ramorum*, is understandable given their significant impact on forest health (Kamoun et al., 2015), and in several countries their control is required by phytosanitary regulations (EU, 2016; DCCEEW, 2023). While research on these species should continue, it is crucial to investigate other forest *Phytophthora* species that could also pose global threats, such as *P. pluvialis*, recently detected in Europe (Pérez-Sierra et al., 2022; Pirronitto et al., 2024). At the same time, it is important to characterize the potential risks to forests associated with newly recognised *Phytophthora* species and continue to study the taxonomic variation and population genetics of *Phytophthora* species (Christova et al., 2021; Scanu et al., 2021).

Our results highlight a gap in the practical application of existing research, likely arising from an incomplete understanding of the processes over time and space. This issue has also been noted in studies on biological control agents against *Phytophthora* species in agriculture (de Andrade Lourenço et al. 2022; Giachero et al. 2022). The challenge lies in developing research strategies that integrate different methods to evaluate the combined effects of microbial biocontrol agents on pathogen growth, disease progression, host vigour, and environmental dynamics. More research and development efforts are essential to validate laboratory and greenhouse findings under field conditions.

7.2 Ecology and diversity of forest *Phytophthora* species (Papers III and IV)

In the study presented in Paper III, our primary objective was to assess the microbial community dynamics and taxonomic composition differences between healthy (V1) and declining (V3) *Quercus robur* trees experiencing dieback. We hypothesized that the composition of microbial (bacteria and fungi) communities in the rhizosphere of oak trees varies depending on the health status of the plant. In addition, we utilized baiting methods, to isolate species from the oomycetes genus *Phytophthora*, which are known for their contributions to the global decline of oak trees. Using metabarcoding, a total of 2563 fungal ASVs and 6647 bacterial ASVs were recorded. The rarefaction curves from our samples showed that the sequencing depth was ample, covering the microbial community comprehensively and confirming the reliability of our results. The overall relative abundance of bacterial and fungal ASVs did not differ significantly between samples from V1 and V3 trees. The most abundant bacterial ASVs at the phylum level were Proteobacteria, Acidobacteriota, and Planctomycetota, together contributing over 65% of the relative abundance. The most dominant fungal ASVs were from the phylum Basidiomycota, followed by Ascomycota and Mortierellomycota, together contributing over 90% of the relative abundance (Fig. 1).

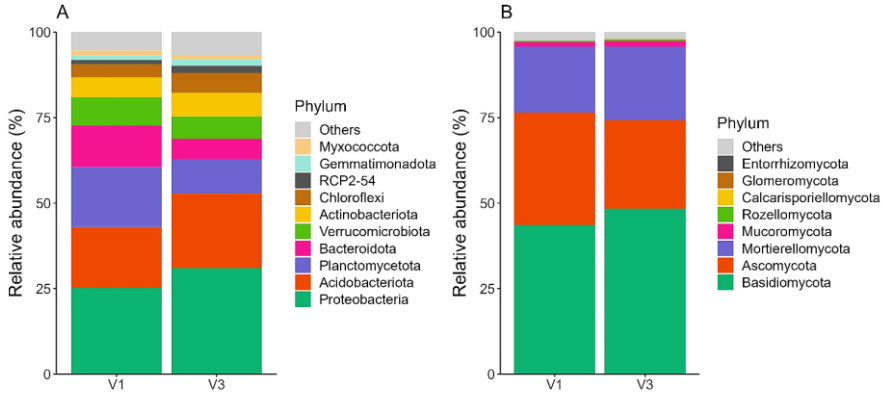

Figure 2. Group mean of the relative abundance of the top 10 phyla between healthy (V1) and declining (V3) *Quercus robur* rhizosphere-soil samples, where (**A**) represents the bacterial and (**B**) represents the fungal phyla.

There were also differences in the relative abundance of specific fungal taxa. Basidiomycota and Ascomycota were more prevalent in the rhizosphere of declining compared to healthy trees. The higher trend of prevalence of Basidiomycota in declining trees may be linked to symptoms such as necrotic areas and dead branches, aligning with previous research that identified Basidiomycota as dominant in declining trees, suggesting their role in tree health (Lawrey et al. 2008; Giordano 2009; Marçais et al. 2011; Sun et al. 2016). Likewise, the increased relative abundance of bacterial phyla like Proteobacteria and Acidobacteriota in declining trees suggests their potential involvement in tree health and disease progression, supported by studies that found these groups dominant in declining trees (Denman et al., 2016; Terhonen et al., 2019; Ding et al., 2021). However, further research is required to test this hypothesis. Our findings show that fungal community composition appears to both influence and be influenced by tree health, with clear differences observed among trees of different health statuses. Nevertheless, abiotic factors like soil pH, salinity, organic matter, and nutrient levels may have a stronger influence on community dynamics (Rath et al., 2019; Wan et al., 2020), though this is unlikely in our study since all samples were collected from the same site. Further research is necessary to pinpoint specific species and clarify their roles in maintaining tree health within this oak stand.

The analysis of alpha diversity using Simpson (D) and Inverse Simpson measures showed significant differences in the bacterial community (species richness and evenness) between healthy (V1) and declining (V3) trees, indicating variations in the dominance of certain bacterial species (Fig. 2). However, no differences were found with the Chao 1 and Shannon indices, suggesting these differences may be slight. For the rhizosphere fungal communities, Chao1, Shannon, Simpson, and Inverse Simpson diversity measures showed no significant differences between V1 and V3 vitality classes ($p > 0.05$).

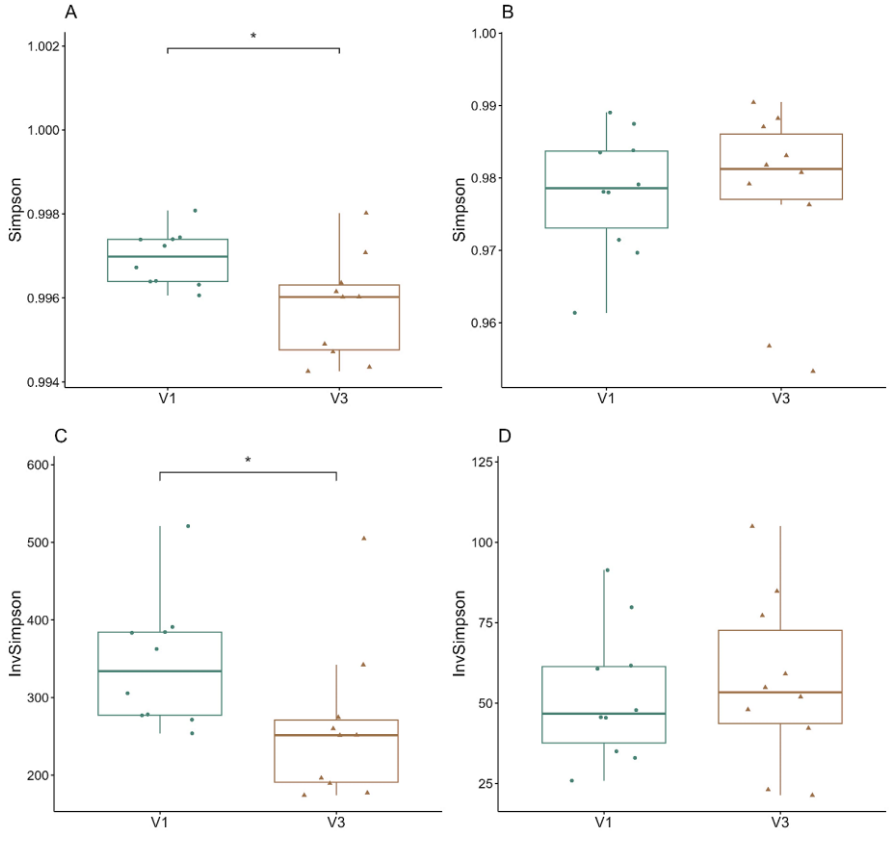

Figure 3. Alpha diversity shown as Simpson (D) and InvSimpson indices between healthy (V1) and declining (V3) *Quercus robur* rhizosphere-soils samples, where results of pairwise comparisons using the Wilcoxon rank sum test were (**A**; **C**) bacterial (p = 0.011) and (**B**; **D**) fungal (p = 0.795) species diversity composition (n = 10).

As the Simpson index prioritizes common or dominant species (species richness) and their relative abundance (evenness), it implies that a few rare species with minimal representation do not significantly impact diversity (Simpson 1949). The variation in results across different indices highlights the complexity of interpreting ecological data. These indices, such as the Shannon and Simpson indices, measure fundamentally different aspects of biodiversity (Tuomisto, 2010). The Shannon index calculates the uncertainty regarding the species identity in a sample, expressed in information units (bits), according to Hurlbert (1971). In contrast, the Simpson index assesses the probability that two individuals randomly selected from a sample will

belong to the same species (Simpson 1949; Hurlbert 1971). Therefore, the selection and comparison of these indices can be challenging because they evaluate distinct characteristics of diversity. Interestingly, while bacterial diversity differed between V1 and V3 trees, the alpha diversity of the fungal community remained consistent across the studied vitality classes. This finding indicates that factors affecting bacterial community composition may not similarly impact fungal communities within the rhizosphere of *Q. robur* trees, as previously revealed (Habiyaremye et al., 2021).

The beta-diversity analysis showed significant differences in the composition of fungal rhizosphere communities between V1 and V3 *Q. robur* trees, indicating distinct community composition associated with different tree vitalities (PERMANOVA R = 0.067, $p = 0.001$). However, this variation was observed only in the fungal, not in the bacterial communities (PERMANOVA R = 0.072, $p = 0.109$) (Fig. 3). This finding underscores the significant role that soil fungal communities may play in enhancing plant resistance or resilience to different stressors (Garrastatxu et al., 2024)

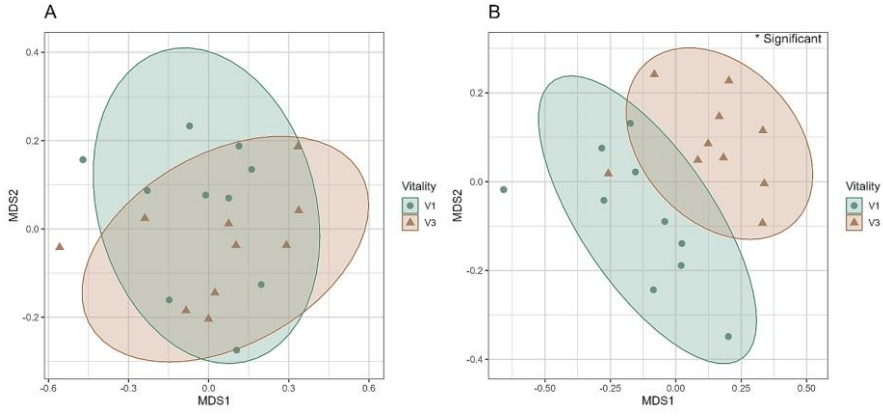

Figure 4. Beta diversity shown as non-metric Multidimensional Scaling (NMDS) of Bray–Curtis dissimilarity matrices which display the differences in (**A**) bacterial ($p = 0.088$) and (**B**) fungal ($p = 0.001$) community composition in rhizosphere-soil samples of healthy (V1) and declining (V3) *Quercus robur*.

The differential abundance analysis further revealed significant differences in certain bacterial genera between the two vitality classes at the order level.

However, no significant differences were observed in the differential abundance of fungal taxa between these vitality classes. This analysis assigns a significance value to each comparison, pinpointing the taxa that exhibit significant variations. Bacteria in the orders Rhizobiales, Subgroup 2, Acidobacteriales, Elsterales, and Gemmatimonadales were more differentially abundant in V3 trees, while Chitinophagales, Gemmatales, Sphingobacteriales, and Planctomycetales were more differentially prevalent in V1 trees. Rhizobiales are known for their roles in nitrogen fixation and potential pathogenicity (Carvalho et al., 2010), while Acidobacteriales, Subgroup 2, Elsterales, and Gemmatimonadales are important for microbial community structure and nutrient cycling (Conradie and Jacobs 2020; Kalam et al. 2020; Liu et al. 2022; Mujakić et al. 2022; Huang et al. 2023), potentially influencing nutrient dynamics in V3 trees. In contrast, the taxa dominant in V1 trees—Chitinophagales, Gemmatales, Sphingobacteriales, and Planctomycetales—are key indicators in specific plant rhizospheres and play crucial roles in organic carbon cycling (Nunes da Rocha et al. 2009; Dedysh 2020; Zhang et al. 2021; Kuang et al. 2023).

Application of the baiting methods demonstrated the presence of *P. gonapodyides, P. plurivora,* and *P. cactorum*. These species have also been previously identified in broadleaved forests of southern Sweden (Cleary et al., 2017; Redondo et al., 2018b). In addition, the discovery of other potentially pathogenic oomycetes, such as *Pythium* and *Phytopythium* species, highlights the complexity of the microbial community and the potential impact of multiple pathogens on tree health. Similar observations were reported by Augspurger and Wilkinson (2007) and Jankowiak et al. (2015). Our study found that isolating *Phytophthora* species from the rhizosphere samples of healthy trees was more successful than from declining trees. This may be because, although the trees are asymptomatic, there is an ongoing infection, indicating active pathogen colonization and potential future issues. This observation aligns with findings from Jankowiak et al. (2014) and Tkaczyk et al. (2014), who established a significant correlation between changes in the crowns of oak stands and the presence of *Phytophthora* pathogens, which may have a detrimental impact on the host plants. In any case, further research is required to confirm this hypothesis and understand its contribution to the decline.

Overall, this study confirmed our initial hypothesis that microbial communities differ based on the health status of the trees. These findings

align with previous research that has observed changes in the soil microbiome due to biotic disturbances in forests, with microbial communities in the soil of declining trees showing significant differences compared to those associated with healthy trees (Pinho et al., 2020; Gómez-Aparicio et al., 2022). Future research should aim to clarify the functional roles of these microbial communities and their implications for managing dieback disease in *Q. robur* forests.

In Paper IV, the study aimed to identify *Phytophthora* species associated with symptomatic trees across 23 sites between Svealand and Götaland. Among the 186 trees sampled, 78 tested positive for *Phytophthora* species. This finding suggests that our isolation efforts might not have been fully successful or other factors like drought or other diseases could have caused the observed symptoms. It also implies that *Phytophthora* might have affected several asymptomatic trees. However, further research is needed to confirm this hypothesis.

Ninety–one isolates were identified as *Phytophthora* species, while others included pathogenic oomycetes such as *Phytopythium* and *Pythium* species, as well as fungi like *Mortiella* spp., *Neonectria coccinea,* and the mycoparasite *Clonostachys rosea*. The detection of eight *Phytophthora* species (*P. syringae, P. lacustris, P. plurivora, P. gonapodyides, P. cactorum, P. inundata,* and the hybrid species *P.* × *cambivora,* and *P.* × *alni*) from bark cankers and rhizosphere soils using traditional culturing-based methods suggests their potential role in the decline of broadleaf forests in urban and peri–urban areas in Sweden. Soil baiting proved more effective than tissue plating, yielding a higher number of *Phytophthora* isolates. *Phytophthora* × *cambivora* (35.9%) and *P. plurivora* (24.3%) were the most abundant species in tissues and rhizosphere soil samples, respectively. We found some differences in the efficacy of isolating *Phytophthora* species using mixed host baits, suggesting a potential effect on detection efficiency. Comparable variability in isolation success has been documented in previous research (Jung et al. 2002; Vettraino et al. 2005; Matsiakh et al. 2021). The difficulty in isolating *Phytophthora* may arise from the sampling approach, as many trees examined already exhibited advanced symptoms, increasing susceptibility to infection by other pathogens and reducing the probability of isolating only *Phytophthora* (Drenth and Sendall 2001; Jung et al. 2009). Moreover, the age range among the sampled trees, where lesions varied in freshness, could potentially explain why *Phytophthora* detection rates were

lower in symptomatic trees. Despite clear evidence of tree decline at some sites, soil baiting sometimes failed to detect *Phytophthora*. Though, a negative result does not necessarily indicate the absence of *Phytophthora*, as detection efficiency can be influenced by many factors using traditional techniques (Cooke et al. 2007), such as seasonal changes as reported by Jung et al. (2002) and O'Brien et al. (2009). Conventional PCR assays have shown that traditional methods can yield false negatives. For example, Williams et al. (2009) found that nested PCR detected *P. cinnamomi* in all 336 soil samples, while baiting identified it in only seven soil samples. However, nested PCR has the potential to produce more false positives due to human error (Hayden et al. 2004). Hence, it is important to consider the limitations associated with isolation techniques.

Seven of the eight *Phytophthora* species reported here were previously isolated in Sweden within forest streams, stem lesions, and rhizosphere soils of broadleaved trees (Jönsson et al. 2003; Jönsson et al. 2003; Jönsson 2006; Cleary et al. 2016, 2017; Redondo et al. 2018b; 2018a). Our study expands on this knowledge by identifying these species in bark cankers and rhizosphere soils across different urban and peri–urban forest environments between Svealand and Götaland, with additional data from citizen scientist volunteers. Interestingly, *P. gonapodyides* was recorded for the first time on *Fagus sylvatica* trees in Sweden (Cleary et al. 2016). The study also documented the first report of *P. inundata* in alder trees and the first case of *P.* × *cambivora* on elm trees in the country, broadening our understanding of their potential host range.

