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RESEARCH PAPERS

Phytophthora in forestry, natural environments, agriculture, and horticulture of the Mediterranean Basin and emerging *Phytophthora* threats from other regions

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Summary. *Phytophthora* is one of the most destructive genera of plant pathogens, comprising more than 260 described species, with numerous cryptic and undescribed

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taxa that remain undetected. These oomycetes cause severe diseases in agriculture, horticulture, forestry and natural ecosystems resulting in major economic losses, altered forest dynamics and biodiversity decline. The Mediterranean Basin is particularly vulnerable to these pathogens, due to high crop diversity, rich endemic flora, intensive plant trade networks, and climatic conditions that favour pathogen establishment and spread. Most damaging *Phytophthora* species are exotic, introduced primarily through infected nursery stock, contaminated soil or irrigation and river water. Their impacts are also affected by environmental stresses, climate change, intensive cultivation and interactions and connectivity among agricultural, forest and natural landscapes. New diagnostic tools and global surveys have revealed significant and previously undiscovered diversity and ongoing biosecurity risks for these pathogens. Effective management and mitigation require harmonised surveillance systems, robust early detection tools, production of pathogen-free planting material, improved hygiene and cultivation practices, and breeding for host tolerance. These approaches must be integrated within broad landscape-level strategies, to safeguard biodiversity and enhance ecosystem resilience across the Mediterranean Basin ecosystems.

Keywords. Pathways, detection, surveillance, management.

INTRODUCTION

The Mediterranean Basin is a well-known global hotspot for flora biodiversity, with about 25,000 native species, more than half of which are endemic (Cuttelod *et al.,* 2008). However, there has been a drastic decline in the diversity of plant species across the ecosystems in the region (Biçici and Çinar, 1990; Gritti et *al.,* 2006; Scanu *et al*., 2015; Médail, 2017; Peñuelas and Sardans, 2021; Bregant *et al*., 2024a; Morales-Rodríguez *et al*., 2025). Several plant diseases have negatively impacted vegetation in the Mediterranean Basin, amongst which, those caused by *Phytophthora* species are emerging. Species of *Phytophthora* are among the most destructive plant pathogens, causing severe losses in agriculture, forestry, horticulture and natural ecosystems (Erwin and Ribeiro, 1996; Brasier, 2008; Hansen *et al*., 2012; Lamour, 2013; Burgess *et al*., 2017; Jung *et al*., 2018a, 2022, 2024; Chen *et al*., 2022; Abad *et al*. 2023). These oomycetes are responsible for root and collar rots, bark cankers, fruit rots, and foliar and twig blights, affecting a wide range of agricultural crops, forest trees, ornamental plants, and key species in natural ecosystems (Figures 1 and 2). The ecological and economic impacts of these pathogens are serious, often leading to long-term ecosystem degradation, reduced biodiversity, and compromised ecosystem services (Shearer and Tippett, 1989; Marks and Smith, 1991; Brasier, 1996; Jung *et al*., 2018a; Fadli *et al*., 2022; Dalal *et al*., 2025; Horta Jung *et al*., 2025). Despite this international relevance, the Mediterranean Basin is an underexplored hotspot of vulnerability to *Phytophthora* disease emergence.

Symptoms of *Phytophthora* outbreaks have been known in the Mediterranean area since the 19th century (Lopes-Pimentel, 1947; Cacciola and Magnano di San Lio, 2008; Jung *et al*., 2018a; Saville *et al*., 2021). Nevertheless, most available information on *Phytophthora* derives from isolated case reports, taxonomic descriptions, or nursery-based surveys, rather than from integrated, region-wide assessments of pathogenicity, epidemiology, and host susceptibility under Mediterranean climate conditions. Therefore, the threats posed by these pathogens to Mediterranean crops, forests, horticultural systems and natural ecosystems are likely underestimated (Brasier, 2008; Burgess *et al*., 2017). Exceptions are the studies investigating the genetic structure and dynamics of regional populations of *Phytophthora infestans*, the causal agent of late blight of potato and tomato, that have been carried out in several Mediterranean countries within the framework of international surveillance programmes and networks (Collina *et al*., 2004; Beninal *et al*., 2009; Harbaoui *et al*., 2013, 2014; Corbiére *et al*., 2015; Savazzini and Galletti, 2015; Rekad *et al*., 2017; Gunacti *et al*., 2019; Beninal *et al*., 2021; Saville *et al*., 2021; El-Ganainy *et al*., 2022).

Adding to this knowledge gap, Mediterranean ecosystems are already under pressure from climate change, land-use intensification, and a diverse range of biological invasions (Kosmas *et* al., 2002; Gritti et *al.,* 2006; Santini *et al*., 2013; Didier *et al.* 2022). The Mediterranean Basin is characterized by hot, dry summers, mild winters, and pronounced seasonal water stress, and, more recently, has been subject to extreme climatic events characterised by heavy rain, floods and prolonged droughts. These conditions are particularly conducive to *Phytophthora* species that are tolerant of high temperatures, periodic soil drying and episodic rewetting, which can enhance pathogen survival, dispersal, and infection processes (Burgess *et al*., 2017; Jung *et al*., 2017a, 2018a).

There are multiple examples of aggressive introduced *Phytophthora* species associated with plant decline syndromes or destructive disease outbreaks in rainfed and irrigated crops, forests, and natural vegetation in the Mediterranean region. These pathogens affect

many hosts, including vegetables, such as greenhouse tomato, fennel in field, and pepper in fields and greenhouses, as well as staple crops, including potato and legumes, industrial crops such as soybean, flower crops in greenhouses, including gerbera daisy, herbaceous fruit crops, such as strawberry, the woody crop plants citrus, almond, olive, pistachio, and walnut, and fruit trees, forest trees (oak, chestnut, beech, alder), as well as numerous native and ornamental trees and shrubs. *Phytophthora cinnamomi* is widely recognized as a primary cause of oak decline across Mediterranean Europe, affecting *Quercus* spp. in forest, woodland, and silvopastoral systems, and causing extensive tree death and ecosystem-level impacts (Brasier *et al*., 1993; Jung *et al*., 2013a, 2018a; Horta Jung *et al*., 2025). Citrus production is similarly affected by the thermophilic species *P. nicotianae* and *P. citrophthora*, which cause root rot, gummosis, and fruit losses under warm and moist conditions typical of irrigated Mediterranean orchards (Cacciola and Magnano di San Lio, 2008; Vicent and Tuset, 2013).

In addition to these well-known pathogens, several emerging or previously overlooked *Phytophthora* species are increasingly reported from Mediterranean environments. In agricultural systems, *P. oleae* and *P. heterospora* (recently described sister species of *P. palmivora*) have emerged as important pathogens associated with olive decline, a crop of major economic, cultural, and ecological significance in the region (Ruano-Rosa *et al*., 2018; Scanu *et al*., 2021). *Phytophthora heterospora* has been detected in Mediterranean and subtropical environments, and is probably aggressive under warm conditions, although its distribution and host range remain poorly defined (Scanu *et al*., 2021). *Phytophthora niederhauserii* is frequently detected in nurseries, ornamental plantings, and horticultural systems, where it has broad host range and high tolerance to elevated temperatures (Pérez-Sierra *et al.,* 2010; Abad *et al*., 2014; Jung *et al*., 2016). *Phytophthora palmivora* and *P. tropicalis*, traditionally associated with tropical and subtropical regions, are now increasingly reported from nurseries, and Mediterranean agro- and forest ecosystems (Figure 2 J) and natural habitats (Cacciola *et al*., 2007a; Pane *et al*., 2008; 2009; Ahmed *et al*., 2013; Luongo *et al*., 2013; Türkölmez *et al*., 2015a, 2015b, 2016a; Markakis *et al*., 2017; Kurbetli *et al*., 2020; Linaldeddu *et al*., 2020a; Aloi *et al*., 2021; Bregant *et al*., 2024b). This indicates adaptability of these pathogens to warm climates and episodic moisture availability (Drenth and Guest, 2004; Scanu *et al*., 2021).

Further expanding the spectrum of Mediterranean-relevant *Phytophthora* diversity, *P. acerina* has been associated with decline, root rot, bark cankers and death of maple (*Acer pseudoplatanus*), alder (*Alnus glutinosa*), olive, and cork oak trees in Italy (Seddaiu and Linaldeddu, 2020; Linaldeddu *et al*., 2020b; Jung *et al*., 2024), raising concerns about the role of this pathogen in forest and urban tree health under warming climatic conditions (Ginetti *et al*., 2014). *Phytophthora pseudocryptogea* is another emerging species in the Mediterranean region: in recent years, it has been reported in Italy, Portugal, Spain and Türkiye, from several new hosts in nurseries and forest stands, indicating it has established in the geographic area (Aloi *et al*., 2023; Benigno *et al*., 2025a; Horta Jung *et al*., 2025). Some previous reports of *P. cryptogea* as causal agent of crown rot of gerbera daisy in Italy could be imputed to *P. pseudocryptogea*, but the identification of isolates was based on morphological characteristics and the comparison of electrophoretic profiles of mycelium total proteins and isozymes, while no DNA sequences are available. Other recently described species associated with declining Mediterranean maquis vegetation are *P. crassamura* and *P. ornamentata*, both associated with decline symptoms. Additional species, including *P. asparagi*, *P. mediterranea, P. multivora,* and *P. plurivora*, have been increasingly reported from Mediterranean horticultural systems, nurseries, and natural ecosystems, often exhibiting broad host ranges and high tolerance to warm and temporary drought conditions (Jung and Burgess, 2009; Moralejo *et al*., 2009; Jung *et al*., 2016; Riolo *et al*., 2020; Bregant *et al.,* 2021a; Antonelli *et al*., 2023; Mora-Sala *et al*., 2022; Alderotti and Verdiani, 2023; Aloi *et al*., 2023).

Together, these *Phytophthora* species are diverse and heat-tolerant and thermophilic pathogens. Also, there are cryptic or recently resolved *Phytophthora* taxa adapted to Mediterranean conditions (Scanu *et al*., 2015), many of which remain insufficiently studied with respect to pathogenicity, host ranges, epidemiology, and climatic amplitudes.

In agricultural systems, research has largely focused on economically important host–pathogen systems in temperate regions, while Mediterranean-specific pathosystems such as those involving warm-climate crops, including citrus, olive, and stone fruit production, remain comparatively underrepresented in the literature. Similarly, for forestry and natural ecosystems, most *Phytophthora* studies have concentrated on cool and moist forest types of Central and Northern Europe, leaving Mediterranean woodlands, maquis, and garrigue ecosystems insufficiently investigated (Brasier, 1996; Jung *et al*., 2013a, 2016, 2018a; Riolo *et al*., 2020). For many heat-adapted *Phytophthora* species, basic information on host range, optimum temperature, soil moisture thresholds, and interactions with drought-stressed hosts is still lack-

ing, severely limiting accurate disease risk predictions (Burgess *et al*., 2017; Jung *et al*., 2017a).

In forestry and natural ecosystems, interactions between climatic stressors (e.g., drought) and *Phytophthora* pathogenicity are poorly resolved, despite evidence that such interactions can exacerbate tree decline and mortality (Shearer and Tippett, 1989; Jung *et al*., 2003a; Jung, 2009; Scanu *et al*., 2015). Another very important aspect is nursery plant production, which is a significant industrial sector in several regions, and becoming important in entire provinces across the Mediterranean region. Nurseries have crucial roles in agriculture, horticulture and forestry as they support food supply chains, satisfy increasing demands for ornamental indoor and outdoor plants, and produce planting stock for forest establishment. Several national and international nature conservation and restoration initiatives, such as the EU Regulation 2024/1991 on Nature Restoration (Anonymous, 2024), depend directly on successful production of healthy, pest-free nursery plants across various species. Furthermore, nursery production is also crucial for conservation of endangered European species, such as Sicilian fir (*Abies nebrodensis*) (Thomas, 2017) and Serbian spruce (*Picea omorika*) (Mataruga *et al*., 2020), as well as rear-edge populations of widespread European forest tree species, such as Norway spruce (*Picea abies*) and silver fir (*Abies alba*) (Avanzi *et al*., 2024, 2025). Continuous introductions of infected often symptomless nursery plants for planting into previously unaffected areas is a major pathway for spread of Phytophthora diseases (Pérez-Sierra and Jung, 2013; Migliorini *et al*., 2015; Jung *et al*., 2016; Garbelotto *et al*., 2018; Simamora *et al*., 2018; Rooney-Latham *et al*., 2019; Frankel *et al*., 2020a, 2020b; Green *et al*., 2021; Horta Jung *et al*., 2025), with Mediterranean climatic regions being vulnerable to these pathogens. This has been shown for different regions, including Australia (Shearer and Tippet 1989; Scott *et al*. 2009; Rea *et al*. 2010; Jung *et al*. 2013b), California (Frankel *et al*. 2020a, 2020b; Fajardo *et al*. 2025), or Europe (Brasier *et al*. 1993; Pérez-Sierra *et al*. 2013; Scanu *et al*. 2015; Horta Jung *et al*. 2025). Beyond restoration sites and natural ecosystems, significant risks are also associated with ornamental and amenity plantings, as well as urban greenery in general. Several studies have demonstrated presence of invasive *Phytophthora* species in commercial nurseries that produce ornamental plants (Shishkoff, 2007; Moralejo *et al*., 2009; Pérez-Sierra and Jung, 2013; Prigigallo *et al*., 2015; Jung *et al*., 2016; Junker *et al*., 2016; Mora-Sala *et al*., 2022; Migliorini *et al*., 2023; Schiffer-Forsyth *et al*., 2023; Bačová *et al*., 2024; Green *et al*., 2025), indicating significant risks to ornamental plantings and the surrounding environments (Werres *et al*., 2001; Brasier and Jung, 2003; Milenković *et al*., 2018; Redondo *et al*., 2018; Migliorini *et al*., 2019; Green *et al*., 2020; Mrázková *et al*., 2025), including in the Mediterranean Basin (Morales-Rodríguez *et al*., 2023; Pintos *et al*., 2023; Antonelli *et al*., 2024; Tomić *et al*., 2024).

Increasing connectivity among agriculture, horticulture, forestry, and natural ecosystems has intensified the risks of *Phytophthora* dissemination across managed and unmanaged landscapes (Figure 3). Globalized trade in plants-for-planting, particularly ornamental nursery stock, has been identified as a major pathway for the introduction and spread of invasive *Phytophthora* spp., linking horticultural production systems with forests and semi-natural ecosystems (Jung and Blaschke, 2004; Brasier and Jung, 2006; Brasier, 2008; Jung, 2009; Jung *et al*., 2016; Horta Jung *et al*., 2025). Agricultural irrigation systems, shared water sources, and surface runoff, further facilitate pathogen movement between crop fields and adjacent natural habitats, while infested soils adhering to machinery, vehicles and footwear enable cross-sector pathogen transmission (Shearer and Tippett, 1989; Erwin and Ribeiro, 1996; Parlascino *et al*., 2025). Forestry operations and restoration plantings can inadvertently introduce infected nursery stock into wildlands, amplifying landscape-scale epidemics (Jung and Blaschke, 2004; Jung, 2009; Jung *et al*., 2016; Sims *et al*., 2019; Frankel *et al*., 2020a). Urban and peri-urban plantings serve as epidemiological bridges, creating interfaces where ornamental hosts, agricultural crops and native vegetation coexist in proximity, enabling exchange of pathogens (Jung and Burgess, 2009). Together, these interconnected systems form a continuum rather than isolated compartments, allowing *Phytophthora* spp. to move across ecological and production boundaries (Figure 3), thereby increasing biosecurity challenges and the need for integrated, cross-sectoral disease management strategies. In conclusion, *Phytophthora* dissemination therefore operates across integrated socio-ecological systems rather than within isolated sectors, underscoring the need for coordinated biosecurity and disease management strategies that bridge agriculture, horticulture, forestry, and conservation domains.

Despite an increasing number of reports documenting heat-tolerant *Phytophthora* species in Mediterranean agroecosystems and natural habitats, the scientific literature remains focused on temperate and boreal regions. Most *Phytophthora* research conducted in Europe has focused on temperate and boreal regions of Northern and Central Europe, where cool humid climates prevail, so most studies have focused on species adapted to temperate environments. Research priorities, surveillance

efforts, and management strategies have largely centred on species adapted to mild temperature and high-moisture environments. In contrast, little attention has been paid to heat-tolerant and thermophilic *Phytophthora* species that dominate or persist in the Mediterranean Basin. This geographic and climatic bias has created significant knowledge gaps regarding pathogen distributions, host ranges, disease epidemiology, and future risks under Mediterranean climate regimes (Jung *et al*., 2016).

These knowledge gaps are particularly concerning in the context of ongoing climate change. Warming temperatures and increasing aridification are expected to further favour heat-adapted *Phytophthora* species, potentially increasing disease severity in the Mediterranean Basin, and facilitating northward expansion of mesophilic and thermophilic taxa into previously unsuitable regions (Burgess *et al*., 2017; Nechwatal and Jung, 2021). A Mediterranean focus is therefore essential to improve understanding of species diversity, pathogenicity and climate sensitivity in Mediterranean agroecosystems, forests and natural habitats. This is essential to anticipate future disease risks, and to safeguard plant health, biodiversity and ecosystem resilience under accelerating climate change. Failure to adequately characterize *Phytophthora* species adapted to Mediterranean conditions therefore undermines disease risk assessment, early detection efforts, and the development of effective disease management strategies across Europe.

The objective of the present review is to provide a comprehensive overview of the current *Phytophthora* situation in the Mediterranean Basin, synthesizing available knowledge on established and emerging diseases, surveillance, detection and diagnosis, pathways, and management, and addressing research gaps. This review intends to enhance understanding of the role of *Phytophthora* spp. in Mediterranean environments, and stimulate coordinated efforts to mitigate their impacts under current and future environmental change scenarios.

ESTABLISHED AND EMERGING DISEASES ASSOCIATED WITH *PHYTOPHTHORA* SPECIES IN THE MEDITERRANEAN BASIN

Forest Phytophthora diseases

Ink disease

Ink disease is an important and long-recognized disease affecting the genus *Castanea* worldwide (Jung *et al*., 2018a, 2018b; Vannini and Morales-Rodriguez, 2022). Sweet chestnut (*Castanea sativa*) is severely affected in its natural distribution range in Southern Europe, and wherever the host species has been introduced or cultivated (Figure 1 A). The disease was first recorded in Europe in Portugal in 1838, although it is believed to have been present in Spain since 1726 (Lopes-Pimentel, 1947; Crandall *et al*., 1950; Vannini and Vettraino, 2001; Jung *et al*., 2018a). Ink disease has spread across the entire distribution range of *C. sativa* in Europe, emerging as a major constraint for chestnut cultivation and in forest ecosystems. This disease now affects all chestnut-growing Mediterranean countries: from Portugal to Türkiye (Robin *et al*., 1998; Vettraino *et al*., 2005; Tziros and Diamandis, 2014; Şimşek *et al*., 2019; Horta Jung *et al*., 2025).

The name "ink disease" derives from the characteristic dark, ink-like exudates that may appear at the collar region or seep into soil from necrotic tissues at the base of affected trees. Belowground symptoms include progressive necrosis of fine and coarse roots and destruction of root systems, which severely impair water and nutrient uptake. Above ground, infected trees typically have reduced vigour, leaf chlorosis, premature defoliation, crown thinning and, in advanced stages, dieback and mortality (Figure 1 A) (Vettraino *et al*., 2005; Jung *et al*., 2013a, 2018a; Horta Jung *et al*., 2025; Morales-Rodríguez *et al*., 2025). Ink disease also occurs on chestnut seedlings in nurseries, and in new plantations, which usually show rapid or gradual wilting and mortality (Jung *et al*., 2016; Horta Jung *et al*., 2025).