The primary aim of this study was to identify the diversity and distribution of *Phytophthora* species across 23 sites between Svealand and Götaland, as understanding these aspects is crucial for effective management of these pathogens. Further mapping of identified trees and conducting inventories would provide valuable insights into the spatial dynamics of the disease. Consequently, continuous annual surveys—including aerial, soil, and stream assessments—are essential for effective disease management in areas such as Söderåsen national park, as well as in the urban and peri-urban areas evaluated. Furthermore, the citizen science platform has proven valuable in assessing invasive alien species by facilitating early detection, identification, and monitoring of outbreaks. These results underscore the need to develop and implement effective measures to control the spread of these diseases and prevent additional environmental damage.

8. Conclusions and future perspectives

This thesis investigated the increasing threat posed by pathogenic *Phytophthora* species to forest health and productivity in southern-mid Sweden, with a focus on the influence of their interactions with microbial communities and human activities on their impact in forest settings. Understanding these dynamics is crucial for regional pest risk assessments and the development and implementation of effective control measures.

We found that current protocols and legislation have mainly failed to effectively address the problems caused by oomycete pathogens (Paper I). While EU plant trade legislation has recently been tightened, a similarly robust approach to aquaculture regulation is necessary. These pathogens are highly adaptable, and their spread is closely linked to human activities and international trade and transport, making control extremely difficult. Immediate action is required to prevent further global spread. Raising awareness among stakeholders and consumers is essential for progress, with the research community playing a crucial role in disseminating knowledge to society. Future research should prioritize enhancing the accuracy and sophistication of testing and detection methods for oomycete pathogens. In addition, increased governmental and private funding is necessary for research, development, and improvement of phytosanitary infrastructures, supporting IPM strategies with more sustainable tools and measures, ultimately leading to better control and management of these pathogens.

As highlighted in Papers I and IV, immediate action is essential to develop effective strategies for managing and preventing the spread of *Phytophthora* diseases. To address this, we gathered data on the control and management of forest *Phytophthora* in different forest production settings and ecosystems globally, aiming to uncover knowledge gaps and provide insights into potential future research priorities. Our results highlight significant global

research efforts focused on managing and controlling *Phytophthora* pathogens in forest trees (Paper II). However, we observed a gap between research and practical implementation, likely due to a lack of holistic understanding of the processes over time and space. Moreover, our findings emphasised a need for more field experimental data on control strategies, underlining the significant challenge in managing *Phytophthora* diseases in forest ecosystems. Field experiments, though resource-intensive, are essential for validating new treatments, optimizing application methods, and determining appropriate dosages. Future research employing advanced technologies is expected to enhance surveillance and management tools (Paper I and II), while progress in understanding of epidemiology and host resistance will support the design of better management strategies and facilitate breeding programmes.

In analysing the microbial community dynamics and taxonomic differences in the rhizosphere of *Quercus robur* trees (Paper III), we found significant differences in the alpha diversity of bacterial communities and the beta diversity of fungal communities between healthy and declining trees, highlighting the complex connections between these communities and tree vitality. Our results suggest that tree health significantly influences and is influenced by the composition of bacterial and fungal communities, with clear distinctions between trees of different health statuses. Furthermore, we identified differentially abundant bacterial genera between the vitality classes, suggesting their involvement in nutrient cycling and other environmental processes. Our study also confirmed the presence of three *Phytophthora* species in the rhizosphere of *Q. robur* trees, expanding our understanding of their diversity and distribution (Paper III and IV). Interestingly, we were more successful at isolating these species from the rhizosphere samples of healthy trees compared to declining ones, suggesting that the healthy trees may have been affected by Phytophthora root rot, posing a threat. Further research is needed to confirm this hypothesis. Overall, this study underscores the importance of examining rhizosphere microbial communities concerning tree health and disease symptoms, with potential ecological consequences for soil health and ecosystem dynamics. Future investigations should aim to clarify the functional roles of rhizosphere microbial communities and their implications for managing dieback disease in *Q. robur* forests.

As highlighted in Paper I, the involvement of humans in pathways during invasions suggests that surveys conducted by both researchers and citizens should focus on populated areas. Therefore, sampling in these areas is key for detecting *Phytophthora* in the early stages of invasion. Our surveys identified certain *Phytophthora* species for the first time in Sweden, expanding our understanding of their geographical distribution and host range (Paper IV). Comprehensive surveys are crucial for timely development and implementation of effective measures to control and mitigate the spread of *Phytophthora* diseases. In addition, the citizen science platform has improved our ability to identify invasive species and assisted in monitoring efforts. However, we did not specifically evaluate its impact and contribution to the study. Thus, it may be wise to foster public collaboration to identify infected trees and raise awareness about the potential spread of pathogenic *Phytophthora* species across regions. Our results emphasise the urgent need for strategies to curb the spread of *Phytophthora* diseases and prevent further environmental damage.

To broaden our understanding of controlling *Phytophthora* diseases, we must move beyond focusing exclusively on interactions between hosts and pathogens. Instead, we should adopt a holistic perspective where plants are seen as holobionts interacting with a diverse array of macro— and microorganisms. This process requires studying the impacts on resident microorganisms and understanding variations, especially during episodes of dieback or when implementing biological or chemical fungicides. Therefore, future research should embrace multidisciplinary approaches integrating plant pathology, ecology, genetics, climate science, and forest management to comprehensively address *Phytophthora* diseases and develop effective control strategies.

Collectively, these studies underscore the multidimensional challenges posed by *Phytophthora* pathogens and recommend adopting integrated approaches combining legislative rigor, scientific research, public engagement, and practical management strategies. Future research should prioritize enhancing surveillance technologies, understanding microbial ecology, and linking gaps between research findings and practical applications in the field to effectively protect forest ecosystems from the increasing threat of *Phytophthora* diseases.

Looking forward, several key areas emerge as priorities for future research and management:

1. Enhancing detection and testing methods:

Future research should prioritize the development of more accurate and sophisticated testing methods for plant–pathogenic *Phytophthora* species, especially for field use. Advanced molecular techniques and diagnostic tools will improve early detection and enable timely interventions.

2. Integrated pest management strategies:

Implementing IPM strategies that integrate biological, chemical, and silvicultural control methods is essential. Research should prioritize sustainable and eco-friendly pest management options, including low-risk pesticides and biocontrol agents.

3. Public engagement and awareness:

Increasing public awareness and engagement through citizen science platforms and educational initiatives is crucial. By involving the public in monitoring efforts and disseminating knowledge about *Phytophthora* diseases, we can enhance community resilience and support broader management strategies.

4. Field experimental research:

Conducting field experiments is crucial for validating the efficacy of new treatments and optimizing their application. Collaborative research should focus on understanding the combined effects of microbial biocontrol agents and new green pesticides on pathogen growth, disease progression, host vigour, and environmental dynamics.

5. Policy and funding:

Strengthening policies and securing increased governmental and private funding for research, development, and the improvement of phytosanitary infrastructure are necessary to support IPM strategies, and to facilitate the development of more sustainable tools and control measures.

By addressing these future perspectives, we can leverage the findings of this thesis to develop effective strategies for managing *Phytophthora* diseases and protecting forest ecosystems from this escalating threat.

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Acknowledgements

My PhD project has been a mix of challenges and rewards—fascinating, fruitful, and occasionally demanding. Working with *Phytophthora*, both in the lab and out in the forest, presents its challenges, often requiring a re-evaluation of the initial hypotheses. However, I have not faced these challenges alone. Many individuals have offered their support when I needed it most. The unwavering support from my family has been exceptionally encouraging, keeping me focused and motivated even during the most challenging moments.

A mis queridos padres, Ángeles y José, y a mis hermanos, Ángeles, Claudio y Juanjo, así como a mis sobrinos Claudio y Natalia, no encuentro palabras suficientes para expresar mi amor y gratitud por teneros en mi vida. Vuestro amor incondicional, confianza, apoyo y comprensión han sido invaluables a lo largo de todos estos años. Vuestra fortaleza y aliento me han impulsado a ser una mejor persona día tras día. Por todo ello, os estaré eternamente agradecida. Buddy, peque, te estoy infinitamente agradecida por tu amor incondicional y compañía. Te prometo que nuestros paseos serán más largos y que pasaré más tiempo jugando contigo a partir de ahora.

I am deeply grateful to my supervisors, especially Jonas Rönnberg, for your unwavering support, for recognizing my challenges, and for always being there. Your patient guidance, understanding, and encouragement have been invaluable throughout these past years. I also wish to extend my sincere gratitude to my co-supervisors, Laura Grenville-Briggs and Stephen Woodward, for your invaluable contributions. I have learned so much from both of you. Your commitment, diligence, encouragement, kindness, and unwavering support have been deeply appreciated. I would also like to thank all my co-authors for their support and dedication over the years. I am especially grateful to Michelle Cleary and Carmen Romeralo for pushing me

out of my comfort zone and offering new perspectives. Thank you all for the time and effort you put into both the project and supporting me.

I wish to acknowledge my previous supervisor, Johanna Witzell. Thank you for providing me with this opportunity. Your patient guidance, along with your challenging questions and criticisms, has pushed me to explore deeper and broader perspectives. Throughout this journey, I have not only learned about research but also about myself. I am grateful for all the valuable lessons you have taught me.

I am immensely grateful to Annika Felton for her unwavering support, care, and understanding. Thank you for always being there, encouraging me to persevere, and helping me navigate through the challenges of this journey.

I wish to express my sincere gratitude to Violeta for her dedication in assisting with bureaucratic matters and addressing any other needs. Your kindness and support have been invaluable, and I am truly grateful. Additionally, I want to extend my thanks to all the current and former colleagues at the Southern Swedish Forest Research Centre in Alnarp, including Nihad, Klas, Torbjörn, Zhanna, and Tobias, for your ongoing assistance and support every day.

Thank you to the group of postdocs, especially Trini, Leonie, Donnie, Dusan, and Luís, and to all the current and former PhD students I have had the pleasure of working with at the department. Joan, Laura, Jaime, Amanda, Ola, Nora, Matej, Luca, Sara, Sezer, Beatrice, Anna K., Benjamin, Khaled, Ida, Axelina, Kinga, Keeli, Lukas, Derek, Andis, and many others – your contributions have helped create a positive and supportive work environment. Thanks for everything!

I would like to express my gratitude to my colleagues at the Pathology group in Alnarp. Thank you for your support over the years and for your friendship, guidance, and companionship throughout this journey.

Muchísimas gracias por todo a Joan y Laura, no tengo palabras para agradeceros todo vuestro cariño, ayuda, amistad, compañía y por todas las risas y todos los momentos que hemos compartido juntos durante estos años. Ha sido un placer compartir esta experiencia con vosotros. ¡Gràcies per tot!

Gracias también a Jaime, Carmen, Jorge y Nacho, he sido muy afortunada por compartir con vosotros en el camino. Carmen, siempre te estaré

infinitamente agradecida por tus enseñanzas, tu dedicación, tu paciencia y por todo el apoyo prestado tanto en el laboratorio, como con los manuscritos. ¡Muchísimas gracias por todo!

I extend heartfelt thanks to all my PROTECTA colleagues, with whom I have shared unforgettable moments over these years. I am especially grateful to Murillo, Christian, Valentina, and Jennifer for our journey together both as colleagues and friends.

To Maja, thank you for our discussions about oomycetes and for your support and valuable feedback on my manuscripts.

Muchísimas gracias a mis amigos y amigas de vida, quienes han sido mis pilares de aliento y apoyo durante todos estos años. Gracias por estar siempre a mi lado, por todas las risas y por todos los momentos compartidos.

Last but not least, I want to extend my heartfelt thanks to my TBF family. Your care, support, and guidance over the years have been invaluable. It has been a true joy to learn, heal, and grow alongside each of you. I am deeply grateful to have you in my life. Love you all!

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FUNGAL BIOLOGY REVIEWS 40 (2022) 19–36

British Mycological Society promoting fungal science

journal homepage: www.elsevier.com/locate/fbr

Current practices and emerging possibilities for reducing the spread of oomycete pathogens in terrestrial and aquatic production systems in the European Union

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ARTICLE INFO

Article history:
Received 1 April 2021
Received in revised form
2 September 2021
Accepted 13 October 2021

Keywords:
EU legislation and policies
Fish trade
Management practices
Oomycete dispersal pathways
Plant trade

ABSTRACT

Diseases caused by oomycete pathogens are a global threat to forestry, agriculture and aquaculture. Because of their complex life cycles, characterised by dormant resting structures that enable their survival for years under hostile environmental conditions, reducing the spread of oomycetes is a challenging task. In this review, we present an overview of this challenge, starting from the need to understand the natural and anthropogenic dispersal pathways of these pathogens. Focusing on the European Union, we explore current legislation that forms a backbone for biosecurity protocols against the spread of oomycetes through trade and transport. We discuss the options for prevention, containment and long-term management of oomycetes in different production settings, emphasising the importance of prevention as the most cost-efficient strategy to reduce the spread of these pathogens. Finally, we highlight some of the new and emerging technologies and strategies as potential tools in the integrated pest management of animal and plant diseases caused by oomycetes. We emphasise the urgency of actions to halt the global spread of these pathogens.

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https://doi.org/10.1016/j.fbr.2021.10.001
1749-4613/

1. Introduction

Oomycetes are among the most damaging of disease-causing organisms in forestry, agriculture and aquaculture, presenting global threats to natural and anthropogenic environments, and to food production. The plant-pathogenic oomycetes causing highest global losses in agriculture and forestry are in the genus *Phytophthor*a, with *P. cinnamomi*, *P. ramorum* and *P. infestans* (Table 1) amongst the most damaging species. One of the most destructive plant pathogens worldwide is *P. cinnamomi*, which infects over 5000 plant species (Burgess *et al.*, 2017; Hardham and Blackman, 2018). *Phytophthora ramorum* is the causal agent of 'sudden oak death' and 'ramorum blight' diseases across a wide range of hosts, and has an economic impact in the USA alone conservatively estimated at in excess of 10 million USD per annum (Goheen *et al.*, 2002; Dart *et al.*, 2007; Frankel, 2008). Oomycete pathogens are also a serious problem in aquaculture, i.e., cultivation of freshwater and saltwater organisms in natural or artificial reservoirs under controlled conditions (Derevnina *et al.*, 2016). This system has become one of the fastest growing food sectors globally, representing 20% of fish production in the European market, providing both food and high employment (STECF, 2018). Two important oomycete pathogens of the present-day aquaculture industry are *Aphanomyces invadans*, cause of Epizootic Ulcerative Syndrome, EUS (Huchzermeyer and Van der Waal, 2012; Dibyendu &, Arunjyoti, 2014; Hsieh *et al.*, 2016) in many species of warmwater fish and *Saprolegnia parasitica*, cause of saprolegniosis most significantly in coldwater salmonids (Table 1). *Aphanomyces invadans* can cause up to 100% mortality at aquaculture sites (Iberahim *et al.*, 2020), whilst *S. parasitica* is responsible for approximately 10% of all mortality in Scottish salmon farming (Phillips *et al.*, 2008).

The European Union (EU) has invested a considerable amount of financing into control and management of oomycete pathogens in its area, which is reflected by a total of 32 hits in the Cordis research project database and specific mentioning of oomycetes in several regulatory documents (28 hits in EUR Lex). Yet, the currently established management strategies and legislation to control the spread of pathogenic oomycetes in both terrestrial and aquatic production systems have not succeeded as desired. Thus, revision and updating of the strategies to consider the pathways of spread and to reflect the latest scientific knowledge in the field of epidemiology and relevant technological approaches is urgently required. In this review, we provide an overview of the natural and human–driven pathways of oomycete pathogen spread in terrestrial and aquatic ecosystems, identifying potential facilitators and barriers. We also discuss management strategies and problems related to these management approaches, with attention to current legislation and regulations focusing on the EU. Finally, we consider different opportunities to reduce the spread of oomycetes implementing integrated pest management (IPM) strategies, including some new and emerging technologies.

2. Dispersal pathways

Natural dispersal pathways

With free-swimming zoospores, oomycetes are adapted to dispersal in aquatic and moist habitats. For soil-borne *Phytophthora* species, local spread usually takes place after periods of heavy rain or floods, when zoospores are released and swim, chemotactically attracted to plant roots, where they encyst and penetrate the host (Erwin and Ribeiro, 1996). For air-borne *Phytophthora* species, zoospores are released under favourable humidity, and disperse by water splash or are carried by wind in small droplets (Erwin and Ribeiro, 1996; Vannini *et al.*, 2010). The natural life cycle of some *Phytophthora* species occurs in flowing water, which is also the main dispersal pathway (Jung *et al.*, 2011). In some cases, natural hybridisation may occur in water courses (Nagel *et al.*, 2013; Burgess, 2015). *Phytophthora* can also be dispersed over long distances by animals or humans moving infested soil (Cushman and Meentemeyer, 2008). Some *Phytophthora* species produce sexual and asexual structures (oospores, chlamydospores or hyphal aggregations), which enable survival during unfavourable conditions in soil or in plant tissues (Crone *et al.*, 2013; Jung *et al.*, 2013a, b).

Natural dispersion of oomycetes in aquatic environments may sometimes occur through periodic migration of wild salmonids (Kennedy *et al.*, 1991) (Fig. 1). The horizontal transmission of oomycetes, for example, *A. invadans* can also occur through water supplies where secondary zoospores, which adhere to the host prior to infection, can attach to damaged skin of fish and germinate. If the secondary zoospores cannot find a suitable species or encounter unfavourable conditions, encystment occurs until conditions favour transformation into tertiary generations of zoospores. The encysting characteristics displayed by species of *Aphanomyces* play an important role in epidemics (Gon Choudhury *et al.*, 2014; Rezinciuc *et al.*, 2018). Other fish-pathogenic oomycetes, such as *Saprolegnia parasitica* and *S. australis* can form biofilms together with numerous other microorganisms, in which growth occurs. Natural biofilms, therefore, constitute reservoirs of oomycetes in the environment, including in aquaculture (Ali *et al.*, 2013).

Anthropogenic dispersal pathways

Globalisation of trade and extensive travel have resulted in increasing risks of spread of invasive alien pathogens, including oomycetes. Thus, the global trade in live plants (horticulture, agriculture and forestry), and live fish (food fish and ornamental fish trade) should be considered as significant pathways for both plant and fish pathogenic oomycetes. When these organisms are introduced into new ecosystems

Table 1 – Basic information about selected oomycete pathogens in terrestrial and aquatic production systems.

Species	Main hosts/Host range	Morphology/Genetics	Typical damage (type/ symptoms)	Current distribution and risk of spread	References (examples)
Terrestrial systems					
Phytophthora cinnamomi	Broad host range approaching 5000 species: coniferous and deciduous forest trees, woody ornamentals, and orchard crops.	Heterothallic. Typically, only one mating type is found in a region.	Root and collar rot, basal and stem cankers, wilting, chlorosis, decline and mortality.	Present in all continents. Expected to expand its sphere in North America and Europe.	Shea *et al.* (1978); Costa *et al.* (2011); Robin *et al.* (2012); O'Brien and Hardy (2014); Sena *et al.* (2018).
Phytophthora ramorum	Wide host range, affecting over 100 plant species in 40 genera.	Heterothallic. Oospores are hardly found, as the two mating types do not often coincide.	Bleeding stem cankers often cause mortality, necrotic foliage and shoot dieback. Causal agent of Sudden Oak Death.	Europe (mating type A1) and North America (mating type A2). Risk of sexual recombination if both mating types occur in the same region.	Werres *et al.* (2001); Goheen *et al.* (2002); Rizzo *et al.* (2002).
Phytophthora alni	Riparian alder species (*A. glutinosa, A. cordata, A. incana*) in Northern Europe.	Homothallic, with gametangia usually frequent. No chlamydospores are observed.	Small, yellow and sparse summer leaves and crowns, dead twigs and branches, heavy cone production, bleeding at the base of the tree.	Widespread across Europe, recently found in Alaska and Oregon.	Brasier *et al.* (1999); Brasier *et al.* (2004); Hansen (2012).
Phytophthora cambivora	Hardwood forest trees, especially members of the Fagaceae, including chestnut and beech.	Heterothallic. Chlamydospores are absent.	Root rot and stem canker, chlorosis, bleeding cankers, and wilting. The symptoms of ink disease of chestnut are characteristic.	Europe, North America and Asia.	Belisario *et al.* (2006); Ioos *et al.* (2006); Vannini and Vettraino (2011).
Phytophthora infestans	Principal hosts are Solanaceae including *Solanum* spp. (potato) and *Lycopersicon esculentum* (tomato), as well as cultivated species of Solanum.	Heterothallic. Chlamydospores and hyphal swellings are rare.	Seedling blight, unusual odour, abnormal colours on leaves, necrotic areas, necrotic areas and wilting.	Present in all continents.	Fry (2008); Haverkort *et al.* (2008); Cooke *et al.* (2011).
Phytophthora cryptogea	Several ornamental plants and vegetable crops, as well as woody plants (e.g., Malus, Prunus, Pistacia, Cupressus, and Pseudotsuga species)	Heterothallic. Chlamydospores are rare.	Discolouration, leaf fall, necrotic areas, rot, wilting, reduced root system, wood rot, canker on woody stem, dieback, gummosis or resinosis.	Present in all continents.	Ampuero *et al.* (2008); Mostowfizadeh-Ghalamfarsa *et al.* (2010); Olson *et al.* (2011).
Aquatic systems					
Aphanomyces astaci (Crayfish plague)	Responsible for the huge mortality of native population of crayfish.	Asexual reproduction. Polyplanetism ability.	Hardly visible to the eye, in some cases may appear as dark spots and soft abdominal cuticles. Not necessarily lethal, stable host–parasite relationship possible.	North America and Asia; extremely infectious to native crayfish in Europe	Nylund and Westman (2000); Diéguez-Uribeondo *et al.* (2009); Svoboda *et al.* (2017).

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Table 1 (*continued*)

Species	Main hosts/Host range	Morphology/Genetics	Typical damage (type/ symptoms)	Current distribution and risk of spread	References (examples)
Aphanomyces invadans (Epizootic Ulcerative Syndrome)	Seasonal oomycete disease of wild and farmed, fresh and brackish-water fish.	Asexual reproduction. Polyplanetism ability.	Necrotising ulcerative lesions. Often fatal due to farming under the high stocking density/high stress conditions.	Asia, North America, Africa and Australia (spread via both commercial and ornamental fish trade).	Diéguez-Uribeondo *et al.* (2009); Oidtmann (2012); Dibyendu & Arunjyoti (2014).
Halioticida noduliformans (Abalone Tubercle Mycosis)	Affects abalones, European lobster eggs and mantis shrimp.	Asexual reproduction.	White nodules/lesions. In abalone, hyphae can penetrate superficial muscles. In lobsters, infection manifests as discoloured eggs.	East Asia, Europe and Africa.	Atami *et al.* (2009); Macey *et al.* (2011); Holt *et al.* (2018).
Haliphthoros milfordensis	Pathogen of crustaceans and their eggs, such as lobster and shrimp	Asexual reproduction.	Depending on the host, infections take various forms, from penetration of eggs or larvae causing a whitish opaque appearance to lesions in adult individuals.	North America, Asia and Europe.	Fisher *et al.* (1975); Tharp and Bland (1977); Nakamura and Hatai (1995).
Saprolegnia diclina (Saprolegniosis)	Pathogenic to fish and amphibian eggs.	Asexual and sexual reproduction. Polyplanetism ability.	Eggs covered with cotton-like mould. Infection usually first appears in dead eggs, spreading to healthy eggs.	Europe, Australia, Asia, North America, South America.	Diéguez-Uribeondo *et al.* (2007); Fernández-Benéitez *et al.* (2008); Bruno *et al.* (2011); Van Den Berg *et al.* (2013); Sandoval-Sierra *et al.* (2014); Sarowar *et al.* (2019).
Saprolegnia parasitica (Saprolegniosis)	Primarily wild and farmed stocks of salmonids.	Asexual and sexual reproduction. Polyplanetism ability.	Dermal and epidermal damage; white/grey cotton-like growths on the fish skin and gills.	Northern Europe, North America, South America and Asia.	Hatai and Willoughby (1988); Van West (2006); Bruno *et al.* (2011).

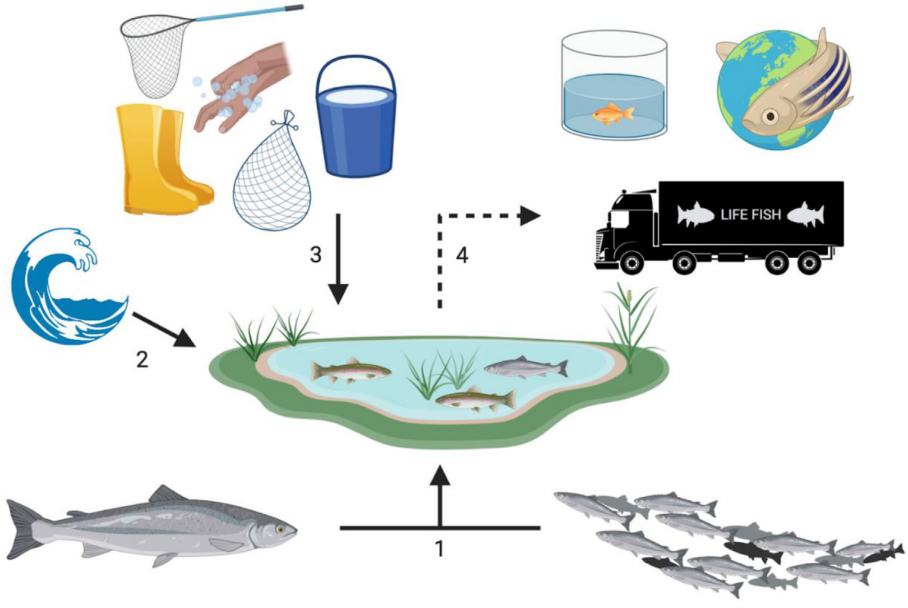

Fig. 1 – Dispersal pathways of oomycetes through the fish trade. 1. Infected fish is introduced into the river/waterways through fish trade or migration of wild fish. 2. Widespread disease outbreak through flooding. 3. Farm to farm transfer. 4. Global pathogen dispersion through the live fish trade. (Created with BioRender.com).

where the native plants have not developed resistance to the invasive organisms, the damage may be severe (Brasier, 2008; Hansen, 2008; van den Berg *et al.*, 2013).

Several studies have identified the international plant trade as one of the most important pathways for introductions of alien oomycetes (Brasier, 2008; Pérez-Sierra *et al.*, 2013; Santini *et al.*, 2013; Jung *et al.*, 2016; Chapman *et al.*, 2017; Puertolas *et al.*, 2021). Conditions in plant nurseries, including high plant densities in monocultures, a plentiful supply of water, inadequate drainage and poor phytosanitary practices, provide perfect conditions for the development and reproduction of oomycetes (Fig. 2). Furthermore, the ability of oomycete species to survive long periods as propagules, possibly multiplying during transport, hidden in soils or in symptomless host tissues, exacerbates the problem (Hong *et al.*, 2008; Vannini *et al.*, 2012).

Urban areas are particularly exposed to *Phytophthora* inoculum due to the recurrent out-planting of ornamental plants that may be symptomless but infected (Alonso Chavez *et al.*, 2016). Many of the ornamental plants and even larger trees used in landscaping are transported over long distances in the international plant trade (Puertolas *et al.*, 2021). In addition, the highly populated areas are exposed to inoculum, e.g., in commodities or the soil carried by humans on vehicles and even on footwear (Hayden *et al.*, 2013). Thus, a large number of human assisted pathways are simultaneously active and enable dispersal of oomycetes. The huge volume and extent of these pathways explains the difficulties in controlling the spread of oomycetes (Hulbert *et al.*, 2017; Garbelotto *et al.*, 2018).

The human-assisted dispersal of aquatic oomycetes also occurs through movement of pathogens in trade, e.g., via the international movement of fish for aquaculture, or the ornamental fish trade (Blazer *et al.*, 2002) (Fig. 1), or accidently in ballast water (Morgan, 2001). Many oomycete life-stages thrive within ornamental fish transport bags. Cysts, in particular, may persist for several weeks under such conditions and can often withstand environmental extremes and chemical treatments (Griffith *et al.*, 1992). Staff movement between aquaculture services, transport vehicles, water-supply channels and use of farm gear (e.g., nets) are also associated with disease transmission.

3. Regulatory framework for controlling oomycetes spread in EU

Global treaties and agreements

The economic profitability of the agriculture, forestry and aquaculture sectors of the EU is highly dependent on global markets and trade. Global markets rely on regulatory systems and treaties aiming to ensure safe trade and to protect biodiversity against alien invasive pests (MacLeod *et al.*, 2010). The World Trade Organization (WTO) governs the Sanitary and Phytosanitary Measures Agreement (the SPS agreement), which involves quarantine and biosecurity measures that help to mitigate the risk of introduction, establishment and spread of pests and diseases in food and feedstocks, advocating harmonised, science-based standards for

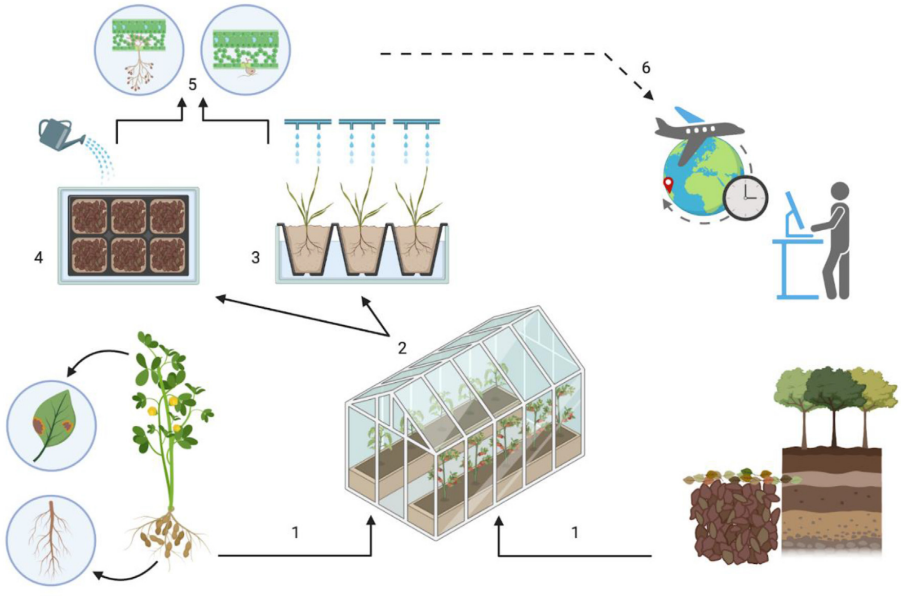

Fig. 2 – Dispersal of *Phytophthora* spp. through plant nurseries. 1. Infected plant material is introduced into the nursery through the plant trade and/ or from the environment. 2. Sporangia produced on infected plants, plant debris or soil spread via water splash or air currents to uninfected plants. Pathogens can also spread via irrigation from contaminated water sources. 3. Cuttings from infected plants contaminate propagation material. 4. The pathogens spread from infected plants and leaf debris via standing water. 5. Infested potting media can lead to infection of roots and stems. 6. Infected plants are sold from nurseries through local, national and international e-commerce platforms all over the world. (Created with BioRender.com).

sustainable production and safe trade. For plants, these standards are developed within the International Plant Protection Convention (IPPC), an intergovernmental treaty that works to secure international cooperation in protecting global plant resources from the introduction and spread of plant pests, and to preserve food security and protect biodiversity, whilst at the same time facilitating trade. The IPPC, hosted by FAO, promotes cooperation among the parties, e.g., through a set of 13 National Reporting Obligations that include description of the organisational arrangements for plant protection, list of regulated pests, and pest reports (www.ippc.int). Importantly, the IPPC develops International Standards on Phytosanitary Measures (ISPMs) and facilitates their implementation to reduce risks to plant production and biodiversity. The current list contains 45 ISPMs, several of which aim to reduce or prevent the spread of pests and pathogens. For instance, ISPM 03 provides guidelines for the export, import and release of biological control agents and other beneficial organisms; whereas ISPM 15 regulates use of wood packaging material in the international trade and ISPM 38 targets international movement of seeds (www.ippc.int). The "sister" organisation of IPPC, World Organisation for Animal Health (OIE), advises on surveillance and control of zoonoses and other infectious transboundary animal diseases, setting the standards for animal health and production (Kahn and Pelgrum, 2010). The EU is a member of the WTO (as are Member States in their own right), therefore these treaties and agreements are strongly forming the policy background for the plant and animal health regulations of the EU.

The spread of oomycetes and other pests is also a concern for the Convention on Biological Diversity (CBD), which is dedicated to protection of biological diversity and promotion of sustainable development. The CBD emphasises management of alien species by pathways (i.e., release, escape, contaminant or stowaway in transport systems, corridors and unaided spread) and distinguishes intentional vs. unintentional introductions, as well as movement via a commodity or a vector (Harrower *et al.*, 2018). Because the focus of CBD is on risks of species movement between countries, it shares common ground with the IPPC and OIE. With increasing numbers of alien species detected (approximately 12 000 and 10–15% of them which are becoming invasive), the EU is concerned about the impacts of newly recognized pests. Consequently, the EU-level regulations related to cross-border spread of oomycete pathogens adhere also to the CBD principles.

In the following sections, we highlight the complexities of implementing the IPPC, OIE and CBD polices through the regulatory system of the EU, and the challenges in restricting the

spread of oomycete diseases of plants or aquatic animals in this regulatory matrix.

Phytosanitary regulations at the EU level

The IPPC is implemented by Regional Plant Protection Organisations (RPPOs), which act as coordinating bodies at a regional level, and by National Plant Protection Organizations (NPPOs), which are the competent phytosanitary authorities at the country level. In Europe and surrounding countries, the RPPO is the European and Mediterranean Plant Protection Organisation (EPPO). All RPPOs collaborate with IPPC, developing ISPMs, sharing information, and proposing approaches for detection, prevention and management of pests. The NPPO is responsible for operational tasks, e.g., surveillance, inspections and pest risk analyses.