The two main causal agents, *P. cinnamomi* and *P.* ×*cambivora*, are widespread in declining chestnut stands across the Mediterranean region, with *P. cinnamomi* prevailing in warmer and drier areas, and *P.* ×*cambivora* under cooler and more humid conditions (Vettraino *et al*., 2005; Perlerou *et al*., 2010; Tziros and Diamandis, 2014; Horta Jung *et al*., 2025). In a recent forest survey in Portugal, *P. cinnamomi* and *P.* ×*cambivora* were found in 12 and five declining chestnut stands, respectively, co-occurring in two stands (Horta Jung *et al*., 2025). In Türkiye, however, *P.* ×*cambivora* was more common, occurring in 13 of the 29 chestnut stands sampled, whereas *P. cinnamomi* was only found in five stands in the Marmara region around Istanbul (Şimşek *et al*., 2019). These contrasting patterns between the Western and Eastern Mediterranean regions probably reflect differences in their histories of plant trade, and consequent accidental pathogen introductions, which were also discussed by Vettraino *et al.* (2005). Minor contributors to ink disease include *P. cactorum*, *P. cryptogea*, *P. gonapodyides*, *P. megasperma*, *P. nicotianae*, *P. plurivora*, *P. pseudosyringae*, *P. syringae*, and *P. sansomeana*, which are infrequently detected in rhizosphere surveys of chestnut stands across the Mediterranean Basin (Per-

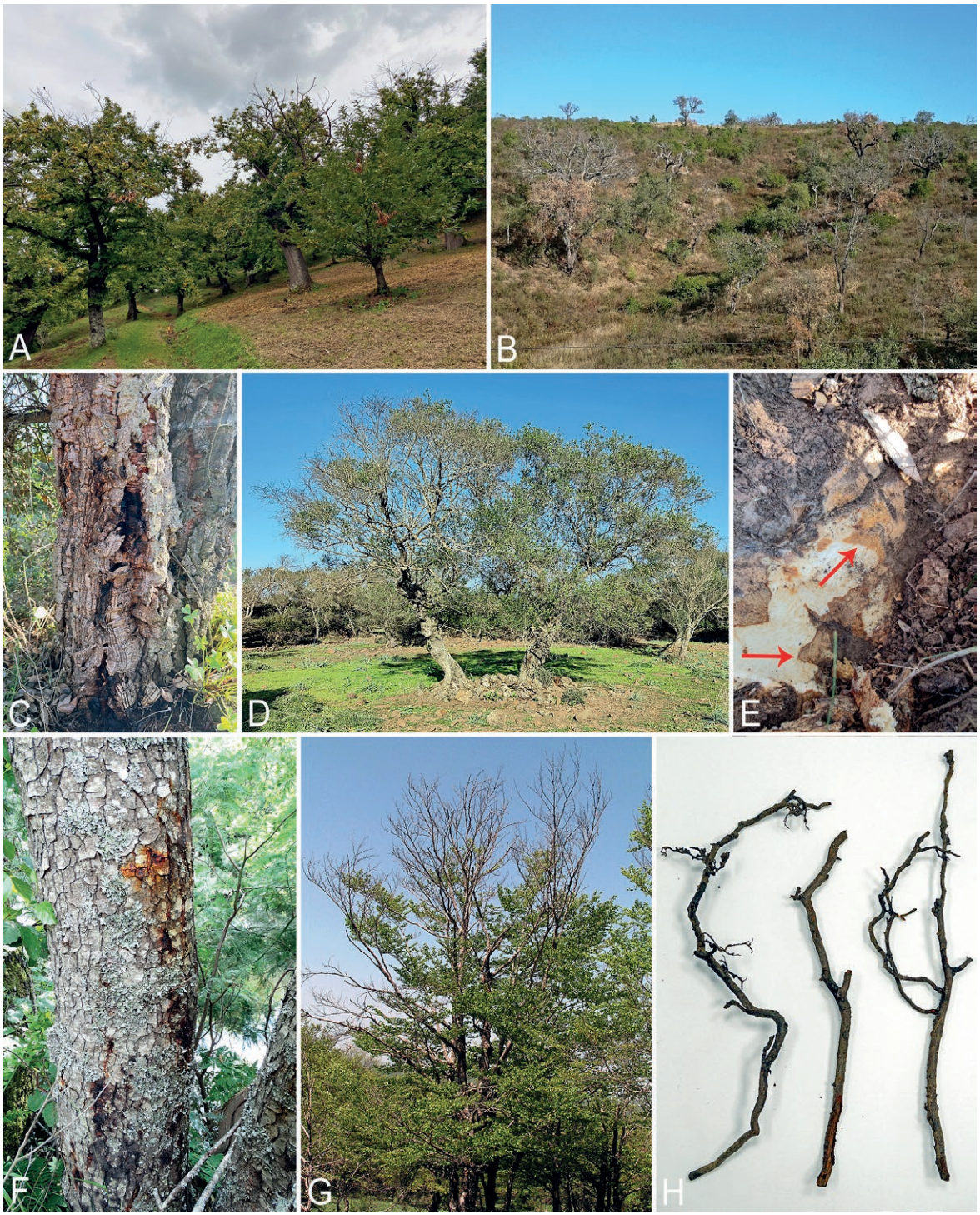

Figure 1. Phytophthora diseases in Mediterranean forests. A. Dieback of chestnut (*Castanea sativa*) trees in Italy, due to ink disease caused by *P. cinnamomi*. B. Severe mortality of cork oaks (*Quercus suber*), due to root and collar rot caused by *P. cinnamomi*, leading to deforestation in Southern Portugal. C. Bleeding bark canker, caused by *P. cinnamomi* on cork oak in Sardinia. D. Thinning and dieback of wild olive trees (*Olea europaea* var. *sylvestris*) in Sardinia, due to root rot caused by various *Phytophthora* spp. E. Inner bark necroses (arrows), caused by *Phytophthora* spp. on a main root of a wild olive tree in Sardinia. F. Bleeding bark cankers (collar rot) on a riparian *Alnus lusitanica* tree in Portugal, caused by *P.* ×*alni*. G. Severe crown dieback of *Fagus sylvatica* in the Nebrodi Mountains of Sicily, due to root and collar rot caused by *P.* ×*cambivora*. H. Small woody roots of a declining *F. sylvatica* in the Nebrodi Mountains of Sicily, with extensive losses of fine and lateral roots due to infections by *P.* ×*cambivora* and *P. megasperma*.

lerou *et al*., 2010; Scanu *et al*., 2010; Jung *et al*., 2013a, 2018a; Şimşek *et al*., 2019; Horta Jung *et al*., 2025). The recently described *P. castanetorum* occurs in declining Italian, Portuguese and Spanish chestnut stands (Jung *et al*., 2017a; Štraus *et al*., 2023).

For decades, the aetiology of ink disease has been interpreted within a simple framework, in which chestnut decline and mortality were attributed primarily to the direct effects of root destruction caused by one or both main causal agents, *P. cinnamomi* and/or *P.* ×*cambivora*. This pathogen-centred view shaped diagnostic approaches and management strategies and still represents the baseline reference for ink disease in the scientific literature (Vannini *et al*., 2009; Vannini and Morales-Rodriguez, 2019). However, as with other *Phytophthora* and fungal diseases, the epidemiology of ink disease is strongly influenced by climatic and soil conditions, landscape heterogeneity, and human activities.

The Mediterranean Basin constitutes a particularly suitable context in which to analyse how these factors interact with the pathogens and the host in determining the disease expression. This region is characterised by pronounced climatic seasonality, with wet or mild winters followed by hot and dry summers, a pattern that imposes considerable physiological constraints on sweet chestnut growth (Freitas *et al*., 2021). Winter rainfall and spring precipitation drive ink disease epidemiology by creating soil moisture that boosts *Phytophthora* zoospore production, dispersal, and root infection during tree growth resumption (Fernandes *et al*., 2021). Subsequent summer droughts stress chestnut trees, limiting root regeneration and vigour, while the pathogens survive in long-lasting structures, especially if both matting types are present, until wet conditions resume (Jung *et al*., 2013b, 2018a; Dorado *et al*., 2023b). This precipitation-driven infection/drought stress cycle encourages progressive disease development under Mediterranean climates.

Climate change is amplifying these seasonal dynamics by increasing temperatures and altering precipitation patterns across the Mediterranean Basin. Rising minimum winter temperatures and a higher frequency of extreme climatic events have been identified as key factors affecting both host performance and pathogen behaviour (Benito-Garzón *et al*., 2013; Freitas *et al*., 2021). From a *Phytophthora* perspective, these changes are particularly relevant because they selectively favour species with higher thermal tolerance and broader ecological plasticity. Evidence from Mediterranean forest ecosystems indicates a progressive shift in *Phytophthora* species dominance, with *P. cinnamomi* increasingly replacing *P.* ×*cambivora* in areas where climatic conditions have become warmer (Morales-Rodríguez *et al*., 2025). This shift has important epidemiological implications, as *P. cinnamomi* shows higher aggressiveness, greater persistence under rising temperature and fluctuating moisture regimes, and a wider host range (Brasier and Jung, 2003; Hardham and Blackman, 2018; Şimşek *et al*., 2019; Brandano *et al*., 2023), thus increasing the likelihood of recurrent infections and long-term disease establishment in chestnut stands.

In addition to stress caused by abiotic factors, in Mediterranean chestnut ecosystems, ink disease develops within a broad context of accumulated biotic stress, that progressively reduces host resilience and increases susceptibility to root pathogens. Sweet chestnut has been repeatedly exposed to successive biological invasions, starting with introduction and establishment of *P. cinnamomi*, followed by the long-standing impacts of chestnut blight caused by *Cryphonectria parasitica*, and more recently by the widespread invasion of the Asian chestnut gall wasp (*Dryocosmus kuriphilus*). Each of these stressors affects different functional components of the host tree, but their combined effects converge in reducing carbon assimilation, altering resource allocation, and weakening defence and recovery capacities. Defoliation and canopy damage caused by *D. kuriphilus* have resulted in prolonged reductions in photosynthetic performance in many Mediterranean areas, from which chestnut stands are still recovering, thereby increasing vulnerability to soilborne pathogens (Morales-Rodríguez *et al*., 2019).

Anthropogenic activities and landscape configuration significantly influence the impact and spatial distribution of ink disease in Mediterranean chestnut ecosystems. A spatially explicit study in Central Italy showed strong association between disease impact and landscape features linked to human presence, particularly road networks and natural drainage systems (Vannini *et al*., 2021). These elements facilitate movement of contaminated soil and surface water, promoting dispersal and accumulation of *Phytophthora* inoculum in downslope areas and sites with persistently high soil moisture. Importantly, such landscape features often connect managed systems (e.g. orchards, forest roads, agroforestry areas) with semi-natural and natural ecosystems, creating a functional continuum through which pathogens, soils, water and human vectors are shared across land-use types. In Mediterranean landscapes, where chestnut stands frequently occur at the interface between agricultural, forestry and natural systems, this connectivity amplifies ink disease spread and reinforces the role of human-mediated pathways in shaping disease epidemics at landscape scales (Vannini *et al*., 2021).

Although ink disease is pathogen-driven, increasing evidence indicates that disease expression in Mediterranean chestnut ecosystems also depends on structure and functionality of the soil and rhizosphere microbiome (Vannini *et al*., 2013; Ruiz Gómez *et al*., 2019). High-throughput sequencing approaches have revealed complex communities of *Phytophthora* and other soil microorganisms, whose functional composition and interactions may modulate pathogen activity and host resilience beyond the effects of the main disease-causing agents (Ruiz Gómez *et al*., 2019).

Under Mediterranean conditions, ink disease should be understood as the result of interactions between soilborne pathogens, climatic factors, and the anthropogenic pressures characteristic of highly connected landscapes.

Oak decline

Mediterranean oak trees are keystone components of forest and agro-silvopastoral ecosystems throughout southern Europe and North Africa (Petroselli *et al*., 2013). Species such as the evergreen cork oak (*Quercus suber*) and holm oak (*Quercus ilex*) dominate extensive woodlands, including the traditional "Montado" and "Dehesa" systems in Portugal and Spain. These systems provide cork and timber, support livestock grazing, and deliver key ecosystem services including biodiversity conservation and soil protection (Carreira *et al*., 2023). However, the long-term sustainability of these ecosystems is increasingly threatened by the complex "oak decline" syndrome, in which soilborne pathogens such as *Phytophthora* species are recognized as major biotic drivers (Brasier *et al*., 1993; Jung *et al*., 1996, 1999, 2017a, 2018a, 2019; Sánchez *et al*., 2002; Vettraino *et al*., 2002; Moreira and Martins, 2005; Camilo-Alves *et al*., 2013; Pérez-Sierra *et al*., 2013; Scanu *et al*., 2013; Moricca *et al*., 2016; Seddaiu *et al*., 2020; Dorado *et al*., 2023a; Horta Jung *et al*., 2025). In the Mediterranean Basin, also several deciduous oak species are affected by *Phytophthora*-mediated oak decline. These include Turkish oak (*Quercus cerris*), Portuguese oak (*Quercus faginea*), Hungarian oak (*Quercus frainetto*), Hartwiss oak (*Quercus hartwissiana*), sessile oak (*Quercus petraea*), pubescent oak (*Quercus pubescens*), Pyrenean oak (*Quercus pyrenaica*), pedunculate oak (*Quercus robur*), and Kasnak oak (*Quercus vulcanica*) (Jung *et al*., 1996, 1999, 2018a, 2019; Vettraino *et al*., 2002; Balci and Halmschlager, 2003; Pérez-Sierra *et al*., 2013; Horta Jung *et al*., 2025).

The first *Phytophthora* species formally associated with oak decline was *P. cinnamomi*, detected in 1991 from declining oak trees in the Iberian Peninsula (Brasier *et al*., 1993). Since then, extensive research has demonstrated the primary role of *P. cinnamomi* as driver of oak decline across Mediterranean regions of Portugal (Figure 1 B), Spain, southern France, and Italy (Figure 1 C) (Brasier, 1996; Robin *et al*., 1998; Sánchez *et al*., 2002; Moreira and Martins, 2005; Camilo-Alves *et al*., 2013; Scanu *et al*., 2013; Frisullo *et al*., 2018; Jung *et al*., 2018a; Horta Jung *et al*., 2025). For many years, *P. cinnamomi* was considered the only *Phytophthora* species responsible for Mediterranean oak decline. However, extensive surveys and pathogenicity tests have revealed a more complex aetiology, involving more than 20 additional *Phytophthora* taxa that contribute to the progressive decline of oak stands, either alone or in combination with *P. cinnamomi* (Jung *et al*., 1996, 1999, 2018a; Corcobado *et al*., 2017). A diverse *Phytophthora* community has been isolated from declining holm oak stands in Spain, with six previously undetected species from this host, including *P. cryptogea, P. gonapodyides, P. megasperma, P. quercina, P. psychrophila*, and *P. syringae* (Pérez-Sierra *et al*., 2013). Similarly, Seddaiu *et al*. (2020) reported a total of eight *Phytophthora* species from declining cork oak trees across sites in Sardinia, including *P. cinnamomi*, *P. gonapodyides*, *P. pseudocryptogea*, *P. psychrophila*, *P. quercina*, *P. syringae*, *P. tyrrhenica*, and *P.* ×*cambivora*. In Sicily, Jung *et al*. (2019) demonstrated the presence of 11 *Phytophthora* species in the rhizospheres of declining evergreen and deciduous oaks, including *P. gonapodyides*, *P. lacustris*, *P. megasperma*, *P. multivora*, *P. platani* (designated as *P. citricola*), *P. plurivora*, *P. pseudocryptogea*, *P. psychrophila*, *P. quercina*, *P. tyrrhenica* and *P.* ×*cambivora*. A recent survey across Portugal unveiled eight *Phytophthora* species from a wide range of declining oak forests, including *P. cinnamomi*, *P. gonapodyides*, *P. plurivora*, *P. pseudosyringae*, *P. quercina*, *P. uliginosa*, *P.* ×*cambivora* and the informally designated hybrid *P.* taxon ×pseudocryptogea-like (Horta Jung *et al*., 2025). In Türkiye, Balci and Halmschlager (2003) found nine *Phytophthora* species associated with decline of six oak species. Surveys in North Africa (Algeria, Morocco and Tunisia) also demonstrated the presence of multiple *Phytophthora* species in declining cork oak stands (Smahi *et al*., 2017; Dorado *et al*., 2023a; Yangui, personal communication). More recently, the exotic and invasive *P. multivora* was reported for the first time on declining evergreen oaks in central and southern Italy, and its pathogenicity was confirmed on cork and holm oak (Jung *et al*., 2019; Aurangzeb *et al*., 2023; Seddaiu and Scanu, unpublished). Jung *et al*. (2024) reported the emerging pathogen *P. acerina* from a declining cork oak tree in northern Italy.

The presence of multiple *Phytophthora* taxa associated with Mediterranean oak decline has been further

corroborated by metabarcoding surveys based on high-throughput amplicon sequencing (HTS), which consistently revealed greater pathogen diversity compared to conventional methods (Català *et al*., 2015; Mora-Sala *et al*., 2018; Ruiz-Gómez *et al*., 2019; Aurangzeb *et al*., 2023; Seddaiu *et al*., 2025). The observed discrepancies in *Phytophthora* diversity across studies may reflect the detection methods employed, but may also be related to different histories of plant and associated pathogen introductions. While soil baiting effectively recovers viable *Phytophthora* from Mediterranean oaks, its success can be influenced by seasonal pathogen activity and the expertise required for isolation and species identification (Pérez-Sierra *et al*., 2022; Sarker *et al*., 2023; Seddaiu *et al*., 2025). Environmental DNA (eDNA) metabarcoding can detect a wider spectrum of known and potentially novel taxa than baiting (La Spada *et al*., 2022; Bačová *et al*., 2024), although its resolution is limited for closely related species (Bose *et al*., 2018; Burgess *et al*., 2022; Seddaiu *et al*., 2025). Furthermore, due to the uneven distribution of *Phytophthora* inoculum in forest soils and the low quantities of soil tested in eDNA metabarcoding approaches, rare *Phytophthora* species with low levels of primary inoculum may not be detected. Therefore, combining culture-based and molecular approaches remains essential for reliable characterization of *Phytophthora* communities in Mediterranean oak ecosystems (Jung *et al*., 2019; La Spada *et al*., 2022; Sarker *et al*., 2023).

Mediterranean oak decline associated with *Phytophthora* species includes two main syndromes: (i) rapid or acute tree death, and (ii) chronic decline and dieback (Brasier *et al*., 1993; Jung *et al*., 1996, 2000, 2018a; Gallego *et al*., 1999; Vettraino *et al*., 2002; Camilo-Alves *et al*., 2013; Horta Jung *et al*., 2025). Acute mortality, typical in Mediterranean regions, is primarily caused by *P. cinnamomi*, which destroys host fine roots and collars, often in strong synergy with summer drought (Brasier *et al*., 1993; Gallego *et al*., 1999; Sánchez *et al*., 2002; Scanu *et al*., 2013; Carluccio *et al*., 2025; Horta Jung *et al*., 2025). Infected trees may collapse within one season, showing extensive fine root losses, necrotic root and collar lesions, black exudates, and phloem/xylem discolouration (Figure 1, B and C). Chronic decline, often associated with *P. quercina* and other less frequently isolated *Phytophthora* species, develops gradually. Symptoms include crown thinning, leaf chlorosis, branch dieback, and epicormic shoots, reflecting progressive fine and small woody root loss and callused lesions on suberized roots (Jung *et al*., 1996, 2000, 2018a; Jönsson *et al*., 2005; Horta Jung *et al*., 2025). Tree weakening is exacerbated by abiotic stress (drought, waterlogging, poor soils) and secondary pests, which can trigger rapid wilting (Brasier *et al*., 1993; Jung *et al*., 1996, 2000; Vettraino *et al*., 2002; Jönsson *et al*., 2003, 2005; Moreira and Martins, 2005).

Several studies have emphasized the interactions between *P. cinnamomi* and site-related stress factors, including shallow or compacted soils (Cabral *et al*., 1993; Moreira and Martins, 2005), and recurrent summer droughts (Brasier *et al*., 1993; Gallego *et al*., 1999; Horta Jung *et al*., 2025). Mediterranean oak ecosystems are becoming extremely vulnerable to climatic changes (Borreguero *et al*., 2026). Experimental and modelling studies predict that rising mean temperatures will increase the activity and impact of *P. cinnamomi* (Brasier and Scott, 1994; Burgess *et al*., 2017; Cidre-González *et al*., 2025), potentially intensifying root and collar rot and making affected oaks more vulnerable to drought. Climatic shifts, such as milder winters, altered precipitation patterns with wetter winters and drier summers, and more frequent extreme rainfall events, have been discussed as key drivers of the unprecedented epidemic extent and duration of the current *Phytophthora*-related oak decline (Jung *et al*., 1996, 2000, 2003a; Pérez-Sierra *et al*., 2013; Seddaiu *et al*., 2020). Mediterranean oak decline exemplifies the synergistic interaction between invasive soilborne pathogens and climate stress, underscoring the urgent need for strict nursery hygiene, careful site selection in afforestation programmes, limitation of soil movement, and long-term monitoring, to mitigate further spread and impact of *Phytophthora* species in oak ecosystems.

Decline and dieback of European beech

European beech (*Fagus sylvatica*) is an important forest tree in Europe, occurring in a wide range of site conditions from Northern Spain, Sicily and Greece to Southern Scandinavia and from the United Kingdom to Romania and Ukraine. Due to its high shade tolerance, dense canopy and heights exceeding 40 m, *F. sylvatica* is a competitive and dominant tree species that often forms pure or nearly pure stands at ecologically optimal sites across Western and Central Europe, and in mountain forests of Eastern and Southern Europe (Walentowski *et al*., 2004; Ellenberg and Leuschner, 2010).

The earliest report of local decline and mortality of beech forests due to Phytophthora root rot came from the United Kingdom in the 1930s (Day, 1938). Since the early 1990s, *Phytophthora* species have been regularly associated with severe decline and dieback of *F. sylvatica* forests and amenity stands across the entire natural range of the host in Europe (Motta *et al*., 2003; Jung *et al*., 2003b, 2005, 2013a, 2016, 2017a, 2018a, 2019; Cacciola *et al*., 2005; Hartmann *et al*., 2006; Orlikowski *et al*., 2006;

Brown and Brasier, 2007; Munda *et al*., 2007; Vettraino *et al*., 2008a; Černý *et. al*., 2009, Jung, 2009; Jung and Burgess, 2009; Schmitz *et al*., 2009; Stępniewska and Dłuszyński, 2010; Telfer *et al*., 2015; Corcobado *et al*., 2020; Riolo *et al*., 2022; Štraus *et al*., 2023; Martínez-Arias *et al*., 2024; Horta Jung *et al*., 2025). The disease is characterized by extensive fine root losses (Figure 1 H), bleeding collar rot cankers, aerial bleeding bark cankers up to 20 m stem height, canopy thinning, and dieback (Figure 1G), and in an advanced state often pale-green to chlorotic small-sized leaves, and eventually scattered or patchy mortality (Jung, 2009; Jung *et al*., 2013a, 2018a; Corcobado *et al*., 2020; Horta Jung *et al*., 2025).

Decline and dieback are usually chronic and patchy, but can reach epidemic levels with acute tree death if heavy or prolonged rainy periods during the vegetative season are followed by severe drought (Jung, 2009; Jung *et al*., 2018a). In addition to mature trees, naturally regenerated seedlings and understorey trees of *F. sylvatica* can also suffer from Phytophthora root and collar rot (Jung, 2009; Jankowiak *et al*., 2023), and twig blight up to 3 m above ground (Nechwatal *et al*., 2011).

Surveys of more than 350 beech stands across Europe unveiled an array of 16 *Phytophthora* species from eight phylogenetic clades being associated with the decline. Most common, and often causing large bark cankers and severe dieback, were *P. plurivora* and *P.* ×*cambivora*, and, more frequently in urban stands, *P. cactorum*. While *P. plurivora* is often dominant on calcareous soils, *P.* ×*cambivora* prefers acidic heavy soils, although these site preferences are not exclusive (Jung, 2009; Jung *et al*., 2013a, 2018a; Corcobado *et al*., 2020). Other species with scattered distributions include *P. chlamydospora*, *P. europaea*, *P. gonapodyides*, *P. pseudosyringae*, *P. psychrophila*, *P. quercina*, *P. syringae*, *P. tubulina*, *P. uliginosa* and *P. vulcanica*, while *P. cinnamomi* is usually restricted to regions with mild winters such as Portugal and the United Kingdom (Motta *et al*., 2003; Jung *et al*., 2003b, 2005, 2013a, 2016, 2017a, 2018a, 2019; Cacciola *et al*., 2005; Hartmann *et al*., 2006; Orlikowski *et al*., 2006; Brown and Brasier, 2007; Munda *et al*., 2007; Vettraino *et al*., 2008a; Černý *et. al*., 2009; Jung, 2009; Jung and Burgess, 2009; Schmitz *et al*., 2009; Stępniewska and Dłuszyński, 2010; Telfer *et al*., 2015; Corcobado *et al*., 2020; Štraus *et al*., 2023; Martínez-Arias *et al*., 2024; Horta Jung *et al*., 2025; Ogris *et al*., 2026).

Currently, the aerial pathogens *P. kernoviae* and *P. ramorum* occur on beech exclusively in the United Kingdom, where the humid climate and the presence of the sporulating leaf host *Rhododendron ponticum* frequently allow the production of caducous sporangia on infected foliage, and their subsequent aerial dispersal onto adjacent beech stems (Brasier *et al*., 2005; Brown and Brasier, 2007; Jung *et al*., 2018a; Kartakis *et al*., 2026). In the eastern United States of America, *P. cactorum*, *P. plurivora* and *P. pini* are causing root rot, bleeding bark cankers and mortality on amenity trees of the non-native *F. sylvatica* (Jung *et al*., 2005; Weiland *et al*., 2010). Likewise in Chile, *P.* ×*cambivora* was isolated from bleeding bark cankers of *F. sylvatica* (Jung *et al*., 2018b). In under-bark inoculation tests and soil infestation trials, *P. cinnamomi*, *P. plurivora* (before 2009 designated as *P. citricola*), and *P.* ×*cambivora* showed high aggressiveness to *F. sylvatica* (Fleischmann *et al*., 2002; Brasier and Jung, 2003; Jung *et al*., 2003b, 2017a, 2017b; Corcobado *et al*., 2022). The most common and/or most aggressive species to *F. sylvatica* are non-native invasive pathogens introduced to Europe from East Asia (*P. cinnamomi*, *P. plurivora*, *P. ramorum*, *P.* ×*cambivora*; Jung *et al*., 2021, 2024; Shakya *et al*., 2021; Mullet *et al*., 2023), North America (*P. cactorum*; Bourret *et al*., 2022), and Chile (*P. kernoviae*; Jung *et al*., 2022). In contrast, the *Phytophthora* species with only scattered distribution in beech stands and usually lower aggressiveness to beech are considered native to Europe (*P. europaea*, *P. pseudosyringae*, *P. psychrophila*, *P. quercina*, *P. tubulina*, *P. uliginosa* and *P. vulcanica*; Brasier and Jung, 2003; Jung *et al*., 2016, 2017a, 2017b; Mullet *et al*., 2024), or of cryptic origin (*P. chlamydospora*, *P. gonapodyides*, *P. syringae*; Jung *et al*., 2016).

Large-scale surveys demonstrated that 80% of beech nursery stands and nearly 100% of beech plantings assessed across Europe were infested with, nine and 11 *Phytophthora* species, respectively, emphasizing the importance of the nursery pathway for the spread of destructive *Phytophthora* pathogens and diseases into forests (Jung *et al*., 2016). As with the declining mature beech stands, the most aggressive pathogens to beech, *P. plurivora*, *P.* ×*cambivora* and *P. cactorum*, were also most common in young beech plantings. Recent surveys have also demonstrated involvement of *Phytophthora* pathogens in decline and dieback of *F. sylvatica* at the southernmost edges of its distribution. In Sicily, the previously unknown species *P. vulcanica* was obtained from a beech forest at Mount Etna, while *P.* ×*cambivora*, *P. gonapodyides* and *P. megasperma* were found associated with bleeding bark cankers and dieback of beech trees in two forests in the Nebrodi Mountains (Jung *et al*., 2017a, 2019; Riolo *et al*., 2022). In one stand, the new species *P. tubulina*, described from a beech forest in Austria, was also detected (T. Jung, M. Horta Jung and S.O. Cacciola, unpublished). Using metabarcoding, *P. vulcanica* was also recently detected in a submediterranean montane forest in the Sistema Central mountain range of Spain in the rhizosphere of a declining *F. syl-*

vatica tree (Martínez-Arias *et al*., 2024). In Portugal, *P. cinnamomi* and *P.* ×*cambivora* were isolated from rhizosphere soil and bark cankers of declining *F. sylvatica* trees in mature, planted montane forests of the National Parks Peneda-Gerês and Serra da Estrela (Horta Jung *et al*., 2025). In Slovenia, during a recent systematic survey of beech forests, *Phytophthora* species (*P. cactorum*, *P. gonapodyides*, *P. hedraiandra*) were only found associated with declining beech trees in areas with afforestations or highly frequented forest trails, highlighting the importance of human activities in the spread of *Phytophthora* pathogens (Ogris *et al*., 2026).

Using the CLIMEX niche model with refined parameter values, updated climate data, and *P. ramorum* occurrence records exclusively from symptomatic forest trees, 10% of the European area was identified as being climatically suitable for infections by *P. ramorum* and disease development in forest trees (Kartakis *et al*., 2026). Overlaying these climatically suitable areas with distribution data of both *F. sylvatica* and important sporulating leaf hosts, 2,577 km^2 of European beech forests, situated mainly in Austria, Germany, Northern Italy, Belgium and the United Kingdom, were found to be at risk, with potential annual economic losses of €96–130 million (Kartakis *et al*., 2026).

Root and collar rot epidemic of alders

First reported from the United Kingdom and Germany in 1995, this destructive alder-specific disease was already spreading rapidly across Western, Central and Northern Europe (Brasier *et al.,* 1995; Gibbs, 1995; Hartmann, 1995; Gibbs *et al.,* 1999, 2003; Streito *et al.,* 2002; Nagy *et al.,* 2003; Jung and Blaschke, 2004; Schumacher *et al.,* 2006; Černý and Strnadová, 2010; Jung *et al.,* 2013a, 2018a; Štěpánková *et al.,* 2013; Haque *et al.,* 2015; Redondo *et al.,* 2015; Trzewik *et al.,* 2015; Corcobado *et al.,* 2023; Gomes Marques *et al.,* 2024; Mizeriene *et al.,* 2025).

Typical symptoms of this disease include root rots, bleeding bark cankers with flame-shaped, orange-brown lesions of the inner bark, and rusty or tarry spots on bark surfaces (Figure 1 F), as well as small-sized and often chlorotic foliage, thinning and dieback of crowns, and sometimes heavy fructification with unusually small cones (Gibbs *et al*., 2003; Jung *et al.,* 2013a, 2018a). The bark cankers usually start from the collar regions of trees (collar rot), but where exceptional flooding has occurred, aerial cankers can occur on stems. Affecting in nature all European alder species (*Alnus* spp.) except *A. viridis*, i.e. *A. cordata*, *A. glutinosa*, *A. incana* and *A. lusitanica* (Figure 1 F), the disease is widespread along rivers and streams, and occurs in wetlands (alder carrs) and in forest plantations. Mortality rates of alder trees can exceed 50% along rivers, and reach 100% in permanently waterlogged swamps and alder carrs (Jung and Blaschke, 2004; Jung *et al.,* 2013a, 2018a; Horta Jung *et al.,* 2025).

The causal agents are the interspecific hybrid *P.* ×*alni* (originally described as *P.* ×*alni* ssp. *alni*; Brasier *et al.,* 2004) and its maternal and paternal parents *P.* ×*multiformis* and *P. uniformis* (originally described as *P.* ×*alni* ssp. *multiformis* and *P.* ×*alni* ssp. *uniformis*, respectively; Brasier *et al.,* 2004). These pathogens together form the "*P.* ×*alni* complex" (Brasier *et al.,* 2004; Ioos *et al.,* 2006; Husson *et al.,* 2015; Aguayo *et al.,* 2016). While *P. uniformis* was introduced to Europe from the Pacific Northwest of North America (Adams *et al.,* 2010; Aguayo *et al.,* 2013), the origin of *P.* ×*multiformis* remains unknown. Other *Phytophthora* species, including *P. plurivora*, *P. alpina*, *P. cactorum*, *P. gonapodyides*, *P. lacustris*, *P. multivora*, *P. polonica*, *P. pseudosyringae* and *P. siskiyouensis*, are occasionally reported to cause root rot or limited bark cankers on riparian alder trees, but usually do not lead to epidemic mortality (Jung and Blaschke, 2004; Belbahri *et al.,* 2006; Jung *et al.,* 2013a, 2018a, 2024; Haque *et al.,* 2014; Pérez-Sierra *et al.,* 2015; Aday Kaya *et al.,* 2018; O'Hanlon *et al.,* 2019; Bregant *et al.,* 2020, 2023a; Corcobado *et al.,* 2023; Rial-Martínez *et al.,* 2023; Tkaczyk *et al.,* 2023; Mizeriene *et al.,* 2025). In their native origin in Oregon and Alaska, *P. siskiyouensis* and *P. uniformis* have scattered distributions in riparian ecosystems, occasionally causing bark cankers and decline of *A. incana* subsp. *tenuifolia* and *A. rubra* trees (Adams *et al.,* 2010; Aguayo *et al.,* 2013; Sims *et al.,* 2015).

Inoculation trials have demonstrated that *P.* ×*alni* can be highly aggressive, particularly on logs from mature *A. glutinosa*, and on saplings it often causes lesions and mortality rates comparable to *P. uniformis* and *P.* ×*multiformis* (Brasier and Kirk, 2001; Zamora-Ballesteros *et al*., 2017; Macháčová *et al*., 2024). Host responses also vary among *Alnus* species, with high susceptibility reported for *A. glutinosa*, *A. incana* and *A. cordata*, intermediate susceptibility for *A. viridis*, and higher tolerance for *A. rubra* (Jung and Blaschke, 2006). Screening tests of *A. glutinosa* genotypes from riparian populations in Bavaria and Belgium demonstrated that susceptibility to *P.* ×*alni* varied widely, with field-surviving trees tending to show higher tolerance (Jung and Blaschke, 2006; Chandelier *et al.,* 2016). These results indicate feasibility of potential future resistance screening programmes.

Extensive surveys along 20,000 km of rivers and streams and in more than 3,000 forest stands in Bavaria, Germany, and in nurseries and planting sites across

Europe, have demonstrated that the primary introduction of the pathogens from the "*P.* ×*alni* complex" to river systems occurred in most of the studied cases by use of infested alder nursery stock for riparian plantings or afforestations in their catchments (Jung and Blaschke, 2004; Schumacher *et al.,* 2006; Jung *et al.,* 2016, 2018a; Bačová *et al.,* 2024; Green *et al.,* 2025). In several rivers, the source of the pathogens could be traced back to commercial fish farms (Jung and Blaschke, 2004).

Before 2010, distribution of the alder epidemic was limited to Southern Europe. There was only one report of *P. uniformis* from an *A. cordata* seedling in a nursery in Tuscany, Italy (Santini *et al.,* 2001), and records of the "*P.* ×*alni* complex" causing bark cankers on riparian *A. glutinosa* trees along the Rhône River in Southern France and several watercourses in Southwestern France (Streito *et al.,* 2002). Later, isolation tests from bleeding bark cankers of riparian *A. glutinosa* trees led to the record of *P.* ×*multiformis* in Sardinia in 2010, and of *P.* ×*multiformis* and *P.* ×*alni* in Croatia in 2012 (Jung *et al.,* 2017b; 2018a). During the past 15 years alder root and collar rot has also spread across Portugal and Spain (Solla *et al.,* 2010; Pintos-Varela *et al.,* 2012, 2017; Jung *et al.,* 2016; Kanoun-Boulé *et al.,* 2016; Gomes Marques *et al.,* 2024; Horta Jung *et al.,* 2025). As in the rest of Europe, in the Iberian peninsula *P.* ×*alni* is the primary cause of the alder epidemic (Solla *et al.,* 2010; Jung *et al.,* 2016; Kanoun-Boulé *et al.,* 2016; Gomes Marques *et al.,* 2024; Horta Jung *et al.,* 2025), although *P. uniformis*, *P.* ×*multiformis* and several other *Phytophthora* species are also occasionally found (Pintos-Varela *et al.,* 2012, 2017; Haque *et al.,* 2014; Kanoun-Boulé *et al.,* 2016; Bregant *et al.,* 2023a; Rial-Martínez *et al.* 2023; Gomes Marques *et al.,* 2025).

Recently, the potential distribution of *P.* ×*alni* in Europe was modelled, based on a dataset with presence and absence records of the pathogen from 1,189 European locations and a range of bioclimatic variables (Gomes Marques *et al.,* 2024). An early model developed in northeastern France demonstrated that disease incidence increased with decreasing distance of stem bases from the midwater lines, and with increasing river width, summer temperatures of river water, riverbank clay content, and with reduced water flow (Thoirain *et al.,* 2007). Using Bayesian belief network methodology to integrate diverse information from scientific literature, expert knowledge, and empirical data on the factors affecting the survival and infection ability of *P.* ×*alni* in riparian habitats, the "Alder Decline Network (ADnet) management tool" has been developed. The ADnet tool indicated mild temperatures and high precipitation as key factors for pathogen survival, and flood timing, water velocity and soil type as having the strongest influences on disease incidence. The ADnet tool helps to predict disease incidences, and supports ecosystem management decisions at local or regional levels across Europe, including the Mediterranean (Gomes Marques *et al.,* 2024).

Extreme unseasonal heavy rain and floodings that promote *Phytophthora* spread and infections of tree roots and bark are increasingly frequent, often alternating with severe droughts and heatwaves which interact synergistically with *Phytophthora* root losses causing tree decline and dieback (Jung *et al.,* 2000; 2018a; Jung, 2009). To identify resilient genotypes and contribute to mitigation of alder decline, Gomes Marques *et al.* (2025) assessed individual and combined effects of a simulated extreme heatwave and infection by *P.* ×*multiformis* on 2-year-old saplings from 11 populations and six genetic groups of *A. glutinosa* and *A. lusitanica* sampled from Sweden to Morocco. Differences in responses to the combined stressors were found between the populations and genetic groups of both alder species. While *A. lusitanica,* as expected, showed higher tolerance to heat stress than *A. glutinosa*, the latter species was generally more resilient than *A. lusitanica* to the combination of both stressors.

A genotype–fitness relationship has been suggested for *P.* ×*alni*, as isolates belonging to the Pxa-1 genotype showed higher fitness and pathogenicity compared to rarer genotypes (Pecka *et al*., 2026). However, information remains limited on the genetic diversity of alder-associated *Phytophthora* species in Mediterranean countries. Most available data come from France, where isolates were largely collected in the northern part of the country; 11 multilocus genotypes (MLGs) were identified among 165 *P.* ×*alni* isolates, three MLGs among 30 *P. uniformis* isolates, and four MLGs among 33 *P.* ×*multiformis* isolates, and three of these MLGs were also detected in the south-eastern 'Durance' population, close to the Mediterranean Sea (Aguayo *et al*., 2016). In Spain, the common European MLGs Pxa-1 (*P.* ×*alni*) and Pu-E1 (*P. uniformis*) were recorded in 11 and 13 isolates, respectively, while a rare *P.* ×*alni* MLG (Pxa-6) was detected in a single isolate (Aguayo *et al*., 2016; Mizeriene *et al*., 2020). Records from other Mediterranean countries are sparse, with Pu-E1 reported once in Slovenia, and an Italian *P. uniformis* isolate was assigned to the infrequent MLG Pu-E2 (Aguayo *et al*., 2016).

PHYTOPHTHORA DISEASES IN AGRICULTURE AND HORTICULTURE

Decline of olive and wild olive

Olive (*Olea europaea*) is a woody crop of major agronomic importance in the Mediterranean Basin, where it

has been cultivated for millennia, and remains a dominant component of agricultural landscapes (Zohary *et al*., 2012). Together with its wild variety (*O. europaea* var. *sylvestris*), *O. europaea* is an iconic tree species in Mediterranean agroecosystems, contributing significantly to regional economies, traditional farming systems, and providing ecosystem services. In recent decades, however, olive cultivation has increasingly been challenged by several emerging and re-emerging diseases, most notably the outbreak of *Xylella fastidiosa* in southern Italy, which has caused extensive tree mortality and severe socio-economic impacts (Calderoni *et al*., 2025).

In the context of increasing phytosanitary threats, soil- and water-borne pathogens have also gained renewed attention, particularly species of *Phytophthora* responsible for destructive root and collar rot diseases in numerous woody crops (Jung *et al*., 2018a; Brasier *et al*., 2022; Chen *et al*., 2022; Legrifi *et al*., 2024).

The first record of *Phytophthora* infecting olive trees in Mediterranean regions was in 1968, when *P. citricola* and *P. megasperma* were identified associated with root and collar rots of olive in Greece (Kouyeas and Chitzanidis, 1968; Erwin and Ribeiro, 1996). *Phytophthora megasperma* was later reported from newly established olive plantations in Spain that were severely affected by wilt, dieback and mortality under waterlogging conditions (Sánchez-Hernández *et al*., 1997; 1998), and in Sicily from new commercial olive plantings (Cacciola *et al*., 2021). Together with *P. megasperma*, *P. palmivora* was repeatedly isolated from diseased olive plants in nurseries and young orchards in Spain (Sánchez-Hernández *et al*., 1998) and southern Italy (Agosteo *et al*., 2000; Cacciola *et al*., 2000), and more recently in North African countries, particularly Morocco and Tunisia (Chliyeh *et al*., 2014; Msairi *et al*., 2016; Gharbi *et al*., 2020). In Italy, *P. palmivora* was also reported to be responsible for wilt and collapse of young olive trees, in association with *Verticillium dahliae* (Lo Giudice *et al*., 2010). Some of the early identifications of *P. palmivora* on olive should probably be re-assigned to the recently described *P. heterospora*, which is a sister species of *P. palmivora* (Scanu *et al*., 2021).

Phytophthora inundata, formally described by Brasier *et al*. (2003), was first isolated from the roots of declining olive trees in flooded sites in Spain (Brasier *et al*., 2003). This pathogen was subsequently reported in Italy, associated with root rot in olive groves in Sicily (Cacciola *et al*., 2007b), and later in Türkiye, causing necrotic collar and stem lesions on young olive trees (Kurbetli *et al*., 2016).

Several other *Phytophthora* taxa have also been reported on cultivated and wild olive, mainly in Italy (Figure 1, D and E) and Spain, including *P. acerina*, *P. asparagi*, *P. bilorbang*, *P. cactorum*, *P. crassamura*, *P. cryptogea*, *P. kelmanii*, *P. niederhauserii*, *P. pini*, *P. plurivora*, *P. pseudocryptogea*, *P. sansomeana*, *P. syringae*, and the yet undescribed *P.* taxon paulensis (Cacciola *et al*., 2011; González *et al*., 2017; Santilli *et al*., 2020; Deidda *et al*., 2022; 2025; Linaldeddu *et al*., 2023; Legrifi *et al*., 2024).

Within the context of increasing pathogen species diversity on olive, two newly described *Phytophthora* species have emerged as pathogens on olive trees in Italy. *Phytophthora heterospora* was isolated in southern Italy from young declining olive trees with root and collar rots (Cacciola *et al*., 2011; Scanu *et al*., 2021). Phylogenetically close to *P. palmivora*, *P. heterospora* can be distinguished by its production of pseudoconidia, a unique feature within *Phytophthora* (Scanu *et al*., 2021). Symptoms on olive caused by *P. heterospora* include leaf chlorosis, wilting, defoliation, and dieback, often associated with orange-brown, flame-shaped necrotic lesions originating from collar infections and extending up the stems (Figure 2, B and C). Severity of symptoms in the field, and results from pathogenicity tests, indicate that *P. heterospora* is an emerging threat to olive cultivation, mainly in young plantations where infections are favoured by particular agronomic practices and recurrent irrigation.

The second species, *P. oleae*, was originally described as the causal agent of fruit rot on mature olive trees in the Calabria region of Italy (Ruano-Rosa *et al*., 2018), and was subsequently isolated from root rots of wild olive trees in Spain and Sardinia, Italy (González and Sánchez, 2020; Deidda *et al*., 2025). In soil infestation tests with wild olive seedlings frequently used as rootstock of cultivated olive, *P. oleae* was highly aggressive, causing significant reductions in root biomass (Deidda *et al*., 2025).

Whether *P. heterospora* and *P. oleae* are recent introductions into olive-growing areas remains unclear, although a possible tropical origin has been suggested (Scanu *et al*., 2021). Both species may have been misidentified in the past, as their morphologically similar close relatives; *P. palmivora* for *P. heterospora*, and members of the *P. citricola* species complex for *P. oleae* (Erwin and Ribeiro, 1996; Scanu *et al*., 2021; Jung *et al*., 2024). A similar scenario may also apply for *P. crassamura*, previously misidentified as *P. megasperma*, and to other Clade 2 species within the *P. citricola* complex (Ruano-Rosa *et al*., 2018; González and Sánchez, 2020; Jung *et al*., 2024; Deidda *et al*., 2025).

These findings highlight the increasing frequency and diversity of *Phytophthora* taxa in olive nurseries and groves, emphasizing the role of infected propagative plant material as major pathway for pathogen dissemination

Figure 2. Phytophthora diseases in Mediterranean tree crops. A. Containerized healthy-looking olive trees (*Olea europaea* var. *europaea*), from a nursery in Italy infested by *Phytophthora heterospora*. B. Young olive tree in a recently established orchard in Sardinia, killed by root and collar rot caused by *P. heterospora*. C. Girdling collar rot canker (arrow showing upper margin), caused by *P. heterospora* on a recently planted olive tree in Sardinia. D. Young planted almond (*Prunus dulcis*) tree in Spain with gum exudation (arrows), indicating inner bark necrosis caused by *P. niederhauserii*. E. Inner bark necrosis (arrows) of a young nursery-grown almond tree, caused by *P. niederhauserii* in Spain. F. Brown rot (arrow) of an orange fruit (*Citrus sinensis*) caused by *P. citrophthora* in Sicily. G. Orange orchard in the Valencian region of Spain that was almost completely submerged during an extreme flood in August 2024. H. Orange tree showing gum exudation and inner bark necrosis of the highly susceptible grafted cultivar above the resistant rootstock, due to *P. citrophthora* infection during the extreme flood of August 2024. I. Avocado (*Persea americana*) tree in Türkiye with small-sized chlorotic foliage, crown thinning and die-back, due to root rot caused by *P. cinnamomi*. J. Persimmon (*Diospyros kaki*) tree in a Spanish orchard, with acute wilting due to root rot caused by *P. palmivora*.

(Cacciola *et al*., 2011; Jung *et al*., 2016; Scanu *et al*., 2021; Figure 2 A). For example, detection of *P. nicotianae* in olive plantations in Argentina was linked to importation of Mediterranean olive varieties from Italy (Vettraino *et al*., 2009), where this pathogen was previously reported in southern regions (Cacciola *et al*., 2007b). Similarly, *P. bilorbang* was detected in Calabria (southern Italy), where it caused root rot on cultivated olive plants, probably as an opportunistic pathogen (Santilli *et al*., 2020). *Phytophthora bilorbang* is widespread in Sardinian nurseries and in wild olive stands (Deidda *et al*., 2022, 2025), further supporting the role of plant movement in dissemination of *Phytophthora* species.