In order to facilitate EU state reporting, enabling enhanced protection against introduction and establishment of harmful organisms, a web-based reporting system, European Network of Plant Health Information Systems (EUROPHYT) has been established. The EUROPHYT allows the NPPOs to enter data regarding interceptions, ensuring rapid alerts, connecting the Member State authorities with the European Food Safety Authority (EFSA) and the Directorate General for Health and Food Safety of the European Commission (DG SANTE).

Implementation of global, regional and national phytosanitary regulations to prevent the spread of oomycete pathogens is challenging. Protocols and rules exist for phytosanitary passports (EU, 2016), which are required for the plant trade within EU territory, along with plant passports that indicate the producing nursery has passed inspections for appropriate phytosanitary procedures related to plant propagation and onward growth. In the absence of a 'passport', compulsory visual inspections must be carried out at borders, looking for symptoms of listed organisms. Regrettably, these inspections are very expensive and usually inefficient (Brasier, 2008; Jung *et al.*, 2018). This problem is not restricted to the EU: for example, the Animal and Plant Health Inspection Service (APHIS) of the USA claims to inspect only approximately 2% of imported plant stock (Brasier, 2008), thereby highlighting how ineffective these practices have been to date. A problem is also that the plant inspection protocols usually only allow for known pests and pathogens to be regulated. Despite the long use of regulations and protocols globally, several invasive *Phytophthora* species were unknown to science before they induced severe damage in invaded environments. Hence, the conclusion must be that the regulations and associated protocols do not efficiently prevent the introduction and establishment of plant-pathogenic oomycetes (Brasier, 2008; Jung et al., 2016, 2018).

Regulation of aquatic animal health

The OIE develops Animal Health Codes and early warning systems to prevent the spread of pests through international trade in animals, promoting animal welfare. It primarily focuses on livestock pathogens although diseases affecting native wildlife are also listed (Shine *et al.*, 2010). Aquatic animals, including both vertebrates (fish) and invertebrates (e.g., shellfish), along with other aquatic products such as plants, are also subject to EU law and policy. Aquaculture is defined as the breeding and rearing of aquatic organisms using methods to increase and improve their production, which remain the property of a natural or legal person in all stages of the life cycle up to harvest (EU, 2013). As in other sectors of the economy, the European Commission decided to standardise aquaculture policy across all EU states through the Common Fisheries Policy (CFP), initially in 1970, and recently reformed in January 2014. Strategic guidelines were introduced, presenting priorities and general objectives to be followed by Member States (EU, 2013). The CFP and all regulations identified four priorities: fisheries management, international policy, market and trade policy, and funding of the policy. The CFP contributed to the development of EU aquaculture, increasing both the quality and quantity of production.

Health of aquatic animals, and the control and prevention of diseases in aquaculture was first covered by EU Directive 2006/88/EC (EU, 2006). Both endemic and exotic diseases threatening aquaculture were listed, including EUS caused by *A. invadans*, which was later removed (EU, 2012) due to reduced detrimental impacts on the EU economy and environment. More recently, Regulation (EU) 2016/429 (EU, 2016) has been established to cover transmissible animal diseases, with amendments to certain legal acts in the field of aquatic and terrestrial animal health. The Articles 172 to 226 (Title II of Part IV) apply specifically to aquaculture animals and products of animal origin. Interestingly, EUS reappeared on the list of diseases (EU, 2016). This reference is the only mention of oomycete diseases in European aquaculture law, but nevertheless the problem of emerging oomycete infections remains. *Saprolegnia* spp. are ubiquitous (Ali *et al.*, 2014), which is likely the reason why saprolegniosis is not included in any of the EU disease lists.

All Member States are required to keep records of transport of aquaculture animals, along with rates of mortality and disease outbreaks (EU, 2006; EU, 2016). In contrast to the plant health control regulations, however, there is no system for reporting outbreaks in aquaculture available for public view. The European Commission has initiated a website, European Market Observatory for fisheries and aquaculture (https://www.eumofa.eu/) with the main goal of increasing the transparency and efficiency of the market, however, it does not inform the general public about disease outbreaks.

As with the plant trade, health certificates are also applied in aquaculture. Animal Health Certification (AHC) is covered by Regulation (EU) 2016/429 (EU, 2016), for live aquatic animals (Articles 208 to 217) and for products of aquatic animal origin (Articles 223 to 224). Certificates contain basic information about the transport, such as content (type of animals/products, quantity), purpose (intended use of aquatic animals/products) and destination. The AHC also confirms that the aquatic animals/products fulfil the relevant animal health criteria and requirements. Because single-unit inspections are far less practical within the international aquaculture trade, regulatory controls do not provide complete protection against the spread of invasive species.

Regulation of Invasive Alien Species (IAS)

Protection of biodiversity against alien invasive species (IAS) is a priority of the CBD, and the EU recognises IAS as a major cause of biodiversity loss and a threat to the economy and health (Genovesi and Shine, 2004). Several oomycete pathogens can be considered as IAS that in a new location may severely threaten the native biodiversity and ecosystems in the region, regardless of whether the species are animals, fungi, other microorganisms or plants. For instance, *P. cinnamomi* is listed as one of the 100 worst invasive alien species in the Global Invasive Species Database (GISD) of the International Union for Conservation of Nature (IUCN) (Lowe *et al.*, 2000). In the EU, preventive and management actions for the introduction and spread of IAS are regulated by Council Regulation (EU) 1143/2014 of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species (EU, 2014). The criteria used for recognition of organisms as IAS are based on evidence-based risk assessments (Carboneras *et al.*, 2018). With minor exceptions, it is prohibited to import, transport, possess, use, breed from, trade or release all IAS into the environment within the territory of the EU.

The current EU regulatory system for IAS does not specifically target the oomycetes, but rather aims to prevent the spread of IAS in general. The list of organisms recognised as IAS is short, prompting Carboneras *et al.* (2018) to conduct extensive research and identify further potential candidates suitable for listing as IAS. However, following the study, only three oomycete potential candidates were mentioned: *Aphanomyces astaci*, *Phytophthora cinnamomi* and *Phytophthora fragariae*. Although none of these species qualified for EU listing (all three are very well established in EU territories already), the strategies against invasive species (EU, 2014) are versatile enough to be used regardless of the presence of the organism on the list.

Several challenges have been identified in the regulatory system for IAS. Shine *et al.* (2010) point out that the EU lacks a joined-up approach to managing invasion pathways from pre-border to post-border and down to control and management at appropriate scales, and that targeted policies are lacking to protect the most vulnerable ecosystems and prevent further escalation of IAS damage elsewhere. The policies are also considered insufficiently precautionary, failing to optimise efforts for prevention and to address the environmental damage at source, although these are recognised as the most cost-effective type of IAS intervention (Shine *et al.*, 2010). Rapid responses remain a matter for national or local concern and a coordination framework to promote consistency across key domains is lacking. For example, there is a gap between regulations that govern climate change adaptation of forestry which could influence the forest landscape in a way that affects the spread of IAS.

4. Prevention, containment and long-term management of oomycetes

Several strategies can be applied to prevent and control the spread of plant or fish pathogenic oomycetes. These strategies follow general disease management principles that were first described for plant diseases by Whetzel (1929), i.e., avoidance, exclusion, eradication, protection, resistance and therapy. These principles are also reflected in the framework of biological invasions (Catford *et al.*, 2012), corresponding to the phases of prevention (avoidance, exclusion), containment (eradication) and long-term management (protection, resistance and therapy). Here, we discuss briefly how these principles are implemented in management of the threat posed by oomycetes in plant production and aquacultures.

Avoidance

Avoidance refers to prevention of the disease by selecting a time of the year or a site where there is no inoculum or where the environment is not favorable for infection. It could be achieved, e.g., by selecting conditions unfavourable to pathogen growth, spread and transmission, or manipulating the environment towards such a state. Factors contributing to such conditions include temperature regime and other environmental variables (e.g., soil characteristics, pond environment), distance from spore sources, and management strategies, such as stocking density or water treatment (Oidtmann, 2012; Hayden *et al.*, 2013).

Avoidance is the main principle implemented in management of *P. cinnamomi* in Australia. One way to influence the environment in forest stands is to open the canopy architecture so that it allows sunlight to enter to the ground floor, which suppresses *Phytophthora* and *Pythium* diseases of seedlings such as damping-off (Panth *et al.*, 2020). This strategy can be effective, although the more open stand structure may promote transmission of airborne species, such as *P. ramorum* (Rizzo *et al.*, 2005; Hayden *et al.*, 2013). The strategy is also implemented by monitoring and mapping the presence of pathogens in relation to susceptible hosts, performing thinning operations or removal of infected plants (Davis *et al.*, 2010; Hayden *et al.*, 2013). Soil characteristics, such as permeable, well drained, loamy soils, with high organic content play important roles in reducing ingress of inoculum into areas climatically unfavourable to pathogens. Consequently, choosing appropriate sites for plantations or reforestation has been shown to reduce the probability of inoculum invasion (Shearer and Crane, 2011; Hüberli *et al.*, 2012; Hayden *et al.*, 2013).

In aquaculture, avoidance strategies are implemented through site choice, water supply and the fish species being cultured. Fish farming systems vary from open systems based on natural water bodies, to semi-closed (flow-through), and closed systems with water recirculation (Lawson, 2013), which in addition, differ in the degree of control over the spread of oomycetes and other pathogens. Rearing of particular fish species depends on temperature and access to high-quality water resources in the selected geographical region, and seasonal changes strongly affects aquatic organisms, including salmonids which are typically bred at low temperatures for good growth (Hevrøy *et al.*, 2013). Adjustment of water temperature can help to suppress the spread of oomycetes in aquacultures but should be used with care - stress caused by temperature changes may affect the fish immune system, rendering the fish susceptible to *Saprolegnia* species (Bly *et al.*, 1993; Alfonso *et al.*, 2020). The EUS caused by *A. invadans* is primarily a disease of tropical aquaculture, with fish farm

outbreaks most severe when water temperature remains between 18 and 22 °C for prolonged periods of time (OIE, 2019a). Thus, it is possible that climate change may reduce the possibilities available to implement avoidance principles in control of oomycetes spread in aquacultures, e.g., in many European countries.

Exclusion

Exclusion aims to prevent the introduction of the pathogen inoculum into a given region (Whetzel, 1929). In the plant trade, it involves avoidance of long-distance movement of plants and soil, and use of locally grown seedlings from disease-free nurseries (Hayden *et al.*, 2013). In nurseries, the exclusion strategies are based on efficient inspections, high sanitary standards that ensure pathogen-free containers, potting media and irrigation water, and avoidance of fungicides including phosphonates, that may suppress symptoms but do not kill the pathogens. Moreover, it is important to avoid contact between containerised plants and the ground in the nursery, and avoid the use of bio-based suppressive composts or fungicides. Attempts to eliminate resting structures in plant or soil material include measures such as composting, solarisation, oven treatment or autoclaving (Swain *et al.*, 2006; Hayden *et al.*, 2013). In forest areas, the principle of exclusion is implemented through monitoring and mapping of pathogen locations, restrictions of vehicle and people movements from infected to uninfected areas and preventing mixing of infected soils with uninfected ones. Cleaning vehicles and footwear before entering uninfected areas and preventing water draining from infected to uninfected areas are other measures contributing to exclusion of oomycetes in forests. Successful exclusion also necessitates education of the general public and forestry workers (Hansen *et al.*, 2000; Colquhoun and Kerp, 2007; Hayden *et al.*, 2013).

In freshwater aquaculture, adoption of appropriate general husbandry practices reduces the likelihood of transmission of *Aphanomyces* and *Saprolegnia* species (OIE, 2019a, 2019b). Exclusion practices include preventing fish movement from upstream to the farm and securing the location of the facility from flooding risks. It is recommended that water supply is from boreholes, springs or wells, or driven through a pipe, channel or natural pipeline in order to suppress potential sources of infection (Ali *et al.*, 2014). Purchase of fish or eggs from farms not meeting adequate sanitary standards must be avoided, and fish inspection by vets or fish health experts should be carried out at a minimum interval of two years. Farm records should be maintained, including data on mortality rates, origin, and destination of exported eggs or fish (OATA, 2006). For *A. invadans*, however, good husbandry practices at a farm level may be difficult to follow due to economic reasons in many of the lower-income countries where the warmwater aquaculture facilities are most vulnerable to EUS (Mohan and Bhatta, 2002). Of paramount importance is adequate disinfection of all material leaving the site - both personnel and fishery products. This action is achieved via use of appropriate biosecurity, including footwear disinfecting mats or baths containing potassium permanganate ($KMnO_4$) when entering/leaving the facility (Faruk *et al.*, 2012). Stringent monitoring for the presence of EUS and quarantine of fish infected with the pathogen are also of key importance for successful exclusion of fish oomycetes (OIE, 2019b). Prevention of water leaks from poorly constructed ponds in addition to flood mitigation prevent *A. invadans* spread into both neighbouring fishponds and the wider environment (OIE, 2019a).

Eradication

Eradication aims to eliminate the pathogen after the introduction, but before it is widely established and spreading. Eradication measures are most effective when applied in the very early stages of the epidemic and at a local scale. The costs related to eradication increase rapidly as the disease spreads, at the same time as the efficacy of the process decreases. It is thus important to carefully evaluate when eradication programmes are used (Alam and Rolfe, 2006). Eradication of oomycetes is generally challenging due to their persistent spores and efficient spread in the environment (Derevnina *et al.*, 2016).

Eradication programmes for plant diseases involve uprooting, cutting and burning host plants. They are usually accompanied by surveys with baiting or other methods of detection, as well as measures aimed at reducing the competitive ability of the pathogen in the soil, such as by applying root barriers, soil surface treatments or fumigation of deep soils (Hansen, 2008; Dunstan *et al.*, 2010). Eradication strategies used to control *P. cinnamomi* in Australia have generally comprised physical and herbicidal removal of all plants in a 4–10 m buffer zone beyond the disease front (Dunstan *et al.*, 2010). In addition, root barriers have been used to restrict the intrusion of roots from nearby sites. Chemicals, such as triadiazole and metalaxyl, and soil fumigation with methamsodium have also been applied. Using these strategies, *P. cinnamomi* was successfully eradicated from one site, and controlled at other treated areas (Dunstan *et al.*, 2010; Hayden *et al.*, 2013). Although locally successful, the landscape effects of these actions remain unknown.

Eradication treatment strategies to reduce impacts of *P. ramorum* in California and Oregon have varied among sites, generally including physical, herbicide, and cutting and burning of hosts within a buffer of 100 m beyond infestation. New technologies, such as the use of high resolution digital aerial imagery have been deployed aiming to monitor the spread into new sites from the air (Rizzo *et al.*, 2005; Hayden *et al.*, 2013; Goheen *et al.*, 2017). While the strategies have been locally successful, spread of *P. ramorum* has continued at the landscape level.

Eradication in aquatic environments is considered almost impossible, because the pathogens can survive as encysted forms or on carriers. Ideal practices to eradicate aquatic oomycetes involve removal of all susceptible fish before starting with new stock, drainage and liming of ponds, exchange and aeration of water, complete disinfection of contaminated apparatus, and restocking (Bruno *et al.*, 2011). In most cases however, the use of all techniques together is not feasible due to high costs and time involved. Yet, similar practices can be effectively applied at hatcheries, including regular disinfection baths and removal of dead fish eggs as potential

sources of infection for other eggs. Regular disinfection throughout the process of fish culture is recommended also to minimise risk of spread and establishment of EUS. Formalin and potassium permanganate in particular have shown recent promise as agents for this task (Paria *et al.*, 2020). The eradication strategy through restocking is also used in fisheries regularly suffering from EUS outbreaks (OIE, 2019a). This approach lowers the reservoir of hosts available to *A. invadans*, reducing likelihood of outbreaks and disease spread, and thus increasing livelihood stability for aquaculturists. In addition to farm sites, this approach may also be undertaken at small-scale wild fisheries. Emphasis here is upon stocking endemic EUS-resistant species such common carp in India (Pradhan *et al.*, 2008), as opposed to the highly susceptible Indian major carp species typically cultured - *Labeo rohita*, *Catla catla* and *Cirrhinus mrigala* (Eknath and Doyle, 1990).

Protection and therapy

Protection is based on the use of chemical or biological barriers that reduce or hinder the development of pathogen infection and disease in hosts, whereas therapy is used when the organisms are already infected, with a main goal of curing the disease. The protective or therapeutic strategies against *Phytophthora* diseases have mainly focused on enforcement of biological mechanisms and use of chemicals (Hayden *et al.*, 2013), along with cultural practices. The concept of biological control, as defined by Eilenberg *et al.* (2001) as *"The use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be"*, has received considerable attention in research over the last 40–50 years. Thus, biological control may, for example, involve use of beneficial microorganisms to antagonise aerial or soil-borne plant pathogens. Numerous microorganisms, under either greenhouse or field conditions, have been reported to provide protection or disease control against oomycetes in plants, including several bacterial strains in the genera *Pseudomonas* spp. (Raaijmakers *et al.*, 2002) and *Bacillus* spp. (Lim and Kim, 2010), the oomycete *Pythium oligandrum* (Rey *et al.*, 2008), the fungus *Trichoderma harzianum* and also plant species in the genus *Acacia* spp. (D'Souza *et al.*, 2004, 2005). It is known that composts and organic soils may suppress growth and survival of oomycetes, thus the use of unsterilized composts may suppress oomycetes species (Hardy and Sivasithamparam, 1991; Fichtner *et al.*, 2009; Hayden *et al.*, 2013; Chilosi *et al.*, 2020). Morales-Rodríguez *et al.* (2016) found that *in vivo* biofumigation with *Brassica carinata* pellets was effective in reducing the inoculum density of *P. cinnamomi*, suggesting that it could be a bio-based alternative to the use of chemicals to control this oomycete pathogen in agroforestry systems such as the "dehesa" or chestnut orchards.