In addition to their presence in cultivated olives (Azenzem *et al*., 2024; Legrifi *et al*., 2024), several of these *Phytophthora* taxa have been shown to cause diseases in natural and seminatural ecosystems (González *et al*., 2017, 2019; Deidda *et al*., 2025). This indicates that olive orchards may act as sites of pathogen introductions, and as potential reservoirs from which invasive *Phytophthora* species can spread into adjacent habitats (Figure 2 B). Spillover events raise concerns for Mediterranean landscapes, where olive-growing areas are often closely interconnected with native vegetation (Figure 3). The movement of infected olive propagative material, combined with water runoff, irrigation practices, and soil transfer through agricultural activities, can facilitate pathogen dispersal beyond original sites of introduction. Once established in natural ecosystems, *Phytophthora* species may persist in soil and water, increasing the likelihood of recurrent infections and long-term ecosystem alteration. Deidda *et al.* (2025) have further highlighted the capacity of introduced *Phytophthora* species to establish in surrounding environments, potentially threatening native plant communities and disrupting ecological balances. These considerations underscore the importance of implementing strict phytosanitary measures in olive nurseries and plantations, alongside effective monitoring and early detection strategies, to limit pathogen spread and reduce risks of long-term economic and ecological impacts (Jung *et al*., 2016; Brasier *et al*., 2022; Morales-Rodríguez *et al*., 2025).

Decline of avocado

Although Mexico is the leading producer of avocado (*Persea americana*) (FAOSTAT 2023), with increasing interest in the economic and nutritional benefits of avocado fruit in the mid to late 20th Century, commercial production has become important in other countries, including in the Mediterranean region. During the past 50 years, avocado production has greatly increased with Israel, Morocco and Spain as the main producers, followed by Türkiye and Portugal (FAOSTAT 2023).

Phytophthora infections are the most important biotic problems affecting production of avocado in all areas where the crop is grown (Coffey, 1992; Pérez-Jimenez, 2008). *Phytophthora cinnamomi*, one of the most polyphagous *Phytophthora* species and presently classified as a regulated non-quarantine pest (RNQP, Annex IV) in the EPPO region (EPPO, 2004; 2025), is the most common species causing avocado root rot, with decline and mortality occurring in conditions of high soil moisture contents, which are conducive to pathogen infection and disease development (Zentmyer, 1980; Erwin and Ribeiro, 1996).

Other species of *Phytophthora* have been reported, though at lower frequencies, from damaged avocado, including *P. cactorum*, *P. mengei* (previously as *P. citricola;* Hong *et al*., 2009), *P. citrophthora*, *P. cryptogea*, *P. heveae*, *P. multivora*, *P. niederhauserii*, *P. nicotianae*, and *P. palmivora* (Erwin and Ribeiro, 1996; Hong *et al*., 2009; Rodriguez-Padron *et al*., 2018; Kurbetli *et al*., 2020). In Israel, *P. cinnamomi* was first isolated from avocado in 1982, and the number of orchards infested increased during subsequent years (Baum and Pinkas, 1988; Pérez-Jimenez, 2008). In Türkiye, *P. cinnamomi* was by far the most common species isolated from declining avocado trees (Figure 2 I) in Antalya and Mersin provinces, with only two additional isolates of other species recovered, one of *P. cryptogea* and one of *P. palmivora* (Kurbetli *et al*., 2020). In Italy, *P. cinnamomi* was first reported as causal agent of Phytophthora root rot of avocado in 1998 (Cacciola *et al*., 1998).

As Phytophthora root rot progresses in avocado, feeder roots are increasingly destroyed, resulting in a reduced ability to absorb water, leading to symptoms of drought (Zentmyer, 1980; Phillips, 1993; Pérez-Jimenez, 2008). Chlorotic foliage, smaller than normal, develops on affected trees, followed by wilting and early leaf abscission; affected trees have sparse crowns and produce reduced quantities of small fruits (Figure 2 I).

Losses of avocado caused by *P. cinnamomi* vary. In Mexico, Téliz (2000) reported that disease incidence ranged between 5-90% in avocado growing areas. Some regions in California had 60-90% infection (Coffey, 1989). In the Mediterranean Basin where disease has been recorded, high numbers of infected orchards are reported: for example, in Andalusia (Spain), 40% of orchards were affected (Pérez-Jiménez *et al*., 2005). More recently, it was demonstrated that approximately half of the avocado orchards established in the Canary Islands of Spain were affected by Phytophthora root rot (Rodriguez-Padron *et al*., 2018).

Phytophthora diseases of citrus

Phytophthora species are the most severe soil-borne pathogens of citrus in the Mediterranean Basin, and Phytophthora diseases are among the major limiting factors to the citrus industry in this macro-region. Seedling damping-off, foot and crown rot, fibrous root rot, leaf and twig blight, Phytophthora gummosis and fruit brown rot (Figure 2, F to H) are a long-recognized disease complex caused by these pathogens, affecting trees and fruits through the pre- and post-harvest phases of citrus production (Cacciola and Magnano di San Lio, 2008; Rovetto *et al*., 2024a). Phytophthora disease outbreaks result from the aquatic nature of the *Phytophthora* infectious stage. Infection cycles are triggered by the release and dispersal of zoospores in free water, and infections of plant roots and aerial tissues depend on soil water and wetting duration, respectively (Judelson and Blanco, 2005; Cacciola and Magnano di San Lio, 2008). Root asphyxiation due to soil waterlogging is a major predisposing factor to belowground *Phytophthora* infections of citrus trees, while rain splashing of soilborne inoculum is responsible for aerial infections. The increasingly frequent flooding events in the Mediterranean Basin due to extreme weather conditions such as the floodings in Spain in 2024, are likely to favour development of new *Phytophthora* infections, because zoospores can reach and infect the stems of susceptible cultivars above the grafting points of resistant rootstocks (Figure 2, G and H).

Phytophthora citrophthora and *P. nicotianae* are the most common species affecting citrus orchards of the Mediterranean Basin (Cacciola and Magnano di San Lio, 2008; Kurbetli, 2024). *Phytophthora citrophthora* is likely responsible for the pandemic of Phytophthora gummosis and foot and crown rot that impacted the citrus industry during the second half of the 19th century, and from which originated the widespread use of *Phytophthora*-resistant rootstocks, such as sour orange (*Citrus* × *aurantium*), in commercial citrus orchards. *Phytophthora citrophthora* is the main causal agent of trunk and scaffold branch gummoses. This pathogen is also responsible for outbreaks of fruit brown rot, as it adapts to a partially aerial lifestyle (Jung *et al*., 2024), and is active during cool months in the Mediterranean Basin, when fruits of most commercial citrus varieties ripen between late autumn and early spring (Dirac *et al*., 2003; Cacciola and Magnano di San Lio, 2008; Alvarez *et al*., 2009a; Khanchouch *et al*., 2017). Ripe fruits are more susceptible to *Phytophthora* infection than immature fruits, and in the Mediterranean climate this period is also the wettest time of the year.. Although originally described as having persistent sporangia, Jung *et al*. (2024) demonstrated that *P. citrophthora* and its closely related species *P. pseudocitrophthora* and *P.* ×*lusitanica* produce low proportions of caducous sporangia facilitating aerial infections.

Occasionally, in late spring and early autumn, citrus brown rot outbreaks may be caused by *P. nicotianae*, which exclusively produces non-caducous sporangia. However, these outbreaks are not as severe as those caused by *P. citrophthora*, and generally remain confined to fruits in the lower tree canopy, close to the ground, which are exposed to rain splash.

In Sicily during recent years, severe outbreaks of fruit brown rot caused by *P. citrophthora* (Figure 2 F) affecting fruits throughout plant canopies, have occurred after Mediterranean-type hurricanes known as 'medicanes' (Cacciola and Gullino, 2019). In Spain and Tunisia, branch gummosis caused by *P. citrophthora* was reported on clementine (*Citrus* × *clementina*), which is more susceptible than other citrus varieties (Alvarez *et al*., 2008). Emergence of this disease was favoured by mechanical branch girdling, an agronomic practice applied specifically to increase fruit production in this *Citrus* variety (Vicent *et al*., 2012).

In Italy and Spain, snail and slug feeding on fruit infected by brown rot have been suggested to contribute to spread of *P. citrophthora* inoculum in citrus orchards (Magnano di San Lio and Pennisi, 1984; Alvarez *et al*., 2009b). Although *P. citrophthora* has long been regarded as a polyphagous species widely distributed across the Mediterranean basin, citrus remain among its most economically important hosts. The recent description of *P. pseudocitrophthora*, the ex-type of which was isolated in Sicily from rhizosphere soil of *Platanus orientalis* in a riparian forest, highlights cryptic diversity within the *P. citrophthora* complex. Because additional *P. pseudocitrophthora* isolates have been recovered from several Mediterranean countries, including citrus-associated substrates in Morocco (*C. limon* rhizosphere) and Portugal (*C. sinensis* fruit), a proportion of historical Mediterranean records attributed to *P. citrophthora* may warrant re-evaluation using molecular multilocus identification approaches (Jung *et al*., 2024).

Phytophthora nicotianae has a particularly wide host range, and higher optimum temperature than *P. citrophthora* (Cacciola and Magnano di San Lio, 2008; Panabières *et al*., 2016). Differences in cardinal temperatures between these two *Phytophthora* species partly explain their ecology and particularly their distinct seasonal patterns. *Phytophthora nicotianae* preferentially infects fibrous roots, and in summer is more active than *P. citrophthora*, which is inhibited by high temperatures. In citrus groves of the Mediterranean Basin, both *Phytoph-*

thora species, which are self-sterile, reproduce clonally, consistent with the exclusive presence of mating type A1 of *P. nicotianae* (Mammella *et al*., 2013; Biasi *et al*., 2016), while the sexual form of *P. citrophthora* has never been observed. Analyses of a global collection of *P. nicotianae* isolates from various host plants, using mitochondrial and nuclear single nucleotide polymorphisms (SNPs) as genetic markers, revealed that isolates from citrus were a distinct subpopulation (Mammella *et al*., 2011; 2013; Biasi *et al*., 2016). Whether this discovery is indicative of host specificity remains to be verified.

In citrus groves of many Mediterranean countries, including Egypt, Italy, Spain and Türkiye, *P. nicotianae* is more widespread than *P. citrophthora*, while in others, such as Tunisia, *P. citrophthora* prevails. A recent survey of commercial citrus orchards in Sicily (southern Italy) recovered *P. nicotianae* from 31 of 50 soil samples and eight of ten sampling sites, using leaf baits, while *P. citrophthora* was recovered from only 21 samples and six sampling sites (Conti Taguali *et al*., 2025). Conversely, analysis of samples using high-throughput metabarcoding targeting either the ITS1 region or the *RPS10* gene as barcodes, showed that *P. citrophthora* was the dominant species, indicating that the method of analysis may affect results.

In general, high throughput metabarcoding and plant baiting detection techniques complement each other for the study of *Phytophthora* communities in citrus orchards (La Spada *et al*., 2022). Baiting proved to be very effective for detecting aggressive species, such as *P. citricola*, *P. citrophthora*, and *P. nicotianae*, and was therefore the technique used to monitor the presence of potentially pathogenic *Phytophthora* species in recycled wastewater from a constructed wetland used for citrus orchard irrigation (Parlascino *et al*., 2025). Frequently, *P. citrophthora* and *P. nicotianae* co-occur in groves, and mixed infections can be found in individual trees and even in individual fruits.

Some studies have addressed relationships between inoculum load of these two *Phytophthora* species in soil, host plant susceptibility, environmental factors, and disease level, to determine critical thresholds of soil inoculum density, and to forecast infection risk and optimize disease management (Cacciola and Magnano di San Lio, 2008; Khanchouch *et al*., 2017; Boudoudou *et al*., 2025). Other *Phytophthora* species have been occasionally recovered from Mediterranean Basin citrus groves, including *P. palmivora*, *P. cactorum*, *P. citricola*, *P. hibernalis* and *P. syringae* (Ahmed *et al*., 2013; Rovetto *et al*., 2024a). These pathogens were recovered in restricted geographical areas and ecological niches from infected tissues and soil, using selective media and plant baits. These pathogens were recovered mostly from soil, and fruits with brown rot symptoms lying on soil surfaces, and only occasionally from symptomatic fruits picked from the trees, but never from bark cankers.

Phytophthora hibernalis and *P. syringae* are active only during winter, due to their low optimum temperature (approx. 20 °C). Although the pathogens may cause local outbreaks of fruit brown rot, generally they do not pose serious threats to citrus production in the Mediterranean Basin. However, possible presence of these two species in soil of citrus orchards imposes restrictions to fruit exports, as both are classified as quarantine pathogens by some citrus producing and importing countries, such as China (Parlascino *et al*., 2025).

The role of *P. citricola* as a citrus pathogen in the Mediterranean Basin should be further assessed. A recent survey of citrus orchards in Sicily showed that this species, although not widespread (three of 50 analysed soil samples), was associated with symptoms of fibrous root rot and decline of citrus trees (Conti Taguali *et al*., 2025). A recent record has further expanded the list of *Phytophthora* species associated with citrus diseases in the Mediterranean Basin. *Phytophthora inundata*, probably an opportunistic but aggressive pathogen, was recovered from fibrous roots of declining mature citrus trees, together with *P. nicotianae* (Bua *et al*., 2025). Co-inoculations of citrus saplings with both species produced more severe root rot symptoms than inoculation with the individual species, indicating additive effects of mixed infections.

Application of high-throughput analytical techniques has provided breakthroughs for exploring the diversity of *Phytophthora* communities in soil of citrus orchards, and has given insights into ecological and agronomic factors shaping their composition, including geographical site, soil type, rootstock type, tree age, cropping system, and climate change (La Spada *et al*., 2022; Conti Taguali *et al*., 2025). Targeted high-throughput metabarcoding analyses of soil samples from Sicilian citrus orchards detected, in addition to *P. citrophthora*, *P. nicotianae* and *P. citricola*, several other known *Phytophthora* species, including *P. occultans*, *P. oleae*, *P. pachypleura*, an amplicon sequence variant (ASV) matching *P. crassamura* and *P. megasperma*, which are closely related and difficult to distinguish, as well as multiple ASVs not corresponding to known *Phytophthora* taxa. These known and unresolved taxa were rare, except for *P. citrophthora*, *P. nicotianae* and *P. citricola*, indicating that citrus orchards are simple agricultural ecosystems. High-throughput metabarcoding techniques can be particularly useful for surveillance systems to prevent introductions and spread of alien invasive species in the Mediterranean Basin, that

are potential threats for the citrus industry. An example is the recently described *P. mekongensis* (Crous *et al*., 2017), which is common in citrus groves of Vietnam causing trunk gummosis and fruit brown rot, and has been demonstrated to be as aggressive as *P. citrophthora* (Puglisi *et al*., 2017; Van Tran *et al*., 2023).

In a survey of nurseries producing ornamentals and fruit trees in southern Italy using a metabarcoding approach, *P. meadii* and *P. meadii*-like phylotypes were detected in roots and soil of citrus plants grown in pots as ornamentals, and in a commercial citrus orchard (Prigigallo *et al*., 2015, 2016). Although this finding was not confirmed by obtaining living cultures, it is noteworthy that *P. meadii* is a well-known citrus pathogen in south-east Asia, a quarantine organism in the United States of America, and a new pathogen for the Mediterranean region.

Phytophthora root and crown rot of Prunus

Prunus (*Rosaceae*) includes important fruit trees cultivated in the Mediterranean Basin, which play key roles in regional economies, and are important for the development of climate-resilient and sustainable horticultural systems in Mediterranean agriculture. Almond (*Prunus dulcis*), peach and nectarine (*Prunus persica*), apricot (*Prunus armeniaca*), sweet cherry (*Prunus avium*), and plums (*Prunus domestica* and *P. salicina*) represent a considerable proportion of Mediterranean fruit production, and have been traditionally grown under a wide range of agroecological conditions (Bassi *et al.,* 2024). In the Mediterranean Basin *Prunus* spp. are exposed to abiotic stresses, including drought, soil salinity or cold temperatures, and frequent biotic stress, in particular root and crown rot caused by different *Phytophthora* species. Recently, Phytophthora diseases have been aggravated by extreme climatic events, such as intensive rains and floods, or prolonged drought, which favour development of these pathogens leading to increased disease severity and potential yield losses.

A wide range of *Phytophthora* species have been recorded on *Prunus* worldwide, and several are present in the Mediterranean Basin. On almonds, *P. niederhauserii* has caused severe disease in nurseries and orchards. This pathogen was first detected in Spain, causing root rot, stem cankers with gum exudations, and death of almond trees (Figure 2, D and E). The pathogen has subsequently been detected in other almond orchards in Spain and Türkiye (Pérez-Sierra *et al*., 2010; Kurbetli and Deĝirmenci, 2011; Beluzán *et al*., 2022). However, *P. niederhauserii* is not confined to *Prunus*, and has been recorded from at least 33 plant species in 25 families in agricultural and ornamental environments (Abad *et al*., 2014). There are also reports of other *Phytophthora* species on almond. In Türkiye, *P. cactorum*, *P. chlamydospora, P. cinnamomi, P. citrophthora*, *P. megasperma*, *P. nicotianae* and *P. plurivora* have been recorded as causes of root and crown rot, and severe losses (Çiftçi *et al*., 2016; Kurbetli and Yilmaz, 2015; Türkölmez *et al*., 2016b; Kurbetli *et al*., 2025). *Phytophthora acerina* has been isolated from almond trees in California (Forbes, 2020) and Australia (Oswald *et al*., 2023). This species could be a potential threat to almond trees in the Mediterranean region as it has already been detected in Italy on *Acer pseudoplatanus* (Ginetti *et al.,* 2014), olive trees (Linaldeddu *et al*., 2020), and on forestry hosts (Seddaiu and Linaldeddu, 2020; Benigno *et al*., 2023; Jung *et al*., 2024).

On peach and nectarine, *P. inundata* and *P. megasperma* were recorded in nurseries and orchards during surveys across Europe (Jung *et al*., 2016). In Greece, *P. cactorum, P. citrophthora, P. cryptogea, P. drechsleri, P. megasperma, P. nicotianae* and *P. syringae* have been identified causing crown and root rot of stone fruits trees. *Phytophthora cactorum* was the most important species, and *P. citrophthora* and *P. syringae* were locally significant, causing serious yield losses in peach orchards (Thomidis, 2003). *Phytophthora niederhauserii* has also been detected in Spanish nurseries on nectarine and flat peach plants (Pérez-Sierra, unpublished results).

On apricot, *P. cactorum, P. citrophthora*, *P. nicotianae* and *P. tropicalis* were identified causing root and crown rot in a Sicilian nursery (Pane *et al*., 2009). In Türkiye, *P. palmivora* was found in commercial orchards, associated with declining trees (Türkölmez *et al*., 2015a).

On sweet cherry, *P. cryptogea* was reported causing root and collar rot in Italy (Vettraino *et al*., 2008b). This finding was of particular concern because of the aggressiveness of this species to this host, but also to other woody horticultural crops including apple, apricot, peach, walnut, and kiwi. *Phytophthora cryptogea* was also involved in sweet cherry decline in Türkiye (Kurbetli, 2014). *Phytophthora palmivora* has been detected causing root and crown rot in eastern Türkiye (Türkölmez *et al*., 2015b). Jung *et al.* (2016), during their surveys of European nurseries and orchards, also reported *P. cactorum* and *P. chlamydospora* on sweet cherry, and *P. cactorum, P. plurivora, P. sansomeana*, and the undescribed *P.* taxon ´sansomeana-like´ on plum.

PHYTOPHTHORA DISEASES IN NURSERY PRODUCTION FACILITIES

Manifestations of symptoms in *Phytophthora*-infested nurseries are diverse, as summarized by Pérez-Sierra

and Jung (2013). On a global scale, multiple studies have reported various symptoms of *Phytophthora* infections in nurseries, including leaf necrosis, wilting of leaves and shoots, and stem cankers with tarry exudates or gummosis. Belowground symptoms are equally severe, including fine and coarse root losses, cankers on mother roots, abnormal root development, and tap root and collar rots (Abad *et al*., 2014; Henricot *et al*., 2014; Reeser *et al*., 2015; Jung *et al*., 2016; Vettraino *et al*., 2016; Beal *et al*., 2018; Milenković *et al*., 2018; Li *et al*., 2019; Horta Jung *et al*., 2025). Despite these clear disease symptoms, the primary risks are posed by asymptomatic yet infected plants. This lack of symptoms may arise from several factors, including host-pathogen incompatibility, host tolerance, unfavorable environmental conditions for disease progression, or the masking of symptoms following applications of fungicides and fungi-static chemicals such as phosphite.

A rich diversity of *Phytophthora* communities has been recorded on symptomless plants in nurseries (Migliorini *et al*., 2015; Prigigallo *et al*., 2015; Jung *et al*., 2016; Chen *et al*., 2022; Bačová *et al*., 2024; Green *et al*., 2025; Horta Jung *et al*., 2025). Asymptomatic infections allow pathogens to go undetected in visual inspections. Therefore, in addition to visual inspection and traditional detection techniques, standardized application of metabarcoding methods (Català *et al*., 2015; Riddell *et al*., 2019; Green *et al*., 2020, 2025; Rossmann *et al*., 2021; Sarker *et al*., 2021, 2023; La Spada *et al*., 2022; Migliorini *et al*., 2023; Bačová *et al*., 2024) is essential for providing reliable and timely diagnoses of *Phytophthora* presence in nurseries. Nevertheless, best management practices (Figure 4) and integrated approaches, as suggested by Jung *et al*. (2016) and Horta Jung *et al*. (2025), must be urgently adopted to reduce risks and avoid introducing *Phytophthora* species into unaffected orchards, forests and regions. This process primarily involves lifting plant production from the ground to elevated benches, using disinfested substrate mixes, pots, and tools, and implementing water disinfection or filtration. Water management has been recognized as particularly important, since the role of water as both a source and a transporter of *Phytophthora* inoculum has been well-documented. This focus includes irrigation and water reservoir systems (Hong and Moorman, 2005; Yang *et al*., 2013, 2014), as well as natural streams and riparian ecosystems (e.g., Brasier *et al*., 2003; Jung *et al*., 2011, 2018b, 2019, 2020; Seddaiu *et al*., 2020; Corcobado *et al*., 2023; Horta Jung *et al*., 2025).

Consequently, water used in nurseries has been shown to be a primary source for the introduction and proliferation of pathogen inoculum (Hulvey *et al*., 2010; Pérez-Sierra and Jung, 2013; Migliorini *et al*., 2015, 2023; Junker *et al*., 2016; Jung *et al*., 2016; Green *et al*. 2021, 2025; Bačová *et al*., 2024). This contamination, in turn, leads through the planting of infected plants to the spread of the pathogens from waterbodies into horticultural, ornamental, forest and restoration plantings, and through cross-sectoral landscape connectivity into various natural and semi-natural ecosystems (Figure 3).

The Mediterranean Basin is recognized as a global biodiversity hotspot (Myers *et al*., 2000). However, this region faces significant ecological pressure from intensive trade in ornamental plants and trees intended for afforestation, which serve as primary pathways for invasive alien pathogens and pests. This problem is particularly evident with *Phytophthora*, where numerous surveys have shown that nurseries in the Mediterranean region are infested with numerous species, posing severe risks to natural and semi-natural ecosystems (Moralejo *et al*., 2009; Migliorini *et al*., 2015, 2023; Prigigallo *et al*., 2015; Jung *et al*., 2016; Mora-Sala *et al*., 2022; Antonelli *et al*., 2023). Italy, with its unique geography and central position in the Mediterranean Basin, harbours a rich diversity of *Phytophthora* species. Studies in nurseries across various crops have recorded a total of more than 40 *Phytophthora* species (Prigigallo *et al*., 2015; Migliorini *et al*., 2015, 2023; Jung *et al*., 2016; Vettraino *et al*., 2016; Antonelli *et al*., 2023; Horta Jung *et al*., 2025).

Besides notorious pathogens like *P. cinnamomi*, *P. citrophthora*, *P. nicotianae*, *P. plurivora* or *P.* × *cambivora* (Jung *et al.,* 2016), additional species have been recently recorded or described (Linaldeddu *et al*., 2020; Scanu *et al*., 2021), as summarized by Antonelli *et al.* (2023). *Phytophthora mediterranea* was also originally isolated from nursery plants of *Myrtus communis* in Italy (Bregant *et al*., 2021a). This pathogen was recently found associated with the decline of *Platanus* trees in urban areas of Athens, Greece (Antonelli *et al*., 2024). The contemporary presence of multiple species in individual nurseries favours the development of interspecific hybrids (Faedda *et al*., 2013).

Extensive *Phytophthora* diversity has also been recorded in ornamental and forest nurseries across Spain (Moralejo *et al*., 2009; Abad *et al*., 2014; Mora-Sala *et al*., 2022). Among other species, *P. cactorum*, *P. cinnamomi*, *P. citrophthora*, *P. crassamura*, *P. multivora*, *P. nicotianae*, *P. niederhauserii*, *P. palmivora*, *P. plurivora*, and *P. pseudocryptogea* have been isolated from various nursery hosts.

In Portugal, 16 *Phytophthora* taxa, including the known pathogens *P. alticola*, *P. cactorum*, *P. cinnamomi*, *P. crassamura*, *P. multivora*, *P. parvispora*, *P. plurivora*, *P. pseudocryptogea*, *P. quercina* and *P.* ×*cambivora*, the

recently introduced *P. quercetorum*, as well as three previously unknown hybrid taxa, were obtained from 13 forest nurseries (Horta Jung *et al*., 2025). *Phytophthora cinnamomi* was present in eight of the nurseries (62%), and *P. pseudocryptogea* and *P.* ×*cambivora* were detected in six of the nurseries (46%).

In response to these escalating pathogen threats, policy frameworks should shift focus towards nursery accreditation schemes. These should use stringent biosecurity measures and protocols and best management practices within the nursery trade, as has been suggested above (Figure 4).

PATHWAYS AND DRIVERS

Mediterranean regions probably share the same major pathway of introduction and spread of *Phytophthora* pathogens as other climatic regions, which is the global, national and regional trade in living plants (Liebhold *et al*., 2012; Jung *et al*., 2016). Mediterranean climatic regions are often densely populated, resulting in constant import of plants-for-planting in gardens and city parks, so these become sources for pathogen spread (Santini *et al*., 2013; Jung *et al*., 2016; Redondo *et al*., 2018). High human population also causes pressures to natural reserve areas which are subjected to inflows of visitors. Such visitors are possibly bridging the contact between the areas where *Phytophthora* has been introduced and areas where the pathogens are then dispersed (Redondo *et al*., 2018). For instance, within a highly visited protected area in the vicinity of Barcelona (Northeast Spain), high incidence of *Phytophthora* was found in forests immediately in contact with areas of high recreational use, including car parking spots, barbeques, or picnic grounds (Štraus *et al*., 2023).

Visitors not only can transport *Phytophthora* propagules from the cities to natural areas, but also may help to spread inoculum within natural areas through movement of soil on shoes or vehicles, as well as increasing soil compaction, and therefore the risk of soil waterlogging (Giordana *et al*., 2020).

Ecosystem restoration efforts may also be pathways for pathogen introductions. Mediterranean landscapes have been degraded for centuries, leading to vegetation loss and soil erosion. Re-naturalisation of degraded lands has been carried out in many protected areas, often by out-planting seedlings grown in *Phytophthora* infested nurseries (Jung *et al*., 2016; Horta Jung *et al*., 2025). Introductions of *Phytophthora* via restoration plantings and afforestation has been documented in Mediterranean areas of Australia, California, Italy, Southwest Spain, and Portugal (Shearer and Tippett, 1989; Scanu *et al*., 2015; Jung *et al*., 2016; Fernández-Habas *et al*., 2019; Frankel *et al*., 2020a; Horta Jung *et al*., 2025).

Use of forests as agroforestry settings is widespread within the Mediterranean Basin. Agroforestry often encompasses the combination of grazing activities in open savannah-like forests, such as Dehesas in Spain or Montados in Portugal (Fernández-Habas *et al*., 2019). Grazing activities involve cattle movement and soil compaction, known factors for *Phytophthora* spread and disease expression. In Mexico, spread of *P. cinnamomi* into oak forests and subsequent tree decline and mortality, were demonstrated to follow cattle tracks (Tainter *et al*., 2000). Feral pigs have long been implicated as potential vectors for spread of the devastating plant pathogen *P. cinnamomi*, due to feeding on infected material, and their rooting and wallowing activities, which make them vectors of pathogen infested soil (Li *et al*., 2014). Trees in agroforestry environments are often exposed to additional stressors, including pruning, and mechanical damage to bark, and they frequently lack natural tree regeneration, so canopy renewal is limited as older trees die (Vicente and Alés, 2006). The role of *Phytophthora* affecting natural regeneration is under-researched, but several studies indicate that these pathogens can have significant impacts (Jung, 2009; Gómez-Aparicio *et al*., 2012; Bily *et al*., 2022; Jankowiak *et al*., 2023; Štraus *et al*., 2023). Mediterranean areas are rich in intricate mosaics of agricultural settings, human settlements, and small patches of semi-natural vegetation, that act as corridors for *Phytophthora* spread, probably facilitating inoculum movement amongst these landscape elements (Figure 3).

The Mediterranean Basin differs from other areas affected by *Phytophthora*, primarily due to its climatic conditions. The Mediterranean climate is characterized by high variability and occurrence of extreme weather events, including severe droughts, floods and heatwaves. *Phytophthora* species have developed adaptations to such conditions, and drought resistance of their resting propagules is a key trait for surviving in Mediterranean climate environments (Erwin and Ribeiro, 1996; Jung *et al*., 2013b, 2018a, 2024; Caballol *et al*., 2024). The effect of drought in the tree hosts goes both-ways: on the one hand, drought may impair the ability to resist *Phytophthora* attacks (Oliva *et al*., 2014), and on the other hand, *Phytophthora*-induced fine root losses reduce the capacity to take up water and, hence, predispose affected trees to droughts, thus exacerbating the effects of drought stress (Jung *et al*., 2000).

As climate changes and ambient temperatures rise, frequency of severe rainfall events is likely to increase, causing river and stream flooding that submerges large areas of crops and forests. Rainfall promotes zoospore

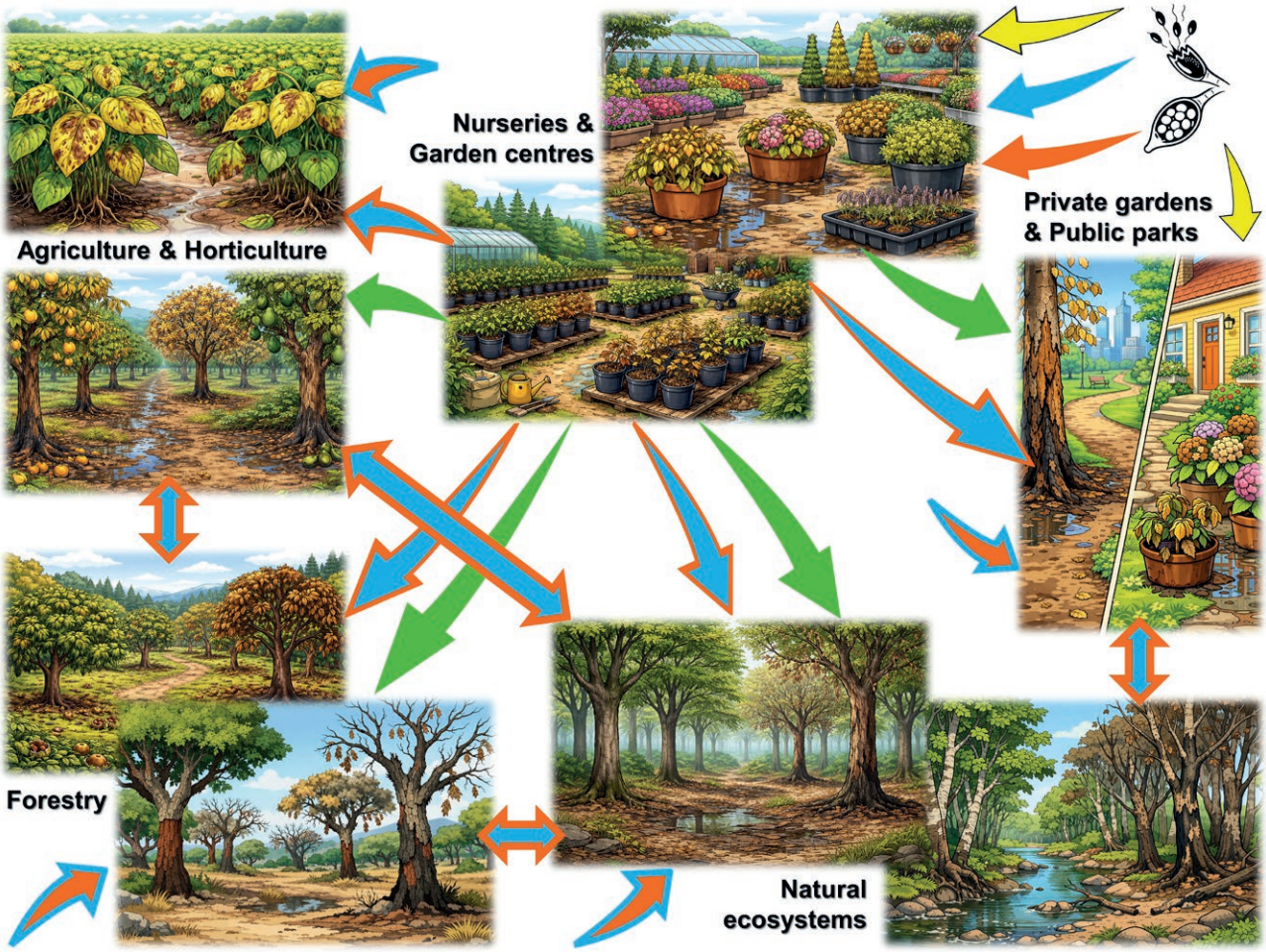

Figure 3. Cross-sector movements of *Phytophthora* inoculum. Living propagules of the pathogens move with infected plants and/or infested soil or water. Alien invasive *Phytophthora* species are introduced into new plantations (commercial production or nature restoration projects) via: (1) planting of infested nursery stock (yellow arrows); (2) irrigation, runoff and natural waterways (blue arrows); and (3) movement of infested material (orange arrows) via other human activities (e.g. work tools, machinery, recreational vehicles, boots) or animal spread. Due to the lack of barriers, after successful introduction into any vulnerable environment, *Phytophthora* can spread to adjacent locations. Figure produced with assistance from ChatGPT (OpenAI, 2026).

production and root infection by *Phytophthora* (Erwin and Ribeiro, 1996; Jung *et al*., 2018a; Chen *et al*., 2022; Serrano *et al*., 2024).

Combined effects of drought and waterlogging have been shown experimentally on several forest tree species (Jung *et al*., 2003a; Corcobado *et al*., 2014), helping to explain patterns of plant mortality observed in the field (Colangelo *et al*., 2018; Fernández-Habas *et al*., 2019). In agricultural settings, the effects can be particularly dramatic in tree orchards, where levels of inoculum surpass resistance thresholds of resistant or tolerant citrus rootstocks. In addition, flooding can also enable zoospores to reach and infect scions of susceptible cultivars above the resistant rootstocks (Figure 2, G and H).

In addition to droughts and floods, heatwaves are climatic stressors that are likely to occur with increased frequency. A recent experiment with *P.* ×*multiformis* and multiple provenances of the alder species *A. glutinosa* and *A. lusitanica,* demonstrated a synergistically deleterious interaction between a simulated heatwave and subsequent *Phytophthora* infections (Gomes Marques *et al*., 2025).

Mediterranean areas have diverse plant communities in natural and agricultural settings. While diversity is generally considered as a barrier for invasive organisms, this may not be particularly strong for *Phytophthora*, as the genus includes many polyphagous species. Indeed, very diverse ecosystems, such as the Jarrah forests in Australia (Shearer and Dillon, 1995), or the Mediter-

ranean shrublands and oak forests of Spain and California, have been affected by wide host range *Phytophthora* species, including *P. cinnamomi*, *P. ramorum* and *P. tentaculata*, amongst others (Brasier *et al*., 1993; Rizzo *et al*., 2002; Jung *et al*., 2018a; Sims and Garbelotto, 2018; Domínguez-Begines *et al*., 2020; Horta Jung *et al*., 2025). A positive correlation between tree diversity and *Phytophthora* species richness has been shown in Europe (Caballol *et al*., 2024), and extremely diverse forests in Southeast and East Asia and South and Central America harbour particularly diverse communities of *Phytophthora* species (Jung *et al*., 2017b, 2017c, 2018b, 2020, 2022, 2024).

PATHOGEN DETECTION, DIAGNOSTICS AND SURVEILLANCE

Detection, diagnosis and surveillance underpin evidence-based assessments of *Phytophthora* occurrence, distribution, and emergence across Mediterranean agricultural, forestry and natural ecosystems, and addresses distinct decision points. Detection provides rapid screening for pathogen presence across multiple matrices. Diagnostics deliver confirmatory, robust identifications (species/lineage) with sufficient evidential strength for reporting. Surveillance integrates these tools within statistically sound, risk-based frameworks that define objectives, target populations, sampling design and prioritization. Because surveillance outcomes depend jointly on sampling effectiveness and on performance of detection and diagnostic tools, the present section of this review summarizes the principal traditional and emerging approaches used for screening (detection) and confirmation (diagnostics), aligned with established survey-and-monitoring frameworks. How these tools are operationally deployed within risk-based Mediterranean surveillance programmes is then outlined (Pérez-Sierra *et al*., 2022; EFSA, 2025a; EFSA, 2025b).

Detection

Detection is usually required for rapid screening for the presence of *Phytophthora* in plant tissues and environmental matrices, and aims to capture early signals, that can be subsequently confirmed and precisely determined by diagnostics when required (Pérez-Sierra *et al*., 2022). In practice, screening most frequently targets symptomatic tissues from putatively infected plants (*e.g*., fine roots, root collar tissues, inner bark at active canker margins), and matrices that act as reservoirs and dissemination pathways for pathogen inoculum, mostly rhizosphere soil/root–soil composites, and water (streams, ponds/reservoirs, irrigation/runoff systems), including nursery-related leachates and irrigation water (Jung *et al.* 1996, 2016; Ghimire *et al*., 2009; Pérez-Sierra *et al*., 2022; Swiecki *et al*., 2024). Because each detection approach is affected by matrix- and method-specific biases, combining independent lines of evidence can increase reliability in pathogen presence screening.

Culture-dependent screening: isolation and baiting

Traditional culture-dependent screening relies on direct isolation from appropriately selected, actively infected plant tissues, which provides evidence of viable propagules, and yields isolates for later confirmation. Direct isolation can, however, be hindered by dormancy of resting structures and by faster-growing competing microorganisms, so indirect baiting approaches are often used to increase recovery probability from soil and water (Pérez-Sierra *et al*., 2022). Soil baiting (commonly using susceptible leaves or fruits) and water baiting (including *in situ* deployment of baits) are widely used to detect *Phytophthora* in rhizosphere soil and aquatic environments, and can recover multiple species present in complex samples (Jung *et al.* 1996, 2013b, 2016, 2019, 2020; Ghimire *et al*., 2009; La Spada *et al*., 2022; Pérez-Sierra *et al*., 2022). Nonetheless, outcomes are intrinsically biased by bait susceptibility and selectivity, interspecific pathogen competition, and contaminant overgrowth (e.g., rapid colonization by competing oomycetes or fungi when highly susceptible or wounded baits are used), seasonal variation, and propagule stage. Under-recovery also results for taxa that are slow-growing, slow to sporulate, in quiescent stages, highly host-associated, difficult to culture, inhibited by antibiotics and fungicides used in selective or semi-selective media to recover *Phytophthora* from baits, or that are otherwise poorly recovered under standard baiting and selective-media conditions. Additional limitations include false negatives, when viable inoculum is present but not effectively attracted to or infective on a chosen bait, as well as requirement for technical skill to obtain clean cultures from microbially diverse substrates (Ghimire *et al*., 2009; La Spada *et al*., 2022; Sarker *et al*., 2023).

These constraints are also evident in nursery screening strategies based on baiting of irrigation leachate from container stock, where success of detections can be variable (particularly in less susceptible hosts), and bait choice can influence sensitivity. Baiting-based detections, when confirmed by culturing, have value as they demonstrate living propagules capable of infections (Chimento *et al.,* 2012; Jung *et al*., 2016; Swiecki *et al*., 2024). These detections also provide isolates for patho-

genicity trials to confirm new *Phytophthora*-host combinations, and taxonomic studies for description of new species (Jung *et al.* 2017a, 2017b, 2017c, 2018b, 2020, 2022, 2024), and for pathogen population genetic and genomic analyses (Jung *et al.*, 2021; Shakya *et al.*, 2021; Mullett *et al.*, 2023, 2024).

Serological screening

Serological-based detection methods, including enzyme-linked immunosorbent assays (ELISA), rely on specific recognition of pathogen antigens by antibodies. They are useful for preliminary rapid screening when large numbers of samples must be rapidly tested. Immunoassays based on ELISA specific for *Phytophthora* are commercially available as kits, in laboratory and on-site versions (EPPO, 2004; Vettraino *et al.*, 2010). Different serological assays have been used to detect *Phytophthora* species of phytopathological concern, including dipsticks and lateral flow devices (Cahill and Hardham, 1994; Lane *et al.*, 2006), and the Agdia ImmunoStrip® (Harkness *et al.*, 2025) has been commonly used. Benefits of using ImmunoStrip® tests include ease-of-use (minimal training is required), possibility of filed use, rapidity (results within 30 min), and cost. Low sensitivity compared to that from molecular methods, has limited routine use and prevented widespread adoption of serological methods. Additional disadvantages are detections of dead and living *Phytophthora* propagules, and possible false positives due to cross reactions with soil particles and some species of *Pythium* and *Phytopythium*.

Targeted molecular screening: PCR/qPCR

Culture-independent targeted assays are widely used for rapid screening of *Phytophthora* directly from extracted DNA, including from symptomatic plant tissues, rhizosphere soil or water samples concentrated by filtration. These approaches include conventional PCR and, increasingly, quantitative real-time PCR (qPCR), which provides high analytical sensitivity and operational scalability for screening programmes (Cooke *et al.*, 2007; Schena *et al.*, 2008). Genus level assays are typically adopted when the objective is the early interception of *Phytophthora* signals across heterogeneous substrates, whereas species-targeted assays are used when *a priori* suspects exist, or when screening focuses on regulated/high-impact taxa. Even when a species-specific qPCR is used at the screening stage, downstream confirmation and robust identification criteria remain necessary for pathogen reporting (Bilodeau *et al.*, 2014). Multiplex real-time PCR is a representative strategy, that combines genus-level targets with species-specific probes, enabling simultaneous broad screening and targeted detection of priority pathogen taxa within a single workflow.

Key limitations need to be acknowledged explicitly in environmental matrices. Firstly, soil- and water-derived extracts commonly contain PCR inhibitors, and incomplete inhibitor removal or suboptimal concentration methods may reduce detection probability, motivating careful attention to extraction and sampling/concentration steps (Schena *et al.*, 2008; Scibetta *et al.*, 2012). Secondly, assay specificity and taxonomic coverage depend on primer/probe designs, and the breadth of validation panels. Cross-reactivity with closely related taxa or incomplete coverage across the expanding diversity of *Phytophthora* can occur, and mismatches at priming/probe sites may generate false negatives in some lineages (Bilodeau *et al.*, 2007; Cooke *et al.*, 2007; Bilodeau *et al.*, 2014). Thirdly, values for qPCR cycle thresholds (Cts) provide useful proxies for target DNA quantity, but do not constitute evidence of viability. Positive signals may derive from non-viable propagules or residual DNA, so molecular detection should be interpreted as presence of target DNA rather than proof of active infection or living inoculum (Bilodeau *et al.*, 2007). A real-time reverse-transcription PCR (RT-PCR) assay, targeting the mRNA of subunit I of the *cytochrome oxidase* gene as a viability marker, was proposed as an alternative approach, based on the assumption that mRNA degradation in dead host plant tissues is more rapid than that of DNA (Chimento *et al.*, 2012; Kunadiya *et al.*, 2021).

Isothermal assays: LAMP and RPA

Isothermal nucleic-acid amplification methods, particularly loop-mediated isothermal amplification (LAMP) and recombinase polymerase amplification (RPA), are complementary rapid screening tools, enabling amplification at constant temperature with minimal instrumentation, and supporting near-field or on-site assessments when laboratory qPCR is impractical (Rovetto *et al.*, 2024b).

In *Phytophthora*, genus- and species-targeted LAMP protocols have been developed for accelerated screening in plant tissues, including approaches that couple genus-level LAMP with species-level discrimination (e.g., quenching-probe formats) to flag priority taxa during quarantine- or nursery-relevant inspections (Hieno *et al.*, 2020). Multiplex LAMP formats further extend this logic by combining genus-level screening with simultaneous detection of multiple high-impact pathogen species and an internal plant control, reducing uncertainty

due to extraction failure or inhibitor carry-over (Hieno *et al*., 2021).

In parallel, RPA has been implemented for rapid screening, using either fluorescence readouts or lateral-flow strip visualization. These enable short sample-to-result times and simplified workflows for *Phytophthora* detection in symptomatic material (Lu *et al*., 2020; Wang *et al*., 2024), and in quarantine contexts using RPA–lateral flow dipstick assays (Dai *et al*., 2019).