Systemically translocated agrochemicals containing phosphonates (including fosetyl-aluminium and potassium salts of phosphorous acid) or phenylamides, or contact chemicals including copper have been used to control plant pathogenic oomycetes (Hayden *et al.*, 2013). At high concentrations, phosphonates act directly to suppress pathogens and at low concentrations act indirectly to stimulate host defences (Garbelotto *et al.*, 2009; King *et al.*, 2010; Pilbeam *et al.*, 2011; Hayden *et al.*, 2013). Phenylamides, of which metalaxyl is the most frequently employed, are water-soluble fungicides that rapidly translocate into plant tissues from roots, shoots and leaves (Cohen and Coffey, 1986). They act specifically on oomycetes by inhibiting ribosomal RNA synthesis and can be very effective at inhibiting sporangial production and chlamydospore germination (Cohen and Coffey, 1986; Erwin and Ribeiro, 1996). However, problems with resistance in the pathogens and restrictions due to negative impacts on the environment and the food chain have limited their use. The combination with, or alternation of, metalaxyl with other fungicides like mefenoxam and the fungi-static potassium phosphite have proven suitable for disease control, reducing symptoms by up to 90 % and plant mortality of *Pinus radiata* to less than 5 % (Ahumada *et al.*, 2013; Hayden *et al.*, 2013; Jung *et al.*, 2018). Copper compounds have been widely used as foliar sprays and trunk paints to suppress airborne oomycetes, but their effect is solely protective, with no effect once infection has occurred. In addition, copper compounds have negative long-term impacts through accumulation in soil and accompanying heavy metal toxicity (Pietrzak and McPhail, 2004; Bünemann *et al.*, 2006; Garbelotto *et al.*, 2009; Hayden *et al.*, 2013).

In aquaculture, protection and therapy strategies to combat oomycete diseases also rely on the use of chemicals. Although no effective chemical treatments exist for EUS, application of agricultural lime ($CaCO_3$) to affected ponds reduces environmental suitability for *A. invadans* and lowers its capacity to cause infection as well as reducing severity of pre-existing lesions (Dibyendu and John, 2020). Liming also has a beneficial effect on the physiology of aquatic animals, providing an additional source of calcium and magnesium (Wurts and Masser, 2004). Saprolegniosis was controlled effectively using malachite green until the negative (carcinogenic, teratogenic and mutagenic) side effects of the chemical were discovered, leading to prohibition in most countries (Meyer and Jorgenson, 1983; Srivastava *et al.*, 2004; Culp *et al.*, 2006). Since then, no equally effective method has been found to protect fish against the disease. Alternative chemical treatments, such as formalin, bronopol, hydrogen peroxide, copper sulphate, methylene blue, potassium permanganate and sodium chloride have been used in aquaculture but so far most have proven unsatisfactory, because their use is typically ineffective, expensive, labour intensive, lacks official approval or the treatments are otherwise dangerous (Oláh and Farkas, 1978; Bailey 1983a, 1983b).

Formalin (37% aqueous solution of formaldehyde) reduces external bacterial or fungal infections, as opposed to internal infections against which it is not effective (Francis-Floyd and Pouder, 2018). The dose rate depends on local regulations and the fish species undergoing treatment. Most European countries have restricted or even prohibited the use of formalin, whereas in the USA, formalin-based products to treat *Saprolegnia* infections on eggs are formally approved by the Food and Drug Administration (Francis-Floyd and Pouder, 2018). Safe use of formalin necessitates monitoring of various factors, such as size of the pond, water temperature, oxygen level in the water and medicinal flow rate (Leal *et al.*, 2018). In recent years there has been growing interest in the use of bronopol (bromo-2-nitropropane-1,3-diol) as a

preventive treatment against a wide range of parasitic microorganisms, including *Saprolegnia* spp. (Verner-Jeffreys and Taylor, 2015). Hydrogen peroxide (H_2O_2) also has potential in the control of saprolegniosis. Products containing hydrogen peroxide are present in EU markets (EMA, 1996), and no negative effects of H_2O_2 on fish and the environment have been observed, when used at appropriate concentrations (Pedersen and Pedersen, 2012; Novakov *et al.*, 2018). The aforementioned therapeutic approaches against fungal/oomycete infections are primarily applicable to fish farmed for human consumption, whereas ornamental fish infections are treated with other protocols (Cardoso *et al.*, 2019).

Limited information is available regarding the potential use of biological control to manage oomycete outbreaks in fish (Petersen *et al.*, 1994; OIE, 2019b). However, two invertebrates, *Gammarus pseudolimnaeus* and *Asellus militaris*, have been reported to control growth of *Saprolegnia* on dead fish eggs (Oseid, 1977). Moreover, probiotics are commonly used in aquaculture to boost natural defences in fish. For example, *Pythium, Rhizophthora* and *Pseudomonas* species have been used as probiotics in treatments against *S. parasitica* (Hatai and Willoughby, 1988; Petersen *et al.*, 1994; Hussein and Hatai, 2001). Use of pro- and prebiotics to prevent fish infection by *A. invadans* is an emerging field which shows strong potential. Currently, this approach has yielded firm commercial success regarding tackling bacterial vibriosis in the shrimp aquaculture industry (Kumar *et al.*, 2016). The usefulness of pro- and prebiotics in EUS management remains understudied (Devi *et al.*, 2019). Currently, there are no vaccines available to minimise the impact of saprolegniosis, but there are several immunostimulatory products commonly used, of plant and microbial origin, to elevate the immune status of fish (Subramani and Michael, 2017). For example, Salar-bec (a vitamin premix immunostimulant) increased *in vitro* serum inhibition of both reproduction and growth of *A. invadans* cysts (Miles *et al.*, 2001; OIE, 2019b).

Resistance

Disease resistance is based on traits that reduce the negative effects of the disease by preventing infection or limiting subsequent pathogen growth and development within the host. There are many reports of effective plant breeding programmes for host resistance to manage different oomycete plant pathogens. A successful long-term breeding programme for Port Orford cedar (*Chamaecyparis lawsoniana*) resulted in commercial production of host genotypes resistant to *P. lateralis* infection (Hayden *et al.*, 2013). Likewise, the occurrence of heritable variation in resistance to oomycetes species has been demonstrated on other tree species, e.g., in *Castanea* spp. to *P. cinnamomi* and *Phytophthora* × *cambivora*, in *Alnus glutinosa* to *Phytophthora* × *alni*, *Eucalyptus marginata* to *P. cinnamomi*, in *Pinus radiata* to *P. cinnamomi,* and in *Lithocarpus densiflorus* to *P. ramorum*, indicating potential for resistance breeding programmes (Robin *et al.*, 2006; Miranda-Fontaíña *et al.*, 2007; Stukely *et al.*, 2007; Hayden *et al.*, 2013; Shearer *et al.*, 2014; Santos *et al.*, 2015; Chandelier *et al.*, 2016; Jung *et al.*, 2018).

In contrast to plants, there are no data available on breeding for oomycete resistance in fish farming (OIE, 2019b). The importance of resistance in limiting the spread of oomycetes in the fish trade could increase in future, if possibilities to achieve and deploy durable resistance using new genetic and molecular techniques become feasible and ethically acceptable. Several methods have been applied to produce Genetically Modified Fish (GMF), such as gene transfer and gene editing (Wang *et al.*, 2021). So far, GMF are only used in sectors related to experimental research, with a single case of GMF in the fish industry. In 2015, the US FDA approved genetically modified salmon, reaching up to twice the size of unmodified individuals (Ledford, 2015). Development and implementation of new breeding programmes, possibly in combination with CRISPR-Cas technology, for oomycete resistance have the potential to reduce the use of chemical treatments in both natural ecosystems and fish farming.

5. The way forward: new and emerging approaches to better control of oomycetes spread

There are several new and emerging technologies that are expected to help in the management and control of oomycetes spread in the near future. Of particular importance are tools for reliable and rapid detection and diagnosis, which will allow timely implementation of rapid response protocols in plant production and aquaculture systems. A selection of these new approaches, their potential and limitations, is presented below.

Improvement of detection and diagnosis

Molecular approaches

Molecular approaches for detection rely on PCR-based methods, usually requiring a well-equipped laboratory and specialist expertise (Aglietti *et al.*, 2019). However, promising technologies and field deployable diagnostic tools, based on molecular approaches, are emerging or already available that will enable rapid, on-site detection of the target pathogens. Oxford Nanopore Technologies offer portable RNA and DNA sequencing devices that enable sequencing in either the laboratory or at the point of sampling (Chalupowicz *et al.*, 2019). Loit *et al.* (2019) compared the relative performance of two third-generation sequencing technologies, MinION (Oxford Nanopore Technologies) and Sequel (Pacific Biosciences) for identification and diagnosis of fungal and oomycetes pathogens from Pinaceae spp. and *Solanum tuberosum*. Sequel was effective for metabarcoding of complex samples, whereas MinION was efficient for utilization in rapid and accurate identification of pathogenic organisms. The disadvantages of these technologies are the high initial investments, and the technical expertise that these devices still require. Moreover, despite the promising avenues opened by the third-generation sequencing technologies, they still need development to overcome some major challenges related to sequencing errors and to data storage and management (Amarasinghe *et al.*, 2020).

Isothermal amplification is another field-based technology that is making progress in the detection of nucleic acids. Winkworth *et al.* (2020) described a method based on a loop-mediated isothermal amplification (LAMP) for the detection of *Phytophthora agathidicida,* responsible for Kauri dieback in

New Zealand. This methodology was highly specific and sensitive, with no cross-reactions against a range of other *Phytophthora* isolates. Dai *et al.* (2019) reported a LAMP method with potential to replace conventional PCR-based and culture-dependent assays for screening of *P. cinnamomi* in regions at risk of infection or contamination. Three LAMP assays capable of detecting quarantine pathogens, including *Phytophthora ramorum*, were developed by Aglietti *et al.* (2019) using the portable instrument Genie. Capron *et al.* (2020) developed a point-of-use real-time PCR system for on-site applications, named in Situ Processing and Efficient Environmental Detection (iSPEED), which demonstrated high capacity to identify a broad spectrum of pathogens, including *Phytophthora ramorum*. In general, the new molecular technologies can be expected to greatly facilitate efficient and rapid diagnosis and monitoring of oomycetes, supporting eradication and management.

Volatile signals

Even in the very early phases of infection, the metabolism of the infected plant may change in a way that is indicative of the causal agent (Jansen *et al.*, 2011). These changes may provide useful biomarkers that can be detected using targeted or global approaches. Liquid and gas chromatography-mass spectrometry (LC-MS and GC–MS), Fourier transform infrared spectroscopy (FTIR) and Nuclear magnetic resonance (NMR) are the main platforms for identification of plant and pathogen derived biomarkers for disease (Pontes *et al.*, 2016; Chen *et al.*, 2017). Volatile Organic Compounds (VOC) represent a plant phenotypic trait that readily responds to disease, and while the pathogen-specificity of these signals has been questioned (Jansen *et al.*, 2011) they could allow non-destructive, rapid detection of a diseased condition in host organisms (Ghaffari *et al.*, 2012). VOCs profiles are usually analysed using dynamic sampling coupled with GC–MS (Jansen *et al.*, 2011), but recent advances in sensors and machine learning technologies have supported development of an alternative approach, the electronic nose (eNose), for detection, recognition and classification of VOC signature patterns (Karakaya *et al.*, 2020). The ENose instrumentation is inspired by the biological olfactory system, and comprises a multisensor array that can detect chemical components and software developed for pattern recognition, allowing non-invasive and inexpensive analysis of VOC profiles (Ghaffari *et al.*, 2012). Cellini *et al.* (2017) reviewed the use of an ENose for plant disease diagnosis and pest detection, concluding that the use of this technology may assist, direct and optimise traditionally adopted diagnostic techniques despite the disadvantages that include low sensitivity and specificity in comparison with microbiological and molecular methods.

Swiecki *et al.* (2018) trained dogs to recognize *Phytophthora* in soil and soil-water suspensions, individual infected plants and plant parts, and discriminate the pathogen odour from other scents (see also Angle *et al.*, 2016). Pathogen-associated changes in phenotype can also be studied using non-destructive imaging and sensor-based detection of anatomical, physiological and biochemical plant properties (Mahlein, 2016; Mishra *et al.*, 2020).

Nanoparticles

Nanotechnology, based on particles smaller than 100 nm, is a growing interdisciplinary science that combines knowledge from different fields including biology, chemistry, physics and engineering (Davari *et al.*, 2017). Its application may lead to the development of improved methods and strategies for disease and pathogen identification (Prasad *et al.*, 2017; Worrall *et al.*, 2018). The commercially available, manufactured nanoparticles (NPs), Zn NPs and ZnO NPs, were found to inhibit spore germination of *Peronospora tabacina* and tobacco leaf infection at 8 and 10 mg L^{-1}, respectively, indicating the potential of NPs as economic, low-dose and potentially non-persistent anti-microbial agents against this oomycete (Wagner *et al.*, 2016). Nandini *et al.* (2017) provided evidence that Selenium nanoparticles produced by *Trichoderma* could suppress the growth, sporulation and zoospore viability of *Sclerospora graminicola* that causes downy mildew on pearl millet (*Pennisetum glaucum*). In aquaculture, nanoparticles have been used for disease diagnosis, vaccine development and to combat antibiotic resistance in bacteria (Shaalan *et al.*, 2016). Shaalan *et al.* (2017) found that silver and zinc oxide nanoparticles showed an inhibitory effect against *A. invadans*, providing evidence for their potential as a tool against this pathogen in aquaculture. Apart from the potential advantages, there are numerous downsides to the use of nanoparticles in terrestrial and aquatic environments including nanoparticle toxicity, exposure hazard, bioaccumulation in food crops and risk of carcinogenesis. In addition, the high set-up costs and problematic manufacturing processes are current challenges to the wider use of nanotechnology (Agrawal and Rathore, 2014).

Open access to real time data

Successful control of international and national dispersal of oomycetes necessitates efficient routines for inspection and monitoring, coupled with a thorough understanding of pathogen traits. In order to minimise the spread of living oomycetes, qualified professionals are needed, with capacity to use suitable tools and technologies to detect, diagnose, demarcate and map newly emerged and re-emerging pathogens, using both existing databases and newly collected information (Bonants *et al.*, 2013). A complete assessment, protection and management protocol should include open access to epidemiological databases, which should be published rapidly and updated as required, in Geographic Information Systems (GIS) Software. An updated epidemiological geographic database, together with vegetation and climatic data can be used in the rapid development of predictive models of the mode and pathways of introduction of invasive alien pathogens (National Research Council, 2002). Internet websites and social media platforms have become increasingly important in the reporting and sharing of information in real time and in enabling awareness raising actions, as well as interactive, collaborative and rapid responses to combat new or re-emerging oomycetes diseases (e.g., the "SOD Blitzes" at University of Berkeley, https://nature.berkeley.edu/garbelottowp/).

6. Concluding remarks

In terrestrial and aquatic food production systems, the current biosecurity protocols and legislation have largely failed to curb the problems caused by oomycete pathogens. In testimony to the severity of this situation, the first report of *P. ramorum* in Del Norte, California, was mere weeks prior to completing this article (Garbelotto *et al.*, 2021). Oomycetes are well adapted to the pathogen life strategy and the intimate relation between their spread and human activities, especially the ever-increasing international trade and transport systems, makes control of these pathogens challenging. Progress can nonetheless be made through increased awareness among stakeholders and consumers, with the research community having great responsibility in supporting knowledge transfer across the academy–society interface. Contemporary research should aim to improve the accuracy and sophistication of testing and detection methods for oomycete pathogens. Increased allocation of governmental and private resources to research and development activities, as well as to phytosanitary infrastructures, is also urgently needed to strengthen the IPM strategies through environmentally sound and socially acceptable tools and measures.

Urgent action is required in order to prevent further and continued global spread of oomycete pathogens. Moving forward, in the EU, plant-trade legislation has recently become more robust, and an equally firm approach to aquaculture regulation is also warranted. The recent assembly of an online database EUROPHYT collating outbreak data on plant-pathogenic oomycetes is proving highly beneficial for global disease monitoring. We recommend that a corresponding resource be produced for aquaculture pathogens.

Declaration of competing interests

None declared.