Recent developments have integrated LAMP into portable platforms (e.g., microfluidic chip and smartphone-readout configurations) for field-deployable screening of regulated *Phytophthora* species and lineages (Mainello-Land *et al*., 2025). As with other molecular screening tools, isothermal assays do not constitute evidence of viable pathogen inoculum, remain constrained by matrix effects and potential inhibitors, and require stringent contamination control. Particularly for first detections, regulated records, or unexpected host–pathogen combinations, positive results should be treated as screening outputs that warrant confirmatory diagnoses and robust identification criteria prior to reporting (Hieno *et al*., 2020; Mainello-Land *et al*., 2025).

HTS/eDNA metabarcoding

Metabarcoding based on high-throughput sequencing (HTS) extends detection from single-target assays to multi-taxon screening, enabling simultaneous interrogation of diverse oomycete/*Phytophthora* assemblages in complex matrices. These assays can support large-scale surveys where pathogen diversity may be underestimated by baiting/isolation (Scibetta *et al*., 2012; Prigigallo *et al*., 2016). Broad screening is typically carried out on environmental DNA (eDNA) extracted from soil, roots/rhizosphere, or water (often after filtration), and results consistently indicate that different substrates and workflows recover partially overlapping assemblages. For example, eDNA from field roots and filtered water fractions can reveal greater richness than culture-based approaches, but still may miss taxa detected by baiting, reinforcing the matrix- and method-dependence of "presence" signals (Khaliq *et al*., 2018; La Spada *et al*., 2022).

The gap between the number of taxa detected by metabarcoding and those recovered by baiting is well recognized, and is explained by biological and procedural selectivity in baiting (e.g., favouring rapidly-sporulating, competitive, bait-infective species), rather than by pervasive false positives in molecular datasets. This supports the method as complementing rather than replacing culture-dependent methods (La Spada *et al*., 2022; Sarker *et al*., 2023).

Several critical constraints apply to HTS/eDNA screening. Primer choice strongly affects observed community composition (primer bias), and marker-dependent resolution may be insufficient for discriminating closely related species complexes when using commonly targeted regions. Primer selection and validation are therefore important for ecological and surveillance-oriented applications (Riit *et al*., 2016; Burgess *et al*., 2022). Long-read sequencing platforms (e.g. PacBio) have been applied to oomycete metabarcoding, enabling recovery of full-length ITS or alternative longer loci, and providing improved species-level resolution compared with short-read ITS1/ITS2-based approaches, particularly within closely related *Phytophthora* species complexes (Redondo *et al*., 2018; Caballol *et al*., 2024). Reference database completeness and curation also directly affect assignment accuracy (database/reference bias), and sequence processing decisions (e.g., error filtering, chimera control, singleton handling) can influence whether low-abundance detections are treated as signals or artefacts, particularly requiring conservative interpretations for "new" or unexpected records (Scibetta *et al*., 2012; Prigigallo *et al*., 2016). In this context, use of synthetic sequence barcode controls within each barcoding run is crucial for detection and quantification of contamination, which can occur in the many stages of PCR-based detection assays (Cock *et al*., 2023; Randall *et al*., 2024). Recent marker developments (e.g., rps10-based oomycete metabarcoding) aim to improve taxonomic resolution and reliability relative to legacy loci, but broad screening remains an inference from recovered DNA, and does not demonstrate viability or pathogenicity in the sampled systems (Khaliq *et al*., 2018; Foster *et al*., 2022).

Non–nucleic-acid-based sensing and phenotyping

Non–nucleic-acid-based sensing approaches are being explored as rapid triage tools for on-site pathogen screening, particularly those leveraging chemical and optical signatures associated with *Phytophthora* infections or propagule presence. Volatile-based strategies (volatilomics) have been investigated to capture disease- or pathogen-associated volatile organic compounds (VOC) fingerprints, including proof-of-concept workflows for detecting asymptomatic infections of *P. ramorum* in ornamental hosts, supporting the feasibility of VOCs as early "presence signals" in nursery-relevant contexts (Thompson *et al*., 2021; Favaro *et al*., 2024; Sherwood *et al*., 2024). Translational sensor implementations of this concept include low-cost electronic-nose platforms aimed at discriminating oomycetes based on volatile patterns, and, more recently, smartphone-read-

able colorimetric VOC sensor arrays proposed for rapid screening of *P. ramorum*, which have potential for detection with portable instruments (Borowik *et al*., 2021; Hossain *et al*., 2025).

Optical sensing approaches have also been applied, based on hyperspectral reflectance/imaging coupled with machine-learning classification for pre-symptomatic detection of *Phytophthora*-associated disease in woody and crop systems. However, these readouts generally reflect host stress signatures, so they require careful validation of specificity across confounding abiotic and biotic stresses (Esterhuizen *et al*., 2025). Fluorescent sensor-array platforms readable with compact devices (including smartphones) provide additional, highly portable and rapid screening. The fluorescent sensor array developed by Santonocito *et al*. (2023) has been applied to detection of *P. nicotianae* and *P. citrophthora*, supporting its relevance as an emerging screening tool in *Phytophthora* detections. While these sensors can offer operational advantages (rapidity, portability, low infrastructure requirements), they remain proof-of-concept and require matrix-aware performance validation (sensitivity/specificity, robustness across taxa and environmental confounders) before routine adoption in *Phytophthora* surveillance.

MALDI-TOF MS protein profiling has also been proposed as a method for identification of *Phytophthora* isolates, but this depends on standardized workflows and curated reference libraries. The method can only be applied to pure cultures, so it is probably a diagnostic reporting tool rather than a detection assay (Božik *et al*., 2021).

Interpreting detection signals: confirmatory requirements

Across all screening options, positive signals, particularly in the case of first detections, regulated taxa, or unexpected host matrix combinations, are commonly escalated to structured diagnostic workflows. This step is essential to obtain robust, reporting grade identification supported by multiple independent lines of evidence prior to any formal notification. Such confirmatory procedures ensure analytical reliability, minimize the risk of false positives, and guarantee compliance with regulatory and phytosanitary reporting standards.

Phytophthora *diagnostics*

Diagnostics for *Phytophthora* in Mediterranean agriculture, nurseries, forestry, and natural environments should aim to produce robust identifications (species and, where needed, lineage) that are supported by explicit taxonomic/phylogenetic contexts, traceable reference sequences, and/or validated targeted assays (Robideau *et al*., 2011; Abad *et al*., 2023). This is particularly critical for *Phytophthora*, where cryptic diversity, rapid radiations, and hybridization can undermine single-marker certainty, which can complicate biosecurity-relevant decisions (Abad *et al*., 2023; Jung *et al*., 2024). For surveillance, "diagnostics" therefore implies strong evidence, from preliminary to confirmed identifications, rather than just positive signals (Abad *et al*., 2023; EPPO, 2025).

Modern *Phytophthora* diagnostics depend on stable phylogenetic structures (major clades/subclades), nomenclatural and taxonomic revision anchored to type material, and harmonized reference resources and loci that enable reproducible placement of isolates and sequences (Abad *et al*., 2023). In practice, confirmatory diagnostics should be understood as attribution of a sample (ideally an isolate, or a well-supported sequence) to a described species, with explicit acknowledgement of cases where placement is only clade-level, or where species boundaries are unresolved (Abad *et al*., 2023; Jung *et al*., 2024). This process is particularly relevant in Mediterranean systems, where introductions and pathway-mediated mixing can bring together diverse pathogen lineages into particular environments, such as nurseries or managed landscapes (Jung *et al*., 2016).

Signs/symptoms, isolation and pathogenicity

Assessments of signs and symptoms (e.g., decline syndromes, collar/root rots, bleeding cankers) are important, but symptoms are often generic in *Phytophthora* pathosystems and should be treated as starting points (Pérez-Sierra *et al*., 2022). Minimal but explicit linkage between field phenotypes and laboratory confirmation is therefore appropriate, especially for first detections, unexpected host associations, or reports of novel taxa (Pérez-Sierra *et al*., 2022; Abad *et al*., 2023).

Culture-based isolation remains the 'gold standard' diagnostic, because it supports morphological screening, archiving, reference sequencing, and (where required) pathogenicity testing (Pérez-Sierra *et al*., 2022). Fulfilling Koch's postulates is the next logical step to support causality, particularly for novel host–pathogen relationships or newly described taxa. This requires inoculation, symptom reproduction, and re-isolation with identity confirmation (Jung *et al*., 2017a, b; Pérez-Sierra *et al*., 2022). A Mediterranean-specific illustration of this classical diagnostic chain is provided by the delineations of *Phytophthora tyrrhenica* and *Phytophthora vulcanica* from *Fagaceae* forests, where multilocus data supported

pathogen species delimitation, and pathogenicity trials provided evidence for their roles as cryptic pathogens (Jung *et al*., 2017a).

Targeted molecular diagnostics: species-specific PCR/qPCR and multiplex panels

Targeted molecular assays (PCR/qPCR) provide rapid and sensitive confirmation when diagnostic questions are constrained (regulated/high-impact taxa, nursery screening panels, or defined sets of expected species), and these assays are commonly embedded within broader, standardized diagnostic workflows (EPPO, 2025). The EPPO diagnostic standard for *Phytophthora cinnamomi* exemplifies a reporting-grade approach, where molecular tests are positioned alongside sampling and sample handling requirements, culture-based recovery where applicable, and confirmatory identification expectations (EPPO, 2025).

Assay design and validation are not trivial for *Phytophthora*, because closely related taxa may differ by few diagnostic polymorphisms at commonly targeted loci, known diversity is expanding, and mixed infections can occur in nurseries and in multi-host landscapes (Jung *et al*., 2016; Abad *et al*., 2023). Therefore, targeted assays should be interpreted strictly within a validated scope (taxa tested, matrices, performance parameters), and periodically revisited against updated reference frameworks (Abad *et al*., 2023; EPPO, 2025).

An illustrative targeted strategy is multiplex real-time PCR, combining genus-level detection with species-level resolution, and exploiting mitochondrial features and differences in gene order to support simultaneous screening and confirmation for selected taxa (Bilodeau *et al*., 2014). Systematic development of mitochondrial diagnostic markers has also been used to build species-specific assays for economically important *Phytophthora* species, offering scalable options when assay coverage and validation are adequate for particular intended uses (Miles *et al*., 2017).

Sequence-based diagnostics: barcoding, multilocus confirmation, phylogenetic placement

Sequence-based confirmation (often Sanger sequencing) remains the basis for reporting-grade *Phytophthora* diagnostics, because it is portable, auditable, and extendable to unexpected taxa (Abad *et al*., 2023). For *Oomycetes*, DNA barcoding using mitochondrial cytochrome c oxidase subunit I (cox1/COI) combined with the nuclear ribosomal ITS region has been proposed to improve discriminatory power relative to ITS alone, supported by reference datasets (Robideau *et al*., 2011). However, barcoding should be treated as an entry-level confirmation step, rather than an endpoint in several Mediterranean-relevant scenarios, especially for species complexes with limited divergence at ITS/COI, novel taxa lacking close references, potential hybrids, and high-impact reporting contexts (Robideau *et al*., 2011; Jung *et al*., 2017a, 2017b, 2022, 2024; Abad *et al*., 2023).

In these cases, multilocus datasets and explicit phylogenetic placement become essential to support defensible species-level conclusions, particularly where cryptic diversity or reticulate evolution is suspected (Jung *et al*., 2017a, 2017b, 2022, 2024; Abad *et al*., 2023). The reliability of sequencing-based diagnostics is closely coupled with the quality and traceability of reference sequences, and with taxonomically curated resources that align names, types, and phylogenetic placement (Abad *et al*., 2023).

High resolution approaches: resolving cryptic diversity, hybridization, and complex cases

High resolution approaches are required when standard barcoding and limited multilocus sequencing cannot resolve particular diagnostic questions, such as within rapidly radiating clades, in the presence of introgression/hybridization, or when lineage-level resolution is needed for biosecurity-relevant interpretations (Jung *et al*., 2017a, 2017b, 2022, 2024; Abad *et al*., 2023). International forest surveys have revealed substantial and previously unrecognized diversity within major clades, highlighting that cryptic species, and complex evolutionary histories can be common, with implications for diagnostics and for interpretation of novel detections (Jung *et al*., 2017a, 2017b, 2022, 2024). Operationally, escalation may involve expanded multilocus frameworks, and, in selected cases, genome-informed analyses, to stabilize placements, and to interpret discordant mitochondrial versus nuclear signals consistent with hybridization or incomplete lineage sorting (Jung *et al*., 2017b, 2021, 2024; Abad *et al*., 2023).

Diagnostics in the Mediterranean Basin: scenarios that drive method choice

Diagnostics in Mediterranean ecosystems are scenario-driven, with method selection guided by the host system, the matrices, and balance between expected high-impact taxa and the likelihood of unexpected diversity (Jung *et al*., 2016, 2019; Pérez-Sierra *et al*., 2022).

European nursery systems are key interfaces for *Phytophthora* spread and amplification, and a continent-wide nursery survey has documented widespread infestations and associated high risks to forest, semi-natural, and horticultural ecosystems (Jung *et al*., 2016). A rational diagnostic architecture is rapid screening (genus-level and, where justified, targeted species assays), followed by isolation/baiting from positives, and sequencing-based confirmation, to capture non-panel taxa and achieve reporting-grade outcomes (Robideau *et al*., 2011; Bilodeau *et al*., 2014; Jung *et al*., 2016).

In Mediterranean forests and protected ecosystems, probability of encountering unexpected or cryptic taxa is high, favouring isolation-enabled and sequence-based diagnostics as core confirmatory tools, complemented by pathogenicity evidence for causal attributions (Jung *et al*., 2017a; Pérez-Sierra *et al*., 2022). Description of cryptic pathogenic species from *Fagaceae* forests (Jung *et al*., 2017a) illustrates why multilocus frameworks and phylogenetic placements can be required to avoid misidentifications based on limited loci.

When targets include regulated or high-impact species (e.g., *P. cinnamomi*), harmonized standards and explicit confirmatory requirements enable comparability across laboratories and surveillance programmes. The EPPO standard is an example of such a framework (EPPO, 2025).

Diagnostic outputs as foundations for surveillance data quality

Surveillance depends on diagnostic outputs that are consistent, comparable, and defensible over time. For *Phytophthora* in the Mediterranean Basin, where nursery-mediated pathways intersect with important ecological and economic values, quality of surveillance data is constrained by the weakest links in diagnostic processes (sampling, recovery, confirmation, reference traceability) (Pérez-Sierra *et al*., 2022; EPPO, 2025). Harmonized diagnostic standards for key pathogen taxa and taxonomically anchored references therefore function as infrastructure for reliable surveillance, providing foundations for coherent interpretation across regions and programmes (Abad *et al*., 2023; EPPO, 2025).

Surveillance in Mediterranean ecosystems

Surveillance for *Phytophthora* spp. involves structured monitoring across hosts, habitats, and environmental matrices, to capture presence, distribution, and temporal dynamics of the pathogens. Surveillance is ideally implemented through statistically sound, risk-based surveys, that prioritise high-probability pathways (EFSA, 2025a; EFSA, 2025b).

Risk-based surveillance in the Mediterranean Basin: pathways, matrices and metadata

In the Mediterranean Basin, risk-based surveillance for *Phytophthora* is generally structured around high-probability introduction pathways (particularly plant-for-planting trade and nursery networks), environmental settings that favour pathogen persistence and dispersal (through irrigated systems, drainage infrastructure, and riparian corridors), and host assemblages and habitats that maximize probability of detection (susceptible cultivated hosts, ornamentals, sentinel woody vegetation in managed and semi-natural landscapes) (Antonelli *et al*., 2023; Horta Jung *et al*., 2025). Within this framework, surveillance is strengthened by pairing targeted sampling of appropriate matrices (rhizosphere soil, fine roots, symptomatic collar tissues, irrigation/surface waters) with relevant metadata (site type, water source, host identity, symptom class, sampling season). This allows detections to be interpreted in relation to likely exposure and introduction routes (Prigigallo *et al*., 2015).

Nurseries and the plants-for-planting pathway as priority nodes

Plant nurseries are priorities because they concentrate diverse hosts, substrates, and water systems, and also permit efficient sampling for early interception of multiple pathogen taxa (Jung *et al*., 2016). Evidence from Italy indicates that *Phytophthora* taxa can be repeatedly detected in nurseries over time, supporting the rationale for systematic screening across plant material, potting media, and nursery water systems (Antonelli *et al*., 2023). In southern Italy, nursery-focused molecular surveys have also shown that community-level approaches (metabarcoding) applied to soil/root matrices can reveal broader diversity than conventional recovery alone, supporting risk-based allocation of sampling effort to nursery compartments and potting media most likely to harbour latent pathogen inoculum (Prigigallo *et al*., 2015, 2016).

Irrigated agroecosystems and water-mediated dissemination

Irrigated perennial crop production in Mediterranean agroecosystems and its watering systems are priorities for surveillance. In Sicily, combined baiting and

metabarcoding applied to citrus orchard rhizosphere soils was effective for *Phytophthora* detection, and highlighted the value of integrating "classic" recovery methods with HTS-based pathogen community screening (Conti Taguali *et al*., 2025). Survey evidence from Spanish almond orchards affected by root and crown rot further supports structured sampling in orchard matrices (roots/crown tissues and associated substrates) for Mediterranean perennial crops, including recovery and identification of *Phytophthora* taxa within broader oomycete communities (Beluzán *et al*., 2022). In Mediterranean island agroecosystems, surveys associated with crown and root rot of artichoke (in Sardinia) have similarly linked field sampling and isolate-based identifications with documented *Phytophthora* diversity in production systems (Bregant *et al*., 2021b). Since irrigated agroecosystems are connected to propagation chains, nursery surveys in Spain that explicitly included water from irrigation ponds have confirmed inclusion of nursery water systems as high-yield surveillance points (Mora-Sala *et al*., 2022).

Forests, natural environments and protected areas: compartment-focused and integrated terrestrial–aquatic surveillance

In Mediterranean forests and natural environments, risk-based surveillance prioritizes compartments where inoculum is likely to accumulate (streams, riparian belts, seasonally waterlogged microsites), and host stands dominated by susceptible evergreen sclerophylls and *Fagaceae* that can function as sentinels for decline syndromes. In northern Spain, eDNA-based surveys from soil and water demonstrated that genus-targeted high-throughput sequencing detected diverse *Phytophthora* communities, even when symptom expression was limited or spatially patchy. This provided evidence for prioritizing confirmatory sampling and follow-up diagnostics (Català *et al*., 2015). In holm oak forests, integration of metabarcoding with targeted real-time assays also supported detection of multiple taxa associated with decline complexes, illustrating how surveillance can combine broad community screening with focused assays for high-concern pathogen taxa within single risk-based workflows (Català *et al*., 2017; Mora-Sala *et al*., 2018).

Mediterranean protected areas also justify surveillance designs that integrate terrestrial and aquatic sampling. In Sicilian Protected Natural Areas, leaf baiting from rhizosphere soils and rivers recovered a rich assemblage of *Phytophthora* species. These results emphasize the operational value of combining soil/root-zone sampling with stream baiting in Mediterranean landscapes that are characterized by strong connectivity between catchments and adjacent vegetation (Jung *et al*., 2019). Complementary research in eastern Sicily showed that *Phytophthora* community composition and distribution can differ across aquatic, riparian, and terrestrial habitats within a single protected area, reinforcing the utility of stratified sampling designs at fine spatial scales (Riolo *et al*., 2020). Surveys of Mediterranean maquis vegetation in Sardinia consistently detected multi-species pathogen complexes, and included descriptions of novel taxa, underscoring that symptom-driven inspections alone are insufficient for identifying pathogen diversity in Mediterranean biodiversity hotspots (Scanu *et al*., 2015). A country-wide survey of forests, streams and nurseries in Portugal, using baiting techniques and direct isolations, demonstrated high *Phytophthora* diversities with numerous new *Phytophthora*-host combinations, and the interconnections between the different systems (Horta Jung *et al*., 2025). At the broader European scale that includes Mediterranean regions, discovery of multiple cryptic pathogenic species from *Fagaceae* forests further highlights the surveillance value of recovering living isolates from targeted substrates, enabling robust pathogen identification and characterization (Jung *et al*., 2017a).

Tiered surveillance strategies and supporting layers

Mediterranean studies comparing baiting/isolation and sequencing-based community profiling indicate that methodological complementarity is structurally relevant for surveillance design. Early pyrosequencing-based work in Italian chestnut forest soils showed that sequence-based profiling can detect a broader resident community than baiting alone, while still benefiting from culture recovery for obtaining viable isolates (Vannini *et al*., 2013). More recent Sicilian studies similarly indicate that metabarcoding and baiting recover partially overlapping subsets of taxa, supporting a dual-track logic in which metabarcoding expands breadth (including low-abundance and difficult-to-isolate lineages) and baiting secures living isolates for confirmatory workflows (La Spada *et al*., 2022). Similar results were obtained in a recent survey of Czech nurseries (Bačová *et al*., 2024). Accordingly, surveillance in Mediterranean ecosystems should be focused on sampling at high-risk nodes (notably nurseries and irrigated systems) combined with environmental surveillance in riparian/catchment contexts and using more than one approach to maximise the likelihood of detection (La Spada *et al*., 2022; Conti Taguali *et al*., 2025). In Mediterranean forest systems, risk-based surveillance can be further strengthened by integrating remote sensing/thermal–

hyperspectral imaging to capture early canopy-level signals compatible with *Phytophthora*-associated decline before widespread symptom expression (Hornero *et al*., 2021). Likewise, spatial risk forecasting (e.g., habitat suitability and process-informed approaches) has been applied to *P. cinnamomi* across Mediterranean regions (France, Italy, Portugal, Spain) to support sampling prioritization under present and projected climatic conditions (Cidre-González *et al*., 2025).

Management of disease caused by Phytophthora

Due to their multicyclic nature, Phytophthora diseases are strongly influenced by environmental conditions. Climate change is expected to be a major factor affecting dynamics of invasive *Phytophthora* spp. inoculum (Jung *et al*., 2000, 2018a; Serrano *et al*., 2021, 2024). To mitigate this threat, coordinated and stringent actions are required across diverse ecosystems of the Mediterranean Basin, to reduce inoculum levels and the incidence of *Phytophthora*-induced diseases. The array of Phytophthora disease management strategies and phytosanitary regulatory measures is reviewed below.

Management of Phytophthora diseases in agricultural systems

Agronomic and cultural practices

From phytosanitary perspectives, agronomic practices should eliminate the factors that predispose plants to disease, and create environmental conditions that are unfavourable to pathogens. Preventive agronomic measures are essential management strategies for Phytophthora diseases of crops. These measures include pre-planting actions such as conducting soil chemical and structural analyses, levelling terrain or creation of raised beds or ridges (Figure 5 D) depending on the crop, and improving drainage to prevent waterlogging and soil saturation. These measures are particularly important for permanent tree crops on heavy soils. In commercial citrus, avocado and fruit tree orchards, use of raised-bed planting is becoming more common as a soil-management approach and an alternative to underground drainage.

Young plantations can also be predisposed to *Phytophthora*. Planting young trees too deeply predisposes them to crown and foot rot. Plastic plant protectors used in young plantations to prevent physical damage should be avoided, as they create conditions favouring development of *Phytophthora* diseases. Plant protectors must allow adequate air circulation and prevent accumulation of water at plant bases. Mesh-type protectors that ensure adequate ventilation are recommended. For mature trees, removal of soil from around stem bases eliminates asphyxiation and excess moisture, and contributes to prevention of crown rots and basal trunk gummoses, or helps recovery in trees that are already infected.

Grafting on resistant rootstocks is the most widely used method to prevent root and crown rot and trunk gummosis of citrus, avocado, and other fruit trees. Bud unions usually need to be at least 40 cm above the ground to avoid infections of susceptible scions caused by water splashing. However, the grafts can increase susceptibility of resistant rootstocks to *Phytophthora* (Camisón *et al*., 2023). "Inarching" (also "bridge-grafting"; Figure 6 F), is a particular grafting type, which substitutes original rootstocks by growing saplings of a different rootstock variety close to the trunks of mature trees (two to three saplings per tree), and then grafting the saplings into each trunk or the scaffold branches. This method was previously used in citrus orchards to save trees infected by foot rot and trunk gummosis, or to replace *Phytophthora*-susceptible rootstocks with tolerant ones. This technique is still in use in gardens to rescue old high value trees. Another historical practice, now largely abandoned, is surgical removal of infected bark from trunks of trees affected by bleeding cankers, usually followed by wound disinfection with copper-based products (Cacciola and Magnano di San Lio, 2008).

Pruning favours aeration within tree canopies, and in evergreen trees such as citrus, makes environments unfavourable to aerial *Phytophthora* infections, thus reducing incidence of fruit brown rot and twig blight. 'Skirting' a particular type of pruning, is widely used in commercial citrus orchards. This consists of removing the lower parts of tree canopies close to the ground, to reduce risk of fruit brown rot infections due to water splashing. For fruit brown rot, presence of weeds in citrus orchards during winter reduces risk of infections, as weeds cushion rain impact on soil, reducing splash infections by soilborne inoculum. Conversely, incidence of fruit brown rot is greater in citrus orchards where herbicides are used to clean the soil from weeds than where weed control is absent. The use of localized irrigation systems, such as drip or micro-sprinklers, introduced to optimize water use and save energy, has contributed to reduction of incidence of foot rot and trunk gummosis in citrus, fruit and nut crops of the Mediterranean region. In contrast, introduction of irrigation in typically rainfed crops, (e.g. olive) has contributed to emergence of Phytophthora diseases, previously regarded as being of minor concern (Cacciola *et al*., 2011; Azenzem *et al*., 2024).

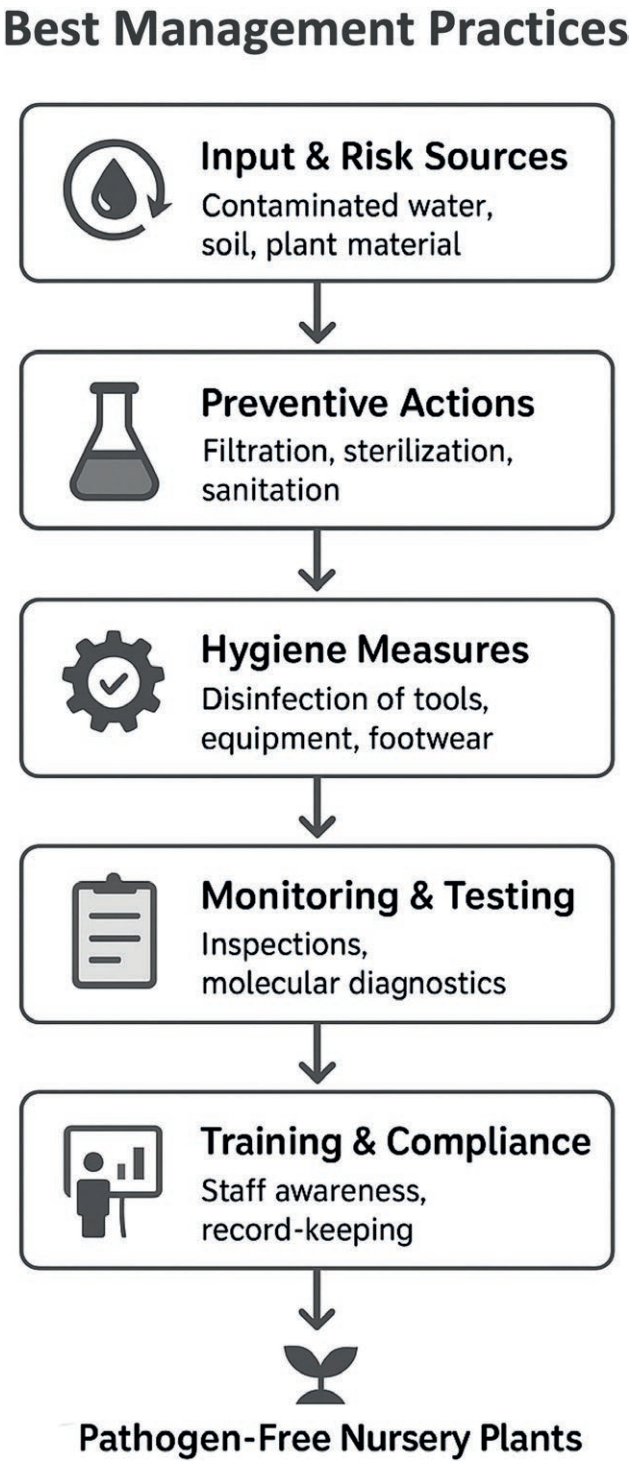

Figure 4. Best management practices for production of pathogen-free nursery plants.

Phytophthora diseases are affected by soil fertilization. Nitrate nitrogen (N) is preferable to ammonium N, because ammonium N nourishes species such as *P. nicotianae* (Cacciola and Magnano di San Lio, 2008). However, the relationships between fertilizer application and Phytophthora diseases have been only occasionally investigated, while there are several reports of the effects of soil amendments on these diseases. In greenhouse and field crop agroecosystems, soil amendments, solarization and plastic mulching help reduce soilborne diseases in general. In a trial in northern Spain (Núñez-Zofío *et al*., 2009), organic soil amendments followed by solarisation reduced incidence of *P. capsici* in pepper. However, most reports from the Mediterranean region have focused on effects of soil amendments on avocado root rot caused by *P. cinnamomi*. Several amendments have been tested, including organic mulching, addition of calcium (Ca) sources (gypsum), and silicon-based soil dressings, as reviewed by Farooq *et al*. (2024). Addition of gypsum was based on the observation that increased calcium availability in soil could create conditions unfavourable to *P. cinnamomi* (Falcon *et al*., 1984; Messenger *et al*., 2000). Gypsum and other calcium fertilizers also increased the tolerance of *Q. ilex* to root rot caused by *P. cinnamomi* in oak dehesa ecosystems (Serrano *et al*., 2012, 2013).

Tolerant cultivars

Following *Phytophthora*-related disease outbreaks in the 1890s in citrus orchards in the Mediterranean region, rootstocks of tree crops have been selected primarily based on their resistance or tolerance to the pathogens (Cacciola and Magnano di San Lio, 2008). Plant breeding for tolerant rootstocks is ongoing. This is also the case for avocado and fruit trees. Challenges for development of varieties and rootstocks resistant to *Phytophthora* limit intensification of some crop production (Kurbetli *et al*., 2020; Fadli *et al*., 2022; Linaldeddu *et al*., 2023; Caruso *et al*., 2024). In addition, breeding of cultivars resistant to multiple *Phytophthora* species is difficult. For example, sour orange (*Citrus aurantium* L) rootstocks which are resistant to *P. citrophthora*, and, hence, are often used for *Citrus sinensis* (Lahlali *et al*., 2021; Boudoudou *et al*., 2024; Dalal *et al*., 2025). Citrange Troyer hybrids are resistant to *P. nicotianae* in Moroccan citrus orchards (Boudoudou *et al*., 2024).

Biological control

Many microbial biocontrol agents (MBCAs) preventively and curatively suppress development of *Phytophthora* species infecting vegetable, field, and tree crops (de Andrade Lourenço *et al*., 2022; Gilardi *et al*.,

Figure 5. Preventive measures for controlling *Phytophthora* pathogens. A. Display of signs to warn of the presence of the pathogen and indicate facilities for cleaning footwear. B. Footbaths for disinfecting livestock hooves. C. Vehicle passageways for disinfecting wheels. D. Planting citrus trees on soil ridges to channel water and prevent waterlogging in the root systems. E. Planting selected holm oak genotypes for their combined tolerance to *Phytophthora cinnamomi* and water stress. F. Replacing holm oaks in severely infested areas with ash, stone pine and carob trees.

2024). Zouaoui *et al*. (2019) deployed endophytic bacterial strains of *Halomonas elongata*, *Bacillus amyloliquefaciens*, and *Paenibacillus polymyxa* to control *P. citrophthora* in clementine (*Citrus* × *clementina*) orchards in Tunisia, and all the assessed isolates reduced necrotic lesions under greenhouse conditions, with one isolate of *H. elongata* (L80), identified as the best candidate. Similarly, isolates 6L10, 6ba6, and 3ss9 of *Pseudomonas fluorescens* with biosurfactant ability when combined with olive oil, reduced *P. capsici* incidence in Turkish pepper greenhouses by 57 to 81% (Özyilmaz and Benlioglu, 2013). Surfactin and fengycin B biosurfactants from *Bacillus* spp. and *Pseudomonas* spp. effectively controlled *P. infestans* sporangium production and zoospore release (Daaboub *et al*., 2022). The biocontrol agent *Bacillus amyloliquefaciens* subsp. *plantarum* [isolate D747; Amylo-X LC (Biogard, Grassobbio)], prevented *P. palmivora* damage in *Punica granatum* and did not allow synergism of *P. palmivora* and *Coniella granati* in pomegranate trees under regular watering and drought (Tundo *et al*., 2025).

Antagonistic *Trichoderma* species suppressed *Phytophthora* species in Moroccan olive orchards (Legrifi *et al*., 2024). *Trichoderma asperellum* isolate T34 and *T. atroviride* isolates have been widely used against *Phytophthora* spp. in pepper greenhouse production in Spain (Segarra *et al*., 2013; Martins *et al*., 2022). *Fusarium solani* FUS25 and a mixture of *T. asperellum* and *T. gamsii* reduced incidence of *P. capsici* infections in sweet pepper by 60 to 65%, and increased plant fresh weights, in Italian hydroponics systems (Gilardi *et al*., 2021). Beyond direct antagonism, *Trichoderma*-based biocontrol may also operate through host-mediated mechanisms within tripartite host plant–beneficial microbe–pathogen interactions. Under controlled conditions, *T. asperellum* and *T. atroviride* reduced tomato root rot caused by *P. nicotianae*, and were associated with transcriptional re-programming involving plant defence-related genes, *Trichoderma* mycoparasitism-related genes, and *P. nicotianae* effector genes (La Spada *et al*., 2020). Treatments with *Trichoderma* spp. were linked to modulation of *P. nicotianae* effector expression, including up-regulation of necrosis-inducing proteins (PnNPP1.1 and PnNPP1.3), and down-regulation of CRN and CBEL effectors (PpCRN4 and PpCBEL4), supporting the assumption that biocontrol efficacy may reflect both direct antagonism and interference with pathogen virulence (La Spada *et al*., 2020). Under experimental conditions, a biological plant protection product based on *T. gamsii* and *T. harzianum*, applied to soil, was effective against citrus root rot caused by *P. nicotianae*. However, in Italy, current authorization for use of this product on citrus is limited to the control of *Armillaria mellea* and *Dematophora* (*syn*. *Rosellinia*) *necatrix*. A natural product based on lemon peel powder fermented by *Lactiplantibacillus plantarum* was effective against Phytophthora brown rot of citrus and apple fruits (La Spada *et al*., 2024).

Organic composts can suppress many soilborne plant pathogens, including *Phytophthora* species, when these compounds are applied alone or with biocontrol agents, followed by plastic mulching (Núñez-Zofío *et al*., 2009; Bellini *et al*., 2020). Compost extracts reduce severity of Phytophthora diseases by at least 60% (Jiménez *et al*., 2025). *Trichoderma*-enriched compost at 10% v/v reduced *P. capsici* incidence in squash (*Cucurbita pepo* var. *cylindrica* L.) (Bellini *et al*., 2020). Similarly, combining MBCAs with organic composts suppressed *P. infestans* in potato (Daaboub *et al*., 2022). Compost extracts can also be used as biofertilizers and plant protection substances (Jiménez *et al*., 2025).

Disease management with chemicals

Between the late 1970s and the early 1980s, the widespread use of phosphonates, including fosetyl-Al and K or Na phosphonate (Manghi *et al*., 2021) started almost simultaneously with the introduction of synthetic fungicides with specific activity against oomycetes, including acylalanines (phenylamides). These compounds were an important breakthrough in management of Phytophthora diseases. The most successful of these were metalaxyl, later replaced by its isomer mefenoxam. Uses of these chemicals was important in agriculture, due to their efficacy against oomycetes and their systemic activity within plants.

Phosphonates, the derivatives of phosphorous acid (H_3PO_3), move in plant symplasts, and are particularly effective against oomycete pathogens when applied as foliar sprays (Figure 6 D; Solla *et al*., 2021). They have also been used as soil treatments (Figure 6 C) (González and Sánchez, 2020), although there are conflicting opinions on effectiveness of soil treatments, and concerns about their environmental impacts (Nguyen, 2025). Phosphonates are also used for tree endotherapy as trunk injections (Figure 6 E) This application method has low environmental impacts, and is particularly suitable for care and protection of single trees in parks and urban areas (Garbelotto *et al*., 2007; Benigno *et al*., 2025b).

Phosphorous acid derivatives have two dose-dependent modes of action: induction of plant resistance, and direct biocidal activity on targeted pathogens (La Spada *et al*., 2021). Plant-mediated resistance has been investigated, but it is not fully understood. After several years

Figure 6. Direct control measures for *Phytophthora*. A. Calcium amendment with $CaCO_3$ in dehesa pastureland. B. Manual dusting of a garlic-based formulation on cork oak trees. C. Pressure injection of fungicide into the soil next to a holm oak tree. D. Foliar spraying of potassium phosphonate diluted in water. E. Injection of phosetyl aluminium into trunks. F. Inarching (i.e., approach grafting) to repair citrus trunks damaged by *Phytophthora* species.

of large-scale successful applications to control diseases caused by oomycetes, it has been proven that phosphonates have a wide activity spectrum, which also includes fungi (Aiello *et al*., 2013).

In some Mediterranean citrus-producing countries (e.g. Egypt), phosphonates are recommended and widely used, together with other fungicides for post-harvest treatments against citrus fruit moulds. This use is not permitted in EU countries. Also in EU countries, phosphonates are not permitted in organic agriculture, and their use as fertilizers has been banned by EU Reg. 1009/2019.

Acylalanines are a chemical group of highly specific, systemic fungicides for the control of oomycetes, including species of *Phytophthora*, *Plasmopara*, *Bremia* and *Albugo*. They have protective and curative activity, and have been widely used to control soilborne Phytophthora diseases, downy mildews and white rusts of economically important crops including potato, tomato, grapevine, leafy vegetables, soybean, sunflower, and ornamentals. Their mechanism of action is inhibition of RNA synthesis in oomycete cells, through specific interference with RNA polymerase I. Acylalanines are in Group 4 of the Fungicide Resistance Action Committee (FRAC) classification (high resistance development risk) (Hermann *et al*., 2020).

Acylalanines are acropetally translocated in plant apoplasts. Soil treatments with these synthetic compounds after drench, surface spray or through irrigation system applications, even at low concentrations, effectively reduce *Phytophthora* inoculum density in soils, making these products particularly suitable for management of soilborne *Phytophthora* species. However, dosages and efficacy vary with soil type, target crops (turf, nurseries, ornamentals, and horticultural crops). In citrus production, mefenoxam is also registered for spray applications against fruit brown rot. However, the manufacturer advises against the use of this product in nurseries, to prevent risks of selection and dissemination of acylalanine-resistant strains of *Phytophthora* over large areas.

Sensitivity of diverse *Phytophthora* species to phosphonates and acylalanines may vary. For example, in citrus fosetyl-Al suppresses *P. citrophthora* more effectively than *P. nicotianae*, whereas mefenoxam (syn. metalaxyl-M) is more effective against *P. nicotianae* (Cacciola and Magnano di San Lio, 2008). This can have implications for control of different *Phytophthora* pathogens and the diseases they cause in particular host plants. Similarly, for crown and leather rots of strawberry, K phosphonate was more effective against *P. cactorum* than *P. nicotianae* (Marin *et al*., 2023). In the Mediterranean region, metalaxyl resistance in *P. capsici* populations in greenhouse pepper crops has been recorded since the 1990s (Pennisi *et al*., 1998), and metalaxyl-resistant *P. infestans* isolates were first reported from potato crops in 1997 in Morocco (Sedegui *et al*.,1997). Subsequently acylalaine-resistant populations of *Phytophthora* have emerged across the Mediterranean region in several crops, including almond, potato, ornamentals, and others (Pérez-Sierra *et al*., 2011; Savazzini and Galletti, 2015; Aiello *et al*., 2018).

Despite introduction of phosphonates and acylalanines, the traditional use of copper fungicides retains a key role for management of Phytophthora diseases in the Mediterranean region. Copper fungicides are used to control fruit brown rot in citrus orchards (Cacciola and Magnano di San Lio, 208). A survey report by Lahlali *et al*. (2021) in Morocco confirmed the widespread use of copper oxychloride in citrus orchards to combat *Phytophthora* pathogens. However, use of copper-based fungicides is increasingly limited in the European Union due to regulatory restrictions, because of concerns related to copper accumulation in soils and the resulting environmental impacts (European Commission, 2018; EFSA, 2018). Loss of effectiveness of synthetic fungicides because of selection of resistant *Phytophthora* populations, concerns for human health and environmental impacts, and increasing restrictions on the use of synthetic chemicals for crop protection, have encouraged the search for alternative more safe and eco-friendly methods for Phytophthora disease management.

Integrated disease management programmes

Integrating pre-emptive cultural, biological, and chemical disease control approaches, and biosecurity measures in agroecosystem, helps to sustainably address phytosanitary challenges posed by *Phytophthora* infections (Ouaznati *et al*., 2024; Legrifi *et al*., 2025). Periodic monitoring of *Phytophthora* inoculum across an agroecosystem is a prerequisite for a holistic approach to manage *Phytophthora* infestations in soil and irrigation water. Samples of soil and suspected plant parts are analysed, especially in citrus orchards (Cacciola and Magnano di San Lio, 2008). Legrifi *et al*. (2024) reported deployment of new tools for detecting and evaluating disease severity in olive plantations. Serological assays (e.g. double sandwich antibody enzyme-linked immunosorbent assays; DSA-ELISA), and molecular analyses using related polymerase chain reactions (PCR) for infected plant parts, soil and water resources, all help reduce disease risks (Gilardi *et al*., 2021; Hussain *et al*., 2025).

Harmonised integrated production and protection practices include preference for tolerant plant cultivars, optimal irrigation and improved soil drainage to avoid water saturation, as well as regulation of agrometeorological conditions in greenhouses. Prioritising the appli-

cation of microbial biocontrol agents MBCAs is encouraged, whereas chemical fungicides should be considered only as a last resort (Hanafi, 2003; Hussain *et al*., 2025).

Disease management in nurseries

Producing *Phytophthora*-free planting material in nurseries is important because nurseries are primary sources of *Phytophthora* species through infected saplings or plantlets. Trade of infected plants is a potential source for spread of already existing or invasive *Phytophthora* species (Jung and Blaschke, 2004; Cacciola and Magnano di San Lio, 2008; Jung, 2009; Moralejo *et al*., 2009; Pérez-Sierra and Jung, 2013; Jung *et al*., 2016; Bregant *et al.,* 2021; Mora-Sala *et al*., 2022; Horta Jung *et al*., 2025). The most effective way to avoid *Phytophthora* infections is to prevent their entry and spread within nursery facilities. Appropriate procedures include thermo-sterilisation of growing substrates, use of disinfested or single-use pots and containers, filtering or disinfestation of irrigation water, use of localized irrigation systems (e.g. spaghetti tube or drip irrigation) to optimize water use and prevent inoculum spread, growing nursery stock without direct contact with soil, lifting plant production onto raised benches and tables, avoiding rotation of crops on infected beds, removing dead or infected plant material, disinfecting tools, vehicles, and footwear, staff training, surveillance and early detection, and purchasing plants only from other nurseries with equally high biosecurity standards (Figure 4). All of these practices can reduce *Phytophthora* inoculum levels in nurseries (Pérez-Sierra and Jung, 2013; Jung *et al*., 2016; Horta Jung *et al*., 2025). In addition, potting mix should be stored on ground cover or concrete surfaces. There should also be barriers between potted ornamental plant containers and soil (Gullino *et al*., 2025).

Adequate analyses of irrigation water and treatment by filtering (slow media, sand, lava grains, pumice), applying heat or ultrasound, electrostatic precipitation or chlorination can also reduce inoculum levels (Ufer *et al*., 2008; Pérez-Sierra and Jung, 2013; Rodríguez-Padrón *et al*., 2019). Water use should be optimised with localized irrigation systems, such as spaghetti tube or drip irrigation, and sprinkler irrigation, surface runoff and excess or stagnant water favouring pathogen sporulation should be avoided (Pérez-Sierra and Jung, 2013; Taoussi and Lahlali, 2025).

Biological control

This remains an underexplored research area, and in many cases biological control agents are used in combinations with chemical treatments. Gilardi *et al*. (2014) assessed use of biological control agents, including *T. asperellum* ICC012, *T. gamsii* ICC080, and *B. subtilis* QST713, which suppressed *P. nicotianae* in a greenhouse tomato nursery. Additionally, a 7 d treatment interval with chemicals (fosetyl-Al, acibenzolar-S-methyl, and phosphite-based fertilizers) was recommended to control the disease (Gilardi *et al*., 2014). Mokhtari *et al*. (2024) reduced infections by *P. capsici* in sweet pepper nurseries by adjusting temperature (>20 °C) and relative humidity (<80%), and regularly applying 10^7 CFU mL^{-1} of *Trichoderma* spore suspensions. The commercial product Remedier® (*Trichoderma asperellum* strain ICC 012 + *T. gamsii* strain ICC 080) applied as soil drench also reduced root rot of potted citrus saplings caused by *P. citrophthora*. However, this product is not registered for nursery use (S.O. Cacciola, personal communication).