Acknowledgements

This work was financially supported by the European Union's Horizon 2020 (H2020) Marie Skłodowska-Curie Actions Innovative Training Networks PROTECTA H2020-MSCA-ITN-2017 call, under grant agreement number 766048 (CBC, NLG, & MES), Swedish Research Council Formas grant 2018-00966 and Nordic Forest Research (SNS-123) (JW), Prime Minister Fellowship, Bangladesh (TR), NERC [NE/R008140/1 (DSJ & PvW)], University of Aberdeen (SW & PvW), the BBSRC [BB/P020224/1, BB/M026566/1 (PvW)], Newton Fund GRP Aquaculture [BB/N005058/1 (PvW)]. We would like to thank Dr Debbie McLaggan (UoA) for proof-reading the manuscript.

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II

Received: 8 November 2023 | Revised: 13 June 2024 | Accepted: 1 July 2024

DOI: 10.1111/efp.12878

Forest Pathology WILEY

REVIEW ARTICLE

Control and management of *Phytophthora* damage in forestry—A systematic mapping study

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Funding information
European Union's Horizon 2020 (H2020) Marie Skłodowska-Curie Actions Innovative Training Networks PROTECTA H2020-MSCA-ITN-2017 call, under grant agreement number, Grant/Award Number: 766048; European Union's Horizon 2020 Research and Innovation Programme under the Marie Skłodowska-Curie, Grant/Award Number: 845419

Abstract

Plant pathogens in the genus *Phytophthora* are a severe threat to forest plantations, ecosystems and tree nurseries. Especially in forests and natural ecosystems, there is a lack of effective measures to control and manage these pathogens. In this study, we conducted a systematic mapping review to collate evidence regarding the control and management of forest *Phytophthora* in different production settings and ecosystems. The study aimed to reveal possible knowledge gaps, thus guiding future research priorities. We extracted information from nine databases, limiting the search to studies published during the time period from January 2010 to December 2022. The articles were shared between three reviewers who classified the reports using a set of inclusion/exclusion criteria. A total of 561 articles were included and mapped in a database using pre-defined coding, and critically appraised for relevance and reliability. The analysis showed that biological or bio-based measures were the most studied interventions, followed by genetics or breeding programmes, whereas chemical and silvicultural management approaches were less studied. Most of the studies were conducted in Europe, North America, Australia and New Zealand. *Phytophthora cinnamomi* has been the most studied species followed by *P. ramorum*. We discuss the current knowledge gaps in the implementation of existing research, likely due to a lack of holistic understanding of the processes over time and space, and suggest future research that is needed to manage *Phytophthora* in forest ecosystems.

KEYWORDS
biocontrol mechanisms, breeding programs, control strategies, oomycetes, pesticides, *Phytophthora* damage

1 | INTRODUCTION

Throughout the world, pathogens in the genus *Phytophthora* (Oomycetes) cause significant yield losses in tree nurseries, natural forests and plantations (Benavent-Celma et al., 2022; Hansen, 2015; Jung et al., 2018; Shamoun et al., 2018). Moreover, these species have been linked to mortality and reduced stability of trees and forests in urban and peri-urban settings (Hansen, 2015; Hayden, Garbelotto, et al., 2013; Jung et al., 2018) and conservation areas (Hansen, 2015; Jung et al., 2018; Štraus et al., 2023). Trees can get infected at any age, with infections leading to the expression of diverse symptoms, such as root and collar rot, necrotic cankers and fine root deterioration, leaf chlorosis and necrosis, crown transparency, bleeding bark cankers and plant death,

depending on the specific pathogen and host involved (Erwin & Ribeiro, 1996; Jung et al., 2018). However, infections can also be asymptomatic, especially in young plants, which complicates the detection of *Phytophthora* in plants for planting (Brasier, 2008; Jung et al., 2016, 2018). Trade in living plants and plant products has been identified as the main pathway for the introduction of newly recognized pathogens, and asymptomatic plant transportation can easily escape controls at borders and custom inspections (Benavent-Celma et al., 2022; Brasier, 2008; Jung et al., 2018; Scott, Burgess, & Hardy, 2013; Shamoun et al., 2018). Once established in nature, *Phytophthora* species may become invasive and have major ecological and economic consequences, as is evident from *Phytophthora* introductions that have devastated forests in the United Kingdom, Australia and the United States (Garbelotto et al., 2001; Hee et al., 2013; King et al., 2015; Pérez-Sierra et al., 2022, 2024). In Europe, nursery surveys have detected widespread and almost ubiquitous infestations with more than 20 *Phytophthora* species in field- and container-grown nursery stock of forest trees, ornamental plants and irrigation systems (Jung et al., 2016), further illustrating the extent of the problem.

The lifecycle of *Phytophthora* species makes the control and management of these pathogens highly challenging. The motile zoospores enable rapid infection of new host plants and dormant resting structures (chlamydospores, hyphal aggregations and oospores) allow them to survive unfavourable environmental conditions over long periods (Erwin & Ribeiro, 1996; Judelson & Blanco, 2005; Jung et al., 2018; McCarren et al., 2005). As oomycetes, *Phytophthora* species exhibit resistance to fungicides, especially those designed to target fungal physiology and impact cell structures. This resistance is due to fundamental differences in physiology and biochemistry between oomycetes and fungi (Adomako et al., 2017; Hu et al., 2008; Olson & Benson, 2013), which adds to the difficulty in managing these pathogens in plant production systems. Potential management options include silvicultural measures (Daniels et al., 2022; Goheen et al., 2017; Hansen et al., 2019), chemical treatments (Garbelotto et al., 2009; Hansen et al., 2019; Hardy et al., 2001; Silva et al., 2016), biological or bio-based methods and deployment of genetic resistance genes or resistance breeding (Hayden, Garbelotto, et al., 2013; Jung et al., 2018; Santos et al., 2015). Research evidence showing the applicability and efficiency of these measures has accumulated over several decades, but it comes from different hosts and *Phytophthora* species interactions, experimental settings and continents. A systematic overview of these studies will help in making recommendations for best practices in different situations and identify the possible research gaps where experimental evidence is missing.

Systematic mapping is an evidence collation method that has recently emerged in environmental sciences (James et al., 2016). Systematic mapping (scoping) studies aim to outline the research area by searching, classifying and tallying the available literature on a topic, resulting in an inventory of publications that cover the different categories related to the topic (Petersen et al., 2015). A mapping inventory enables the discovery of research trends, biases and gaps, providing valuable information for a systematic review. The goal and approach of systematic mapping differ from a systematic review: unlike a systematic review, systematic mapping does not attempt to answer specific research questions by evaluating the evidence but instead collates, describes and catalogues available evidence (e.g. primary, secondary, theoretical and economic), aiming at revealing the structure of the research related to the topic or question of interest (James et al., 2016). Importantly, a mapping approach does not necessarily include a quality assessment (Petersen et al., 2015). The method is particularly suitable in cases where systematic review is challenging, for example, due to the heterogeneous quality of the available papers, due to quantitative and qualitative research, and different methodologies and outcomes (James et al., 2016). Here, we used a systematic mapping approach to collate evidence regarding the management of forest Phytophthoras across diverse production settings and ecosystems, including forest nurseries, production forests and natural ecosystems. Our study addressed two questions:

1. Which control or management measures, used in forests and nurseries, have been most thoroughly addressed in original research studies, and which require more investigation?
2. Is the research biased towards specific regions, environments (nursery, plantation, natural forests) or species (host tree and *Phytophthora* species)?

The study aimed to reveal knowledge gaps, providing insights into potential future research priorities.

2 | METHODS

2.1 | Information sources and literature search

We followed the Collaboration for Environmental Evidence guidelines and Standards for Evidence Synthesis in Environmental Management (Version 5.1) (Pullin et al., 2023) to make the process more reliable when setting up the eligibility criteria. These included the PICO framework structure of the review question, details on PICO key elements (Problem or Population, Intervention, Comparison, control or comparator, and Outcomes), as well as formulating the general questions addressed to compile the systematic map report. We used the following databases to find relevant articles: Web of Science Core Collection, BIOSIS Citation Index, CABI CAB Abstracts, Current Contents Connect, Data Citation Index, KCI Korean Journal Database, MEDLINE (gateway.ovid.com), Russian Science Citation Index and SciELO Citation Index. Search results were limited to studies published between January 2010 and December 2022, aiming to focus on recent developments in research that display the latest changes in forest management priorities and legislation up to 2022. This decision aligns with guidance on setting limits in literature searches to ensure focused and timely

reviews (Cooper et al., 2018; Helbach et al., 2022). Searches were conducted in March 2023, and the search language was set as Auto.

2.2 | Search strategy and selection process

We included search terms for environments (forest settings), pathogens (*Phytophthora* species), measures (chemical, biological, breeding/genetics, silvicultural) and outcomes (symptoms, disease damage, susceptibility, resistance) in the searches, aiming to obtain a search that is comprehensive enough to adequately cover the topic of interest. The search strings were composed as ((forest*) AND (tree* OR seedling*) AND (*Phytophthora*) AND (manage* OR control* OR measure* OR intervention*) AND (silvicultur* OR chemical* OR natural OR biological OR bio-based OR phosph* OR breeding) AND (symptom* OR disease* OR damage OR susceptib* OR resistance OR protecti*)). The term 'Forest*', was selected to encompass different forest-related environments, including plantations, urban and peri-urban areas, and natural ecosystems. To ensure the inclusion of nurseries, terms like 'tree*' and 'seedling*' were also included in the search. The term '*Phytophthora*' was used to refer to all *Phytophthora* species in the search. Although not fully comprehensive, we believe that a representative collection of the published scientific literature covering management of forest *Phytophthora* in different production settings and ecosystems was captured.

2.3 | Eligibility criteria

To structure and focus the literature retrieval, we used the PICO framework (Schardt et al., 2007) where Population (P) = forest (tree(s) or seedling(s)) and *Phytophthora*; Intervention (I) = management/control, measure(s) or intervention(s): silviculture/silvicultural, chemical(s), natural, phosphite, biological/bio-based, genetic (resistance) or breeding; Comparator (C) = no interventions or variation in them; and Outcomes (O) = symptom(s), disease, damage, susceptible/susceptibility, resistant/resistance or protection/protective.

We defined three inclusion criteria: (1) *Phytophthora* management studies/trials, (2) relevance for forest ecosystems or forestry and (3) inclusion of settings such as forest settings, nurseries, experimental orchards, greenhouses and laboratory facilities. Articles failing to meet at least the first two of the three criteria were excluded. Articles were excluded if they met any of the following exclusion criteria: (1) published in a language other than English; (2) not focused on forest *Phytophthora* management or control measures or (3) not dealing with seedlings, trees or shrubs.

2.4 | Data extraction

Data were collected and extracted by a team of three independent reviewers, and the information was organized in a common file according to 12 coding variables. The results of the literature search, motivations for rejections and the categorization of the studies included are presented as Table S1.

2.5 | Data analysis

We conducted descriptive analyses to summarize characteristics of the studies used in the analyses, including geographic distribution, type of management or control measures executed, study settings or facilities and *Phytophthora* species evaluated. Analyses were performed in R environment v. 4.3.1 (R Core Team, 2022) by grouping studies by outcome categories and examining characteristics of the studies mentioned above. Visualization of the data was done using the ggplot2 package v. 3.4.1 (Wickham et al., 2023).

3 | RESULTS

In total, 561 references passed the initial filtering process. After removing duplicates and papers that did not meet the criteria, a total of 126 papers were included in the final analysis (Dataset S2). The selection of studies is summarized in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram in Figure 1.

3.1 | Distribution of publications across the intervention categories

The most thoroughly addressed management or control measures in original research studies between 2010 and 2022 focused on biological or bio-based measures (32.5%) followed by genetics or breeding programmes (27.8%), chemical control (27%) and finally silvicultural approaches (5.5%). Only a few of the selected studies (7.2%) used more than one approach, for example, a combination of biological or chemical methods with silviculture (Figure 2).

3.2 | Biological or bio-based measures

The studies focusing on biological or bio-based measures discussed approaches such as the use of plant extracts that can enhance host defence responses and tolerance to *Phytophthora* species (Hao et al., 2012) or secondary metabolites produced by the host plant during interactions with endophytic fungi, bacteria or mycoviruses (i.e. viruses that infect fungi) (Lackus et al., 2018; Macías-Rubalcava et al., 2010). These interactions can also initiate the release of volatile compounds and elicitins, which trigger host defence responses and can promote resistance to *Phytophthora* species (Medeira et al., 2012; Poimala et al., 2022; Tellenbach et al., 2013; Xie et al., 2015). Other studies tested the antimicrobial activity of bacterial and fungal extracts against *Phytophthora* species (Lawrence et al., 2019; Lefort et al., 2013;

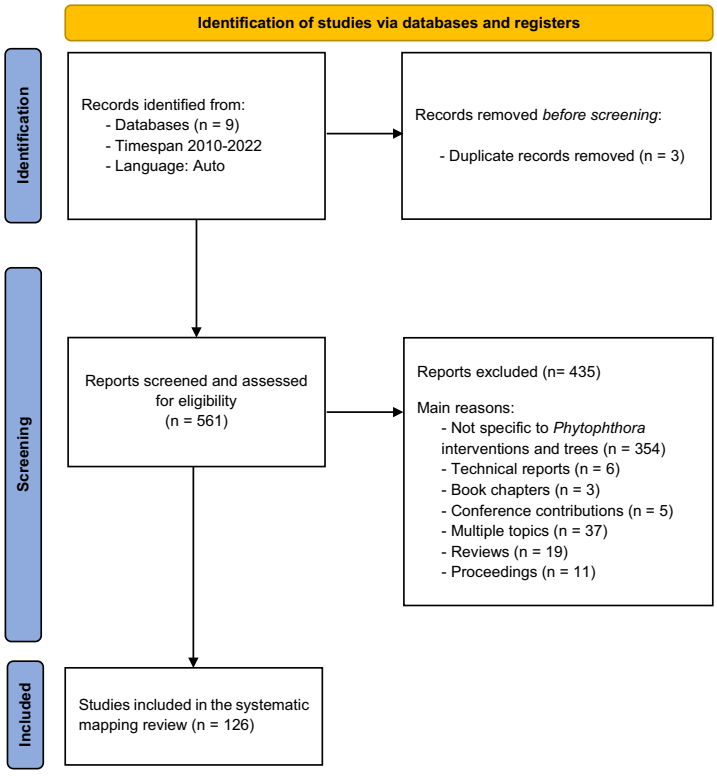

FIGURE 1 PRISMA flow diagram of the study (based on Page et al., 2021).

Masi et al., 2016; Mondol et al., 2016). Finally, some of the articles included the application of bio-fertilizers to reduce plant vulnerability to *Phytophthora* species (López-Sánchez et al., 2022) and bio-fumigation to control vegetative and reproductive structures (Morales-Rodríguez et al., 2016; Ríos et al., 2016, 2017). Specifically, these studies described measures such as inhibition of mycelial growth or sporangia and gametangium (oogonium and antheridia) formation and reducing the motility of zoospores and their germination rate.

3.3 | Genetic or breeding measures

Another common topic was the genetic basis of resistance and plant defence mechanisms against *Phytophthora* (Figure 2). Several of these studies focused on the evaluation and comparison of mechanisms of susceptibility and resistance to *Phytophthora* infections in host trees. To assess these mechanisms, many experiments used an approach based on plant screening by inoculation aiming to identify and select resistant individuals within susceptible taxa. In some cases, genes encoding certain antifungal proteins were introduced to boost resistance (Abraham et al., 2013). For example, the *Raphanus sativus*-antifungal protein 2 (Rs-AFP2) was introduced into *Eucalyptus urophylla* aiming to enhance resistance to *Phytophthora capsici* (Ouyang et al., 2012). Other screening programmes were focused on selecting plants that were most likely to produce active secondary compounds with an anti-*Phytophthora* activity (e.g. Lawrence et al., 2019).

3.4 | Chemical measures

In studies on the use of chemical management approaches, the primary focus was on the evaluation and comparison of direct activities, and effectiveness (Romero et al., 2019) (Horner et al., 2015; Miyake & Nagai, 2017) of agrochemicals to suppress or slow down the development of the disease. The aspects examined included uptake of products (Rolando et al., 2017), phytotoxicity (Horner et al., 2015; Scott et al., 2016; Scott, Dell, et al., 2013), resistance of pathogen species to fungicides (Silva et al., 2016), inhibition of mycelial growth (González et al., 2017; Miyake & Nagai, 2017; Singh et al., 2010), effect on sporangia and oospore formation (Miyake & Nagai, 2017; Serrano et al., 2011) or zoospore germination (Miyake & Nagai, 2017). Whilst studies focusing on tree treatments investigated the efficacy of chemicals to reduce disease incidence and severity (Reglinski et al., 2010), measured as

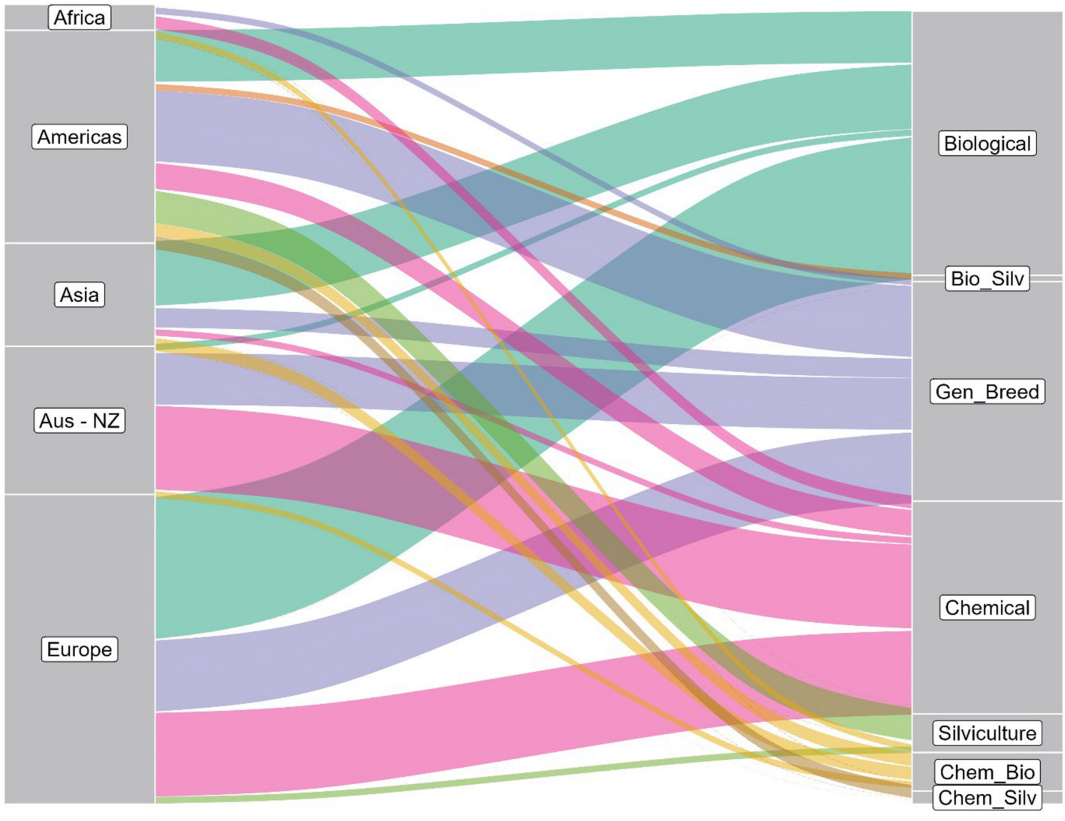

FIGURE 2 The most assessed approaches by geographic distribution are included in the systematic mapping review. Aus – NZ, Australia & New Zealand; Bio_Silv, Biological and Silvicultural; Chem_Bio, Chemical and Biological; Chem_Silv, Chemical and Silvicultural; Gen_Breed, Genetics & Breeding.

the degree of damage (Swiecki & Bernhardt, 2017), root density and infection rates (Oszako et al., 2018), canopy health scores (Horner et al., 2015), *damping-off* severity (Januszek et al., 2014), lesion activity, progression and length (Rolando et al., 2014; Scott et al., 2016), host mortality rates (Stasikowski et al., 2014; Swiecki & Bernhardt, 2017), defence responses and disease progress after treatments (Hansen et al., 2019; Horner et al., 2015; Romero et al., 2019).

Overall, systemic fungicides such as metalaxyl, fosetyl-Al and potassium phosphite were the most frequently utilized, constituting 60% of the included studies, probably because systemic action enables translocation of active ingredients throughout the plant, ensuring effective movement to all host tissues. When applied at low concentrations, some systemic fungicides may activate defence responses (Hardy et al., 2001), making these products highly cost-effective. Tables comprising the most commonly studied chemical products and inorganic amendments have been listed in Appendices 1 and 2.

3.5 | Silvicultural measures

The silvicultural approaches addressed in the analysed publications included strategies such as containment measures to mitigate the chances of spread by limiting access to forests or natural environments and the establishment of quarantine areas (Daniels et al., 2022; Goheen et al., 2017; Valachovic et al., 2017). Early detection methods, encompassing aerial and ground surveys, as well as stream baitings were carried out (Goheen et al., 2017; Kanaskie et al., 2011). Demarcation of infested areas, and eradication treatments involving herbicide applications, uprooting, clear-cutting and burning were also included (Goheen et al., 2017; Swiecki & Bernhardt, 2017). Additionally, the establishment of buffer areas beyond the disease front was recommended, with the removal of host plants in areas where disease spread was likely (Goheen et al., 2017; O'Hanlon et al., 2018; Valachovic et al., 2017). Research and continuous monitoring were also emphasized as crucial components of these comprehensive management strategies (Goheen et al., 2017;

Kanaskie et al., 2011; O'Hanlon et al., 2018; Valachovic et al., 2017). Most of the analysed silvicultural measures aimed to control *P. ramorum*, *P. cinnamomi* or *P. cactorum*.

Under nursery conditions, root pruning has been tested to control *P. cactorum* infection of *Quercus robur* seedlings (Łakomy et al., 2019). Measures studied to control the spread of *P. ramorum* have included physical removal of hosts, herbicide applications, with cutting and burning of hosts within a buffer area of 100 m of a known disease outbreak (Goheen et al., 2017; Valachovic et al., 2017), and monitoring using baitings (i.e. a laboratory technique which consists of soil sample submerged in water with pieces of the bait (tree leaves) floated on the water surface) and, more recently, high resolution digital aerial imagery. Post-treatment monitoring conducted over several years has revealed that, despite elimination of the pathogen from initially affected sites, the spread could continue (Daniels et al., 2022; Goheen et al., 2017; Hansen et al., 2019; Valachovic et al., 2017).

3.6 | Geographic bias among the published studies

Most of the captured studies were carried out in Europe (38.9%), followed by both Americas (26.19%), Australia and New Zealand (19.04%), Asia (12.7%) and Africa (3.17%). The majority of the studies addressing biological or bio-based measures were carried out in Europe (22 studies); chemical treatments were mainly studied in Australia and New Zealand (14 studies) and Europe (13 studies); genetics and breeding in Europe (11 studies) and the Americas (11 studies). While the few studies on silvicultural practices for the control and management of *Phytophthora* were carried out in the Americas (8 studies) and Europe (2 studies).

3.7 | Study environments

The studies selected for this review were carried out in laboratory facilities (31 articles), greenhouses (14 articles), forest nurseries (9 articles), and in the field (19 articles). A total of 53 of the included experiments were accomplished by a combination of two or more facilities such as laboratory and greenhouse or laboratory, greenhouse and field.

3.8 | *Phytophthora* and host tree species or genera in the included studies

The publications included in this work covered a total of 32 *Phytophthora* species. The most commonly studied pathogen species was *P. cinnamomi*, followed by *P. ramorum*, *P. palmivora* and *P. cactorum* (Table 1). Other species were included in fewer than 6% of studies (Table 1).

The most common host species of *P. cinnamomi* included in the articles were in the genus *Quercus*, followed by *Eucalyptus* spp., *Banksia* spp., *Castanea* spp. and gymnosperms such as *Agathis australis* (kauri). The host species of *P. ramorum* were most commonly trees in the genus *Notholicarpus*, followed by *Umbellularia californica*, *Quercus agrifolia*, *Quercus kelloggii*, *Rhododendron* spp. and conifers such as *Larix kaempferi*. The host species of *P. palmivora* were most commonly trees in the genus *Hevea*, followed by *Durio* spp., *Ficus* spp., *Acer* spp., *Olea* spp. and conifers such as *Tsuga heterophylla*. The host species of *P. cactorum*, were most commonly trees in the genus *Quercus*, followed by *Fagus sylvatica*, *Acer* spp., *Populus* spp. and conifers such as *Pinus sylvestris*, *Picea abies*, *Abies fraseri* and *Pinus radiata*.

TABLE 1 Number and percentage of studies on the most representative *Phytophthora* species included in the systematic mapping review.

Phytophthora species	No. studies	Percentage (%)
Phytophthora cinnamomi	56	44.4
Phytophthora ramorum	17	13.5
Phytophthora cactorum; *Phytophthora palmivora*	10	7.9
Phytophthora pluvialis	8	6.3
Phytophthora plurivora	7	5.5
Phytophthora alni; *Phytophthora capsici*; Multiple species	5	4
Phytophthora agathidicida; *Phytophthora parasitica*; *Phytophthora* x *cambivora*	4	3.2

4 | DISCUSSION

The systematic mapping indicated that the most thoroughly studied control or management methods against *Phytophthora* species in forestry settings over the last 12 years have been biological or bio-based measures. The studied solutions include use of bacteria or fungi as biocontrol agents against different *Phytophthora* species, and employing different modes of action (e.g. induction of plant defences, antibiosis or competition). Fungi from the genus *Trichoderma* spp. are considered strong candidates for future integrated pest management (IPM) strategies (Lefort et al., 2013; Oszako et al., 2019; Ruiz-Gómez et al., 2019; Ruiz-Gómez & Miguel-Rojas, 2021). Nevertheless, current research on interactions between beneficial microorganisms and host species is insufficient for evaluating the effectiveness and feasibility of implementing biological control measures in *Phytophthora*-affected forest settings. The majority of the studies selected were conducted in laboratory and greenhouse settings, and rarely in field conditions. Cabrera-Puerto et al. (2023) and Fuller et al. (2023) highlighted the need for additional research to determine effective methods for the use of biological control agents in forest settings and to understand the potential implications, whether positive or negative, of these agents on non-target microbial species in forest ecosystems. More research is needed to, for example, understand the influence of genetic variability within the species on responses

to *Trichoderma* spp. and bacterial colonization. There is also a need for more research to clarify the mechanisms of induced plant resistance, including studies at the physiological, biochemical and genetic levels to explain this phenomenon. A comprehensive understanding of how microbial biocontrol agents interact with their host and other microbes at the cellular and molecular levels will facilitate the screening of effective and eco-friendly bioagents (Giachero et al., 2022; Siah et al., 2018; Zehra et al., 2021). An improved understanding of the behaviour of microorganisms in their natural habitat would also improve assessments of environmental and human health risks. Future studies should also assess the long-term sustainability of biocontrol approaches.

We found that a considerable share of research has focused on the genetics of *Phytophthora* resistance in a broad array of economically and ecologically important broadleaf and conifer species (e.g. *Quercus* spp., *Castanea* spp., *Eucalyptus* spp., *Banksia* spp., *Fagus* spp., *Notholicarpus* spp., *Agathis australis*, *Pinus* spp., *Picea abies*, *Abies fraseri*), and the results from these studies should provide good support for resistance breeding programs. The introduction of more resistant tree genotypes is a promising avenue to control *Phytophthora* diseases in planted forests (Miranda-Fontaíña et al., 2007; Santos et al., 2015; Stukely et al., 2007). For example, seedling progeny resistant to *P. lateralis* in the conifer species *Chamaecyparis lawsoniana* (Port-Orford-cedar) have been effectively deployed for restoration and reforestation in the Pacific Northwest region of the United States (Sniezko et al., 2020; Sniezko & Dana Nelson, 2022). Further, Santos et al. (2017) and Zhebentyayeva et al. (2019) developed the first interspecific genetic map for chestnuts, enabling the identification of Quantitative Trait Loci (QTL) for *P. cinnamomi* resistance. These studies provide valuable genomic resources for enhancing resistance in chestnuts. Recent investigations utilizing proteomics techniques have identified disease-related genes in the *P. ramorum*-tanoak and *P. cinnamomi*-cork oak pathosystems (Coelho & Schütz, 2022; Hayden et al., 2014), serving as markers for early detection of host-pathogen interactions. Additionally, they provide valuable insights for subsequent experiments employing novel genome editing tools such as CRISPR-Cas (Koonin & Makarova, 2009), which can be used to target the active genes involved in the infection cycle, aiming to annotate and alter their function. Together with RNA interference (gene silencing) and nanotechnology, CRISPR-Cas hold promise for targeting disease-resistant genes or disrupting susceptible genes in forest settings to enhance resistance against *Phytophthora* species (Javed et al., 2021). CRISPR-Cas genome editing has been successfully used in a limited number of model *Phytophthora* species such as *P. sojae* (Fang et al., 2017; Fang & Tyler, 2016), *P. capsici* (Wang et al., 2018), *P. palmivora* (Gumtow et al., 2018) and *P. agathidicida* (Hayhurst, 2023), to investigate the roles of critical genes. Still, some technical limitations must be overcome, including the long time period needed to select tolerant and resistant tree families. Moreover, the genetic variation in pathogen populations complicates the selection of resistant host families (Eikemo et al., 2004).

A large proportion of the studies analysed here addressed the use of chemical treatments against *Phytophthora* diseases, most likely because the utilization of agrochemicals has proven to be effective even though legislation is shifting to more sustainable approaches (Booker, 2021; EU, 2019, 2023). Several of the studies focused on the application and assessment of potassium phosphite, used as an aerial foliar spray over large areas (Dalio et al., 2014; Hardy et al., 2001; Solla et al., 2021) or as trunk injections (Brandano et al., 2023; Horner et al., 2015; Horner & Hough, 2013; Solla et al., 2021). The use of phosphite treatments to suppress *Phytophthora* infections in forestry has in many cases been complicated by regulations, phosphites have been registered to markets either as fungicides, fertilizers or biostimulants, and for example in Spain, potassium phosphite products registered as fertilizers have been prohibited (González et al., 2017, 2020). The analysed studies also point out concerns regarding phytotoxicity when applied in higher doses (Horner et al., 2015; Manghi et al., 2021). Unlike phosphite, which stimulates plant defence against *Phytophthora* species, most fungicides can have persistent environmental effects. The selected literature revealed a trend of shifting from 'older' fungicides to other chemicals, such as cuprous oxide, metalaxyl-M and copper hydroxide, in combination with some *Trichoderma* spp., as well as the usage of inorganic amendments and Brassica-based biofumigation, seeking to innovate and adapt the chemical treatments to the current legislation (Agbeniyi et al., 2014; Fraser et al., 2022; Morales-Rodríguez et al., 2016; Ríos et al., 2017; Rolando et al., 2019; Serrano et al., 2011; Singh et al., 2010). Despite the associated risks (Benavent-Celma et al., 2022; Garbelotto et al., 2009; Hayden, Hardy, & Garbelotto, 2013; Horner et al., 2015; Manghi et al., 2021), these treatments have proven effective in controlling diseases caused by *Phytophthora*. Considering the newly imposed regulations, silicate-based mulch could prove to be a valuable alternative (Dann & Le, 2017). New fungicides such as ethaboxam, fluopicolide, mandipropamid and oxathiapiprolin have been proven effective in reducing *P. cinnamomi* in avocados (Belisle et al., 2019) and oxathiapiprolin was very effective against *P. agathidicida* in *Agathis* (Lacey et al., 2021). Moreover, Khdiar et al. (2023) identified calcium chelate as a potential product capable of triggering plant defence responses against plant pathogens, specifically *P. cinnamomi*. Likewise, the use of green pesticides, such as those based on the cinnamate anion and bioactive metabolites produced by fungi, have shown an inhibition rate comparable to certain fungicides against *Phytophthora* species, including *P. cinnamomi* and *P.* × *cambivora*, when applied in controlled chamber conditions (Bugatti et al., 2019; Evidente et al., 2011). Further, antifungal compounds of natural and synthetic origin, such as lipopeptides, sesquiterpenoids and two synthetic derivatives (diol and dicarboxylic acid) of polygodial, have demonstrated effectiveness in targeting multiple life stages of *Phytophthora* species (De Zoysa et al., 2023).

The paucity of research on silvicultural methods to control *Phytophthora* spread may be due to the inefficiency of these methods or the high financial costs involved (Goheen et al., 2017; Hoover & Bates, 2012). Studies of silvicultural methods generally demand long-term field studies, which is challenging when research is organized and funded in short projects. Further, it is plausible that the limited amount of research on silvicultural approaches

reflects the exclusion of grey literature, such as Best Management Practices Handbooks, from our analysis. The compiled literature lacks specific studies on silvicultural management of *P. cinnamomi* in Western Australia. However, it is important to briefly mention that implemented strategies include physical removal or herbicide treatment of vegetation, fungicide application to surface and subsurface areas, and the installation of physical barriers to prevent root-to-root spread (Hayden, Hardy, & Garbelotto, 2013; O'Brien & Hardy, 2014). These measures are considered effective for addressing localized infections that have the potential to spread and become more widespread (O'Brien & Hardy, 2014). While the silviculture utilized to control *P. ramorum* focused on reducing primary infection by limiting forest stand connectivity and treating or removing stumps during site preparation, secondary infection reduction was achieved through planting mixed species forests. Even though these silvicultural methods may be considered drastic, they have demonstrated efficacy in enhancing forest resilience to pathogens (Roberts et al., 2020). In the selected literature, silvicultural approaches were studied to develop effective long-term management strategies to contain *P. ramorum* spread in California and Oregon (Goheen et al., 2017; Hansen et al., 2019; Kanaskie et al., 2011). Complete eradication of the inoculum established in forests is known to be very difficult, but Daniels et al. (2022) confirmed the effectiveness of current treatments in reducing the inoculum in understory plants. The study indicated that while wildfire improved understory treatment, it did not lead to a reduction in infected tanoak trees. Nevertheless, eradication efforts have likely considerably slowed down the epidemic (Daniels et al., 2022). However, further research is needed to understand the potential impacts of the NA1 and EU1 lineages of *P. ramorum* and support appropriate control measures for future introductions of non-native pathogens (Daniels et al., 2022; Goheen et al., 2017; Hansen et al., 2019). In California, recent studies are focused on advancing forest disease and wildfire management goals. Quiroga et al. (2023) demonstrated that utilizing common forest fuels and disease prevention treatments effectively addressed numerous stand-level impacts of sudden oak death without causing significant loss of standing basal area. These results indicated that diverse treatment approaches in various disease contexts have resulted in changes in forest structure and host reduction.

In Ireland and the United Kingdom, O'Hanlon et al. (2018) demonstrated the effectiveness of eradication treatments applied to manage *P. ramorum* and continued surveillance, particularly since the initial discoveries in *Larix kaempferi* forests. Additionally, it emphasizes the importance of drawing lessons from the management program in Oregon and applying them to the situations in Ireland and the United Kingdom. More research is needed to address the long-distance dispersal of *P. ramorum* (Peterson et al., 2015), its ability to asymptomatically infect *L. kaempferi* (Harris & Webber, 2016), and challenges in isolating *P. ramorum* cultures from *L. kaempferi* material (O'Hanlon et al., 2018).

In France, eradication measures were implemented in *L. kaempferi* plantations to limit the spread of the epidemic. Continuous monitoring was conducted on native woody hosts within infected clear-cut larch stands and around seven ornamental nurseries that had previously experienced *P. ramorum* infections. After implementing eradication measures, the pathogen was only detected on rhododendrons and chestnut trees (*Castanea sativa* Mill.) near the outbreak areas, presenting the highest risk for the survival of *P. ramorum* in the region, particularly considering that chestnut trees represent 21%–25% of the forest (Beltran et al., 2024).

The selection of studies revealed a geographic bias in global research activities, with European and North American countries, together with New Zealand and Australia producing most of the research. While these biases may mainly reflect the generally high investments in research in these countries, they may also result from the compelling need to discover new solutions to increasing problems related to introduced and invasive *Phytophthora* species. These problems include sudden oak death caused by *P. ramorum* (Rizzo & Garbelotto, 2003), holm oak decline driven by *P. cinnamomi* (Brasier et al., 1993; Camilo-Alves et al., 2013; Frisullo et al., 2018), red needle cast of pine caused by *P. pluvialis* (Dick et al., 2014) and kauri dieback caused by *P. agathidicida* (Bradshaw et al., 2020). In parallel, the lower number of studies focusing on genetics and breeding programs in Asia may reflect the less urgent problems with *Phytophthora* damage in forests, although more research would be needed to test this hypothesis. Recent population studies indicate that some of the tree-pathogenic *Phytophthora* species, such as *P. cinnamomi* and *P. ramorum*, likely originated in East Asia (Jung et al., 2021; Shakya et al., 2021), suggesting that resistance may have developed in trees through co-evolution. Our research highlights also the lack of investigation into the effectiveness of control methods for *Phytophthora* species in Africa.

The fact that most of the selected studies were focused on *P. cinnamomi* and *P. ramorum* was not surprising, considering that these species are among the most harmful forest *Phytophthora* species (Kamoun et al., 2015) and in many countries, their control is demanded by phytosanitary regulations (DCCEEW, 2023; EU, 2016). While it is important to continue research on these species, new research should also be conducted on methods to control other known forest *Phytophthora* species with potential to influence global forests, such as *P. pluvialis* recently discovered in Europe (Pérez-Sierra et al., 2022; Pirronitto et al., 2024), and previously studied in New Zealand (Dick et al., 2014; Fraser et al., 2022; Gómez-Gallego et al., 2019) and in the Pacific Northwest of North America (Brar et al., 2018; Hansen et al., 2017; Reeser et al., 2013).

Our findings underscore a gap in the implementation of existing research, likely due to the lack of holistic understanding of the processes in time and space. The same gap has also been noted in other studies focusing on biological control agents against *Phytophthora* species in agriculture (de Andrade Lourenço et al., 2022; Giachero et al., 2022). In this regard, the challenge is to develop research strategies that integrate diverse techniques to investigate the collective effects of microbial biocontrol agents on pathogen growth, disease progression, host vigour and environmental dynamics. Overall, more research and development efforts are needed to validate the results from laboratory and greenhouse facilities in field conditions.

5 | CONCLUDING REMARKS

Our systematic mapping of the literature reveals an impressive global research activity focused on the management and control of *Phytophthora* pathogens of forest trees. Future research using advanced technologies will likely result in improved tools for surveillance and management, while progress in understanding epidemiology and host resistance will allow the design of better management strategies and facilitate breeding efforts, although there is still a gap to overcome between research and implementation. Managing *Phytophthora* diseases in forest ecosystems remains challenging due to the lack of field experimental data on control strategies. While field experiments can be resource-intensive, they are crucial for demonstrating the efficacy of experimental treatments for disease control and optimizing their application methods and dosage. Hence, future field experiments are imperative to address knowledge gaps concerning the combined effects of microbial biocontrol agents on pathogen growth, disease progression, host vigour and environmental dynamics to improve our ability to manage *Phytophthora* diseases effectively. Multidisciplinary approaches that combine knowledge from plant pathology, ecology, genetics, climate science and forest management are needed in future research to enable a more holistic understanding of *Phytophthora* diseases and the development of effective control and management strategies.

ACKNOWLEDGEMENTS

This work was financially supported by the European Union's Horizon 2020 (H2020) Marie Skłodowska-Curie Actions Innovative Training Networks PROTECTA H2020-MSCA-ITN-2017 caLL, under grant agreement number 766048 (NLG). CR received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement number 845419. We acknowledge the kind contribution of Professor Steve Woodward and Maja Brus-Szkalej, who made valuable comments on an earlier version of this manuscript. We are grateful for the thoughtful reviews of two anonymous reviewers and the editor-in-chief, which helped improve this article.

CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest to disclose.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/efp.12878.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: López-García, N., Romeralo, C., Rönnberg, J., & Witzell, J. (2024). Control and management of *Phytophthora* damage in forestry—A systematic mapping study. *Forest Pathology*, *54*, e12878. https://doi.org/10.1111/efp.12878

APPENDIX 1

Chemical products utilized in the selected literature to control *Phytophthora* of forest trees, their active ingredients, chemical group and mode of action.

Product and manufacturer	Active ingredient (A. I.)	Chemical group	Mode of action
Cuprofix Disperss® UPL Australia Pty Ltd.	200 g/kg copper (copper sulphate/calcium hydroxide)	Inorganic	Protectant
AgriFos®600 Key Industries Ltd. (NZ)	600 g/L phosphite	Phosphonate	Systemic
AgriFos®400 Key Industries Ltd. (NZ)	400 g/L phosphite	Phosphonate	Systemic
Algon's Algatac Algon (NZ) Ltd.	40 g/L copper salts 100 g/L benzyl ammonium chloride	Inorganic	Protectant
Ridomil® Gold SL Syngenta	480 g/L metalaxyl-M	Phenylamide	Systemic
Amistar® Syngenta	250 g/L azoxystrobin	Strobilurin	Local systemic and protectant
AGPRO Cupric-hydroxide 350 SC AGPRO (NZ) Ltd.	350 g/L copper hydroxide	Inorganic copper	Protectant
Chemet® American Chemet Corporation, USA	750 g/kg cuprous oxide	Inorganic copper	Protectant
Dithane® Dow AgroSciences Australia Ltd., NSW	750 g/kg mancozeb	Dithiocarbamate	Protectant
Blizzard™ Orion Crop Protection Ltd. (NZ)	500 g/L chlorothalinal	Chloronitrile	Protectant
Polyram® DF BASF	700 g/kg metiram	Dithiocarbamate	Protectant
Sphinx® Agronica (NZ) Ltd.	500 g/L dimethomorph	Cinnamic acid amide	Local systemic and protectant

APPENDIX 1 (Continued)

Product and manufacturer	Active ingredient (A. I.)	Chemical group	Mode of action
Funguran® OH Spiess Urania Chemicals	500 g/kg copper hydroxide	Inorganic copper	Protectant
Avoguard® Nulandis® (A division of AECI Ltd.)	500 g/L potassium phosphonate	Phosphonate	Systemic
Empress® Intrinsic® BASF	23.3% pyraclostrobin	Strobilurin	Systemic and curative
ON-Gard® 5-0-0 BioWorks	5% nitrogen (N)	Fertilizer	Organic biological fertilizer
Orkestra® Intrinsic® BASF	21.26% pyraclostrobin 21.26% fluxapyroxad	Strobilurin, succinate dehydrogenase inhibitor	Protectant
Pageant® Intrinsic® BASF	12.8% pyraclostrobin 25.2% boscalid	Strobilurin, succinate dehydrogenase inhibitor	Protectant
RootShield Plus^{+} WP BioWorks	1.15% *Trichoderma* harzianum Rifai (T-22) 0.61% T. virens (G-41)	Biofungicide	Protectant
Subdue Maxx® Syngenta	22% mefenoxam	Phenylamide	Systemic
Tartan® Stressgard® Bayer	4.17% trifloxystrobin 20.86% triadimefon	Fungicide	Systemic, preventive and curative
EnerBite® Newpharm©	11% phosphorous pentoxide (P_2O_5) 7.3% potassium oxide (K_2O)	Fertilizer	Systemic
Armetil® 5 G IQV-Mat Holding Group.	5% metalaxil	Phenylamide	Systemic
Aliette® WP 80% Bayer	Fosetyl-Al [Aluminium tris-(ethylphosphonate)]	Organophosphonates	Systemic
Stature® SC BASF	dimethomorph	Cinnamic acid amide	Systemic and preventive
Phyto Fos®-K AMC Chemical – Trichodex	18% soluble potash (K_2O)	Derived from potassium phosphite	Systemic
OTRIA® 5 GR ©Probelte	5% metalaxyl	Phenylamide	Systemic
Zamorph® 50 WP Zagro©	Dimethomorph	Fungicide	Systemic and protective
ZeroTol® 2.0 BioSaf	27.1% hydrogen peroxide 2% peroxyacetic acid	Algaecide, bactericide and fungicide	Systemic
Banol Bayer	600 g/L propamocarb hydrochloride	Carbamate	Systemic, curative and preventative
Thiophanate-Methyl 70 WP Nippon Soda Co. Ltd. Japan	70% thiophanate-methyl	Benzimidazole	Systemic, protective and curative
Pentra-Bark® Quest Products Corp.	99.8% alkylphenol ethoxylate, polysiloxane polyether copolymer, propylene glycol	Synthetic-non-ionic surfactants	Non-ionic wetting agent designed to aid penetration through bark
Actifos® Agropak Sp.J. Poland	10.02% nitrogen (N) 0.02% boron (B) 0.008% copper (Cu) 0.06% iron (Fe) 0.04% manganese (Mn) 0.004% molybdenum (Mo) 0.02% zinc (Zn)	Fertilizer	Systemic
Ridomil® Gold MZ 68 WG Syngenta	64% mancozeb 4% metalaxyl-M	Ethylenebisdithiocarbamate (EBDC) Phenylamide	Systemic and protective
Phosplus® ©Otsuka Chemical Co., Ltd.	605 g/L potassium phosphite	Phosphorous acid	Systemic

APPENDIX 1 (Continued)

Product and manufacturer	Active ingredient (A. I.)	Chemical group	Mode of action
Amistar® Gold Syngenta	125 g/L azoxystrobin 125 g/L difenoconazol	Strobilurins, Triazole	Systemic and translaminar
Daconil® Action™ Syngenta	720 g/L chlorothalonil 2.34 g/L acibenzolar-S-methyl	Chlorinated Benzonitrile	Systemic
Kocide® 2000 DuPont™	53.8% copper hydroxide	Inorganic copper	Protectant
Ranman® Ishihara Sangyo Kaisha, Ltd.	34.5% cyazofamid	Imidazoles	Protectant
Bordeaux WG Grochem Australia Ltd.	200 g/kg tri-basic copper sulphate and lime (calcium hydroxide)	Bactericide and fungicide	Protectant
Kalex® Alba Milagro International S.P.A.	30% phosphoric anhydride 20% potassium oxide	Phosphoric acid	Bio-stimulant
Foli-R-Fos® 400 Bayer	40% mono and di potassium phosphite	Phosphorous acid	Systemic
Ridomil® Gold EC Syngenta	480 g/L metalaxyl-M	Phenylamide	Systemic and protectant
Foschek® 400 Arxada Ltd. (NZ)	400 g/L mono and di potassium phosphite	Phosphorous acid	Systemic
Fosject® 200 Bayer	200 g/L mono and di potassium phosphite	Phosphorous acid	Systemic
Apron® Gold Syngenta	35 g metalaxyl-M	Phenylamide	Systemic and protectant
Actiwett® Etec™ Crop Solutions Ltd. (NZ)	98% alcohol ethoxylate 2% polyethylene glycol	Linear alcohol ethoxylate	Surfactant (adjuvants)
LI-1000® Etec™ Crop Solutions Ltd. (NZ)	100% lecthin, methyl esters of fatty acids and alcohol ethoxylate	Lecithin, methyl esters of fatty acids and alcohol ethoxylate	Surfactant (adjuvants)
Hasten™ BASF	704 g/L ethyl and methyl esters of fatty acids	Derived from food grade canola Oil	Non-ionic surfactants (adjuvants)
Nu-Film-17® Key Industries Ltd. (NZ)	904 g/L di-1-p-menthene (a terpenic non-ionic polymer)	di-1-p-menteno	Adjuvant
Du-Wett Stainless® Etec™ Crop Solutions Ltd. (NZ)	30%–60% alcohol ethoxylate polyalkylene compounds: 10%–30% polyalkylene oxide 10%–30% polyalkyleneoxide silane 1%–5% polyalkyleneoxide	A pH-stable organosilicone polymer containing alcohol ethoxylate and polyalkylene compounds	Non-ionic organosilicone surfactant (adjuvants)
Du-Wett® Etec™ Crop Solutions Ltd. (NZ)	500 g/L trisiloxane ethoxylate	An organosilicone-blend containing siloxane polyalkeneoxide copolymers	Non-ionic organosilicone surfactant (adjuvants)
Du-Wett WeatherMAX® UPL (NZ) Ltd.	60% latex emulsion 30% water 15% siloxane polyalkyleneoxide copolymer	An organosilicone-blend superspreading sticker containing organosilicone and polimer latex	Non-ionic organosilicone surfactant (adjuvants)
Biohumin® Deutschland GmbH, Berlin, Germany	0.5% organic (N) 0.3% (P) 0.5% (S) 1% (Ca) 0.2% (Mg) 0.3% (Fe, Mn, B, Zn) 55% organic substance 20% humic fulvic acids	Composed of leonardite in liquid chelated form	Organic soil fertilizer
Break-Thru® S240 Western Farm Services Inc, Fresno, CA	100% Polyether Modified Trisiloxane	Organomodified trisiloxanes	Systemic Insecticides Fungicides Weedicides

APPENDIX 2

Composition of implants of phosphite, PHOSCAP® and MEDICAP® (Creative Sales, Inc., Fremont, Nebraska, United States of America).

Product and manufacturer	Composition % by weight	Chemical group	Mode of action
MEDICAP MD® Creative Sales, Inc. USA	12% nitrogen (N) 4% phosphate (P_2O_5) 4% soluble potash (k_2O) 4% iron (Fe) 4% manganese (Mn) 4% zinc (Zn)	Derived from potassium nitrate, ammonium phosphate, urea, sulphate of ammonia, ferric ammonium citrate, manganese sulphate and zinc sulphate	Systemic Fertilizer Implants
PHOSCAP® Creative Sales, Inc. USA	50% phosphate (P_2O_5) 30% soluble potash (k_2O) 0.06% magnesium (Mg) 0.02% boron (B) 0.05% copper (Cu) 0.1% iron (Fe) 0.05% manganese (Mn) 0.0005% molybdenum (Mo) 0.05% zinc (Zn)	Derived from mono-potassium phosphite and di-potassium phosphate	Systemic Fertilizer Implants
Zinc – (MEDICAP ZN®) Creative Sales, Inc. USA	30% zinc sulphide	Derived from purified Zinc sulphate	Systemic Fertilizer Implants
Iron – (MEDICAP FE®) Creative Sales, Inc. USA	Ammonium iron (II) citrate about 28% Fe	Derived from Ferric ammonium citrate	Systemic Fertilizer Implants

Acta Universitatis agriculturae Sueciae
Doctoral Thesis No. 2024:67

Pathogenic *Phytophthora* species pose a significant threat to forest ecosystems. This thesis explores their diversity, distribution and interactions with soil microbial communities and human activities. It assesses current legislation and control measures to prevent their spread and the role of soil microbiome in oak decline. Results revealed differences in microbial communities between healthy and declining trees. The isolation of several *Phytophthora* species, including newly identified species, highlights the need for advanced detection methods, public engagement, and stronger legislative measures to protect forests.

Noelia López-García received her BSc and MSc degree in Environmental and Forestry Engineering at the University of Córdoba, Spain, and her double MSc in Mediterranean Forestry and Natural Resources Management at the University of Lleida, Spain, and University of Lisbon, Portugal.

Acta Universitatis agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

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ISSN 1652-6880
ISBN (print version) 978-91-8046-358-4
ISBN (electronic version) 978-91-8046-394-2