Use of chemicals

Pre-nursery treatment of seedbeds or substrates and regular post-nursery spraying suppress *Phytophthora* inoculum development (Antonelli *et al*., 2023; Mora-Sala *et al*., 2022). Fungicide applications may conceal and mask early infections, and their continued use can contribute to development of pathogen resistance. Ornamental plant nurseries, while being hotspots for alien *Phytophthora* species introductions, provide favourable conditions for the selection of fungicide-resistant populations, due to repeated chemical treatments and less stringent regulatory requirements. Resistance of *Phytophthora* species to phosphonates has been reported (Farooq *et al*., 2024), so use of fungicides and phosphonates should be reduced to a minimum, to avoid the spread of *Phytophthora* pathogens through infected, asymptomatic plants into new environments (Jung *et al*., 2016; Horta Jung *et al*., 2025).

Certification schemes

Mediterranean countries must regulate and standardise nursery production and create nursery certification schemes with high biosecurity standards, to ensure production of *Phytophthora*-free planting material along plant supply chains. Certification schemes with effective biosecurity measures and traceability are essential in nurseries for disease-free seedling production and tracking phytosanitary issues (Jung *et al*., 2016; Ouaznati *et al*., 2024; Taoussi and Lahlali, 2025), and studies have recommended monitoring of *Phytophthora* species throughout supply chains, starting in nurseries (Jung *et al*., 2016; Mokhtari

et al., 2024; Benigno *et al*., 2025a). Phytosanitary regulatory measures must be in accordance with EU regulation 2016/2031, the European and Mediterranean Plant Protection Organization (EPPO), and National Plant Protection Organizations (NPPOs) (Montilon *et al*., 2023). Compulsory and voluntary certification programmes introduced in several Mediterranean countries for citrus and fruit trees have provided frameworks for implementing these measures, but much is required to implement these certification schemes in the Mediterranean Basin and elsewhere. A survey of Moroccan avocado (*P. americana*) nurseries found that only 54% had official registrations, and only 2% were registered with territorial plant protection services (Ouaznati *et al*., 2024). Internationally, several highly successful nursery accreditation schemes already exist, including the Nursery Accreditation Scheme Australia (NIASA) and Avocado Nursery Voluntary Accreditation Scheme (ANVAS) in Australia, the Accreditation to Improve Restoration (AIR) and the California Nursery Stock Registration & Certification Program in California, and the Plant Healthy Certification Scheme in the United Kingdom.

Disease management in forest systems

Controlling *Phytophthora* diseases in forest ecosystems presents major challenges due to the complexity and scale of natural environments. In contrast to agricultural settings, forests often lack structured management practices, and infected trees often remain undetected for long periods, allowing pathogens to spread through soil, watercourses, and root-to-root contact. The persistence of long-lived inoculum in soil, presence of multiple susceptible species, and difficulty of applying chemical or physical control measures across large and heterogeneous landscapes, further hinder effective disease management. Additionally, introductions of invasive *Phytophthora* species through planting infected nursery stock increase these challenges, making early detection and disease prevention strategies essential yet difficult to implement.

Surveillance, monitoring and mapping

Surveillance of Phytophthora and other diseases requires understanding of disease epidemiology and management, and of the use of appropriate analytical tools (López-García, 2024). Early detection, surveillance and mapping vegetation for plant diseases using high resolution tools such as Sentinel-2 satellite, Geographic Information Systems (GIS), multispectral cameras, and drones, require research and collaboration for real-time precision (Isbaex *et al*., 2024; Morales-Rodríguez *et al*., 2025). The Italian National Plant Protection Organisation, for example, collaborated with the International Plant Sentinel Network (IPSN) to give timely surveillance of Italy's forest zones, and mapping of existing and emerging plant pathogens (Gullino *et al*., 2025). Innovatively, citizen collaboration in phytopathological data collection through "citizen science" can also contribute to surveillance and mapping. As described by Gullino *et al*. (2025) and Suffert and Suffert (2022), citizen science involves public engagement and voluntary data collection using accessible mobile applications, through which citizens can submit suspicious plant health information from public green areas for further investigation. Coordinated large-scale disease surveys involving trained practitioners, such as foresters and riparian biologists, who survey forests and riparian corridors for disease symptoms that are then verified by experienced plant pathologists, are another efficient surveillance approach. This was demonstrated by the Bavaria-wide survey of alder mortality (Jung and Blaschke, 2004).

Silvicultural practices

Silvicultural practices are important for managing *Phytophthora* diseases in forest ecosystems, by enhancing stand resilience and reducing conditions favourable to pathogen establishment and spread. Although silvicultural measures have been less studied than biological approaches, targeted interventions can help mitigate disease impacts. These include selective thinning, promoting species and structural diversity, and improving regeneration methods, by increasing forest heterogeneity and reducing host densities. Broad silvicultural frameworks aimed at maintaining forest health, such as adaptive management, variable-density thinning, and interventions designed to enhance structural complexity, also contribute to reducing vulnerability to soilborne pathogens by improving overall ecosystem function and resilience. However, despite their potential, silvicultural strategies remain underrepresented in research literature, highlighting the need for further studies on how forest management can effectively reduce *Phytophthora* spread and disease severity under diverse ecological conditions (López-García *et al.,* 2024; Serrano *et al.,* 2024; Morales-Rodríguez *et al.,* 2025). Stakeholder engagement and sensitisation for removal of infected trees and sustainable forest rehabilitation are also important for managing ensembles of tree pathogens (Morales-Rodríguez *et al*., 2025).

Occurrences of *Phytophthora* species increase in dense forest stands during the rainy seasons, so reducing

excessive soil humidity could help to reduce *Phytophthora* occurrence (Serrano *et al*., 2024). Reductions of soil pH in man-made ecosystems can also create unfavourable habitats for these pathogens (Balci and Halmschlager, 2003).

Selective thinning enables solar radiation to reach low forest canopies and soil surfaces, which enhances forest health and yields (Alderotti and Verdiani, 2023). Thinning of 30% of *Q. ilex* in Mediterranean coppices reduced *Phytophthora*-related diseases and tree death (Gavinet *et al*., 2019; Hernández-Lao *et al*., 2024). Breeding for resistance to *P. cinnamomi* and water stress in central and southern Spain (de la Mata *et al*., 2025, 2026) allowed planting of selected genotypes tolerant to *P. cinnamomi* (Figure 5 E). In valleys with highly infested soils, replacement of *Phytophthora*-susceptible species by *Phytophthora*-tolerant tree species (*Fraxinus angustifolia*, *Pinus pinea*, *Ceratonia siliqua*) yielded good results (Figure 5 F). Management of browsers and grazers in dehesas or Mediterranean agro-silvo-pastoralism is a mitigation practice for enhancing selective silviculture (Ruiz-Gómez and Miguel-Rojas, 2021; Alderotti and Verdiani, 2023). Benigno *et al*. (2025b) showed that emerging *P. plurivora* infecting English walnut in Italy can be managed in plantations through policy support on irrigation water use, and in agroforestry through investment in research and policy implementation.

Chemical control

Only a few EU-registered chemicals, including fosetyl-Al, potassium phosphite, calcium (Figure 6A), and zinc, are permissible for forest treatments against soilborne-related diseases (Romero *et al*., 2019; Serrano *et al.,* 2023). Trunk spraying of individual trees or large-scale understory vegetation, as well as canopy spraying with resistance inducers, such as fosetyl-Al and potassium phosphite, suppresses development of *P. cinnamomi* in *Q. ilex* woodlands (Solla *et al*., 2021; Dorado *et al*., 2025). Tree trunks can also be injected with fosetyl-Al or potassium phosphite (Solla *et al*., 2009; Romero *et al*., 2019; Brandano *et al*., 2023) (Figure 6 E). An integrated approach enhances effective management of these pathogens in forests.

Biological control

Innovative biotechnological approaches, including targeted use of biological control agents (helper microorganisms and antagonists), are being explored to manage *Phytophthora* spp. in forest ecosystems (López-Sánchez *et al*., 2022; Morales-Rodríguez *et al*., 2025). These adaptive strategies include the use of native bioagents, including *Trichoderma* species, against *P. cinnamomi* root rot (Ruiz-Gómez and Miguel-Rojas, 2021). Other research has focussed on antifungal effects of essential oils or root exudates (garlic essential oil), which had inhibitory effects on fungi and *P. nicotianae* (Wang *et al.,* 2019). Some trials are ongoing using garlic dust on cork oak in Spain (Figure 6 B).

Integrated holistic approaches

In forest management, the increasing complexity of ink disease in Mediterranean conditions has shifted disease mitigation strategies from pathogen eradication towards more holistic approaches. To date, the most effective treatment remains application of potassium phosphonates, either by foliar spraying or trunk injection, which has been shown to reduce disease severity by directly affecting *Phytophthora* activity while simultaneously inducing host defence responses (Vannini *et al*., 2009; Gouveia *et al*., 2010; Brandano *et al*., 2023). However, reliance on single-input strategies is considered insufficient in systems exposed to multiple and recurrent stressors (Solla *et al*., 2009).

Integrated and holistic pest management strategies are gaining attention, aiming to restore functional balance at the system level rather than only targeting pathogens. Recent approaches combine complementary actions, including soil biofumigation to reduce inoculum pressure, application of antagonistic and plant growth–promoting microorganisms to enhance rhizosphere functionality, and the use of resistance inducers to reinforce host defence capacity. Examples of this integrated approach are the protocols developed within the LIFE FAGESOS project (https://www.lifefagesos.it), where multi-component interventions are designed to act simultaneously on soil, microbiomes and host resilience, reflecting the need for adaptive management strategies in Mediterranean chestnut ecosystems subjected to combined pressures (Morales-Rodríguez *et al*., 2025).

Restoration and reforestation

Reforestation programmes require use of disease-free seedlings (Jung *et al*., 2016), and sometimes also destruction of infected herbaceous species (San-Eufrasio *et al*., 2021). The restoration of forests in which *Phytophthora* spp. are well established, as for *P. cinnamomi* in oak woodlands or *P.* ×*alni* in riparian alder forests, requires use of tree genotypes that are tolerant to *Phytophthora* spp. (Jung and Blaschke, 2006; Alderotti and

Verdiani, 2023; Martínez *et al*., 2020). Practitioner and public awareness of restoration and reforestation activities should be raised to control diseases and mitigate climate change in the Mediterranean basin (Cidre-González *et al*., 2025; Morales-Rodríguez *et al*., 2025).

A promising strategy to restore Mediterranean oak forests under decline is the use of genotypes selected for drought tolerance and *Phytophthora* resistance (Martínez *et al*., 2023; de la Mata *et al*., 2026). The newly funded LIFE RECLOAK project exemplifies this approach, by reforesting affected areas with native holm oak seedlings chosen for their resilience to drought and *P. cinnamomi* across pilot sites in Italy, Spain, and Malta. The project tracks reforestation success, soil biodiversity, carbon sequestration, and holm oak tolerance indicators, while fostering stakeholder engagement and promoting replicable practices, as a holistic, system-level strategy to mitigate dieback and enhance forest ecosystem resilience.

Disease management in natural environments

Controlling *Phytophthora* in natural environments remains challenging, because chemical interventions are often impractical and may disrupt sensitive ecosystems. Recent systematic reviews have indicated that biological and bio-based measures dominate current research efforts, with silvicultural and chemical strategies being comparatively underexplored. In Mediterranean natural ecosystems, integrated pest management (IPM) approaches, combining early detection, monitoring, signing (Figure 5 A), sanitation (Figure 5 B), and restoration of plant communities, have been highlighted as essential for reducing pathogen spread under increasing pressures from climate change and invasive species.

Alien invasive *Phytophthora* species destabilize flora biodiversity by endangering scarce and native plant species. This undermines the resilience and homeostasis of natural environments (Riolo *et al*., 2020; Morales-Rodríguez *et al*., 2025). Therefore, prudent continuous monitoring of *Phytophthora* occurrence should be applied for endemic and threatened plant species, and to ensure biodiversity in Protected Natural Areas (PNAs) (Jung *et al*., 2019; Riolo *et al*., 2020). However, the limited knowledge of pre-existing *Phytophthora* populations hampers rational management strategies for pathogens in PNAs (Riolo *et al*., 2020). Furthermore, the complex diversity of *Phytophthora* species, their long persistence in soil, water and infected plant tissues (Erwin and Ribeiro, 1996; Jung *et al*., 2013b, 2018a), and the connectivity between agricultural, forestry, urban, and natural environments (Figure 3), make disease management difficult across ecosystems (Legrifi *et al*., 2025).

Portable diagnostic tools can be useful for early pathogen detection, especially in remote settings (Frisullo *et al*., 2018; Riolo *et al*., 2020). Environmental DNA (eDNA) based detection in streams and soils provides an early warning and monitoring for *Phytophthora* (Keriö *et al*., 2020; Bass *et al*., 2023). For example, metabarcoding processing of eDNA samples from northern Spain revealed wide pathogen diversity, with 35 *Phytophthora* taxa from water samples and 13 from soil samples (Català *et al*., 2015).

In natural environments, recreational and human-mediated transport should follow strict sanitation and hygienic practices (Figure 5, B and C), and be minimised, as transport is a primary pathway for the dispersal of non-native *Phytophthora* species into new ecosystems (Riolo *et al*., 2020). The movement of contaminated soil on vehicles and agricultural machinery should be avoided or strictly controlled (Figure 5 C) (Shearer and Tippett, 1989). Disinfection stations for tyres and footwear at entry points of protected natural areas can reduce introductions and spread of *Phytophthora* and other soil-borne pathogens within these environments (Shearer and Tippett, 1989; Colquhoun and Hardy, 2000; Morales-Rodríguez *et al*., 2025).

There is urgent need to strengthen legislation, enhance public awareness, and implement comprehensive management measures for *Phytophthora* pathogens, given the ease with which they can spread through human activities, international trade, and ecotourism (Jung *et al*., 2016, 2018a; López-García, 2024). The framework of phytosanitary regulatory measures should be in accordance with EU regulation 2016/2031, EPPO, NPPOs, and other ecological policies. These policies are devised to ensure cross-border monitoring, and reinforce quarantine practices across the ecosystems in the Mediterranean Basin (Montilon *et al*., 2023; FAO, 2024; Vettraino *et al*., 2018). Biosecurity schemes for *Phytophthora* species, including voluntary sanitary certification of nursery forest plants for afforestation or reforestation, should also be considered for surveillance of natural ecosystems (Riolo *et al*., 2020).

NEEDS AND FUTURE RESEARCH DIRECTIONS

Knowledge gaps on emerging diseases in Mediterranean forests

Phytophthora ink disease

In chestnut stands there is the necessity for continued monitoring to understand the factors influencing the reaction between chestnut hosts and the ink dis-

ease pathogens, especially considering climate change and the potential spread of *Phytophthora* species (Marzocchi *et al*., 2024). A challenge in chestnut stand soils includes knowledge of soil biota, since in-depth research is required regarding microbial richness in the absence or presence of *Phytophthora* (Marzocchi *et al*., 2024). There is a lack of knowledge of rhizosphere microorganisms associated with ink disease affected chestnut stands. Despite indications that some microorganisms may be able to inhibit the causal agents, biocontrol has not been well-explored (Choupina *et al*., 2014). For forest management, there is necessity in some areas to replace chestnuts killed by ink disease with other tree species to assure permanent forest cover, highlighting the need for alternative species selection (Heinz and Prospero, 2025).

Early research showed considerable variations in susceptibility/tolerance to *P.* ×*cambivora* within 23 European populations of *C. sativa* (Robin *et al*., 2006), which could provide the basis for resistance screening programmes. Later studies demonstrated resistance of *C. sativa* × *C. mollissima* hybrids to *P. cinnamomi*, and detected Quantitative Trait Loci (QTLs) for resistance against *P. cinnamomi* (Santos *et al*., 2015, 2017). Future research includes obtaining chestnut genotypes resistant to mixed *Phytophthora* infections (Choupina *et al*., 2014), heat stress (Dorado *et al*., 2022, 2023b; Solla *et al*., 2024), and drought stress (Camisón *et al*., 2021; Pérez-Rial *et al*., 2025), which requires further testing of resistance efficacy in the field. Screening is needed for *Phytophthora* resistance in *C. sativa* populations adapted to Mediterranean conditions, and Alcaide *et al*. (2020) reported the knowledge gap, at molecular and genetic levels, on tree resistance to ink disease. This highlights the need for deeper analysis of the resistance genetic structure of chestnut populations, which could be facilitated by the molecular characterization of sequences of the genes involved in host tree resistance.

Future studies could rely on available genomes of *C. mollissima*, *C. crenata*, and *C. sativa* to advance research, highlighting the need to utilize these resources (Pérez-Rial *et al*., 2025). Elucidating pathogen virulence/avirulence factors involved in chestnut-*Phytophthora* interactions (Fernandes *et al*., 2022), and identities and modes of action of toxin(s) produced by *P. cinnamomi* during pathogenesis, would be major advances for disease control, particularly through resistance breeding, and, potentially, targeted genetic manipulation of this pathogen (Brasier and Jung, 2006; Camisón *et al*., 2019).

Phytophthora oak decline

For oak decline caused by *Phytophthora* in Mediterranean forests, several studies have suggested continuing and expanding research on pathogen x *Quercus* interactions, specifically emphasizing the biochemical and molecular signals involved in pathogen virulence and host defence mechanisms (Horta *et al*., 2010; Coelho *et al*., 2021; Saiz-Fernández *et al*., 2022; Contreras-Cornejo *et al*., 2023). Research on the *Phytophthora* secretome to understand release of effectors into rhizospheres, and the early mechanisms of host-pathogen interactions was also suggested by Oßwald *et al*. (2014). Analysis of *Phytophthora* genomes could improve understanding of host ranges, aggressiveness, and effector and suppressor molecules. Oßwald *et al*. (2014) also posed questions about the function of elicitins in susceptible host-pathogen interactions, specifically whether they may act as suppressors of Pattern-Triggered Immunity (PTI), and which PTI compounds would be impaired.

Particularly for holm oak and cork oak decline, further investigation is required to explain the combined effects on tree death by waterlogging, drought stress, insect pests, and *Phytophthora* infections (Moreira and Martin, 2005; Milanović *et al*., 2015, 2020; Ruiz-Gómez *et al*., 2019), and of the genetic basis of tree responses to combined stress (de la Mata *et al*., 2025, 2026). Studies to determine the genetic basis of resistance/tolerance against root rot in Mediterranean environments will allow mitigation of *Phytophthora* diseases in complex forest ecosystems (Alcaide *et al*., 2026). In the field there is the necessity for continuous monitoring, public awareness, and innovative treatment methods to mitigate the impacts of *Phytophthora* in oak forests. The prevalence of *P. quercina* in the Mediterranean area (Jung *et al*., 1999, 2016, 2019; Pérez-Sierra *et al*., 2013; Dorado *et al*., 2023a; Horta Jung *et al*., 2025) warrants further study of this species as a cryptic predisposing factor for oak decline (Colangelo *et al*., 2018; Horta Jung *et al*., 2025).

There are additional knowledge gaps in implementation of existing research, which is likely due to a lack of holistic understanding of processes over time and space. Future research and policy efforts to manage *Phytophthora* in forest ecosystems are required. For example, potassium phosphonate, which is registered for chestnut and has proven efficacy for controlling *Phytophthora*-mediated oak decline (Solla *et al*., 2021), should also be registered for controlling *Phytophthora* in evergreen oak species (Morales-Rodríguez *et al*., 2025). There is also requirement for increased field experimental data to validate new treatments (López-García *et al*., 2024), optimize application methods, and determine appropriate dosages (Dorado *et al*., 2025) for controlling *Phytophthora* diseases in Mediterranean ecosystems.

Phytophthora decline and dieback of European beech

First studies indicated a similar involvement of *Phytophthora* species in beech decline of Southern Europe, as in Central and Northern Europe (Motta *et al*., 2003; Milenkovic *et al*., 2012; Jung *et al*., 2018a, 2019; Horta Jung *et al*., 2025). However, large-scale investigations into pathogen and disease distribution across southern Europe are required to draw general conclusions about the extent and role of *Phytophthora* species in beech decline throughout the Mediterranean basin (Jung, 2009). Increased field research is required to establish associations between specific site conditions, such as soil surface structure, water content, and pH, and climatic conditions, and the occurrence and impacts of *Phytophthora* species (Jung, 2009; Nechwatal *et al*., 2011; Jung et al., 2018a; Corcobado *et al*., 2020). Some *Phytophthora* species (e.g. *P. cactorum*, *P.* ×*cambivora*, *P. plurivora*) can reduce naturally regenerated European beech seedlings (Jankowiak *et al*., 2023), but there is a knowledge gap on the pathogen species involved in natural regeneration failure of beech in Southern Europe. As for research in northern countries, e.g., by Jung *et al*. (2002; 2003b; 2005), Brasier and Jung (2003), and Matsiakh *et al*. (2021), and in Sicily by Jung *et al*. (2017a), there is need for further study to determine the pathogenicity of *Phytophthora* species to southern *F. sylvatica* tree populations. Additional investigation into the root condition of beech stands and other interacting abiotic factors is also required, including effects of drought and heat stress that may cause decline even in the absence of *Phytophthora* (Corcobado *et al*., 2020). As previously studied for *Q. ilex* in Spain (Corcobado *et al*., 2015) and *Q. petraea* and *Q. robur* in Germany (Jung *et al*., 2000), further research is required on relationships between *Phytophthora* presence and root parameters, beech vitality, and frequency and species richness of ectomycorrhizae.

The upsurge in bark necroses on European beech in several countries since 2000 indicates a period of increased disease activity requiring further research attention (Brasier *et al*., 2006). This should include the dissemination of *Phytophthora* species via the international nursery trade as an area requiring urgent attention by plant health agencies and the nursery trade. There is a clear need to prevent pathogen spread through infested nursery stock (Jung, 2009; Jung *et al*., 2005; 2016), to produce *Phytophthora*-free beech planting material, and to develop silvicultural treatments for declining mature *F. sylvatica* stands.

Phytophthora root and collar rot epidemic in *Alnus*

In nurseries, there is urgent requirement for inexpensive and rapid molecular-based detection protocols for alder-associated *Phytophthora* species, as visual inspection for detection of these pathogens is inadequate because infected plants may remain asymptomatic. Effort should also be made to adopt a code of good practice, including growing alders from seed, avoiding surface water during irrigation, and implementing 3-year fallows in forest nursery beds to prevent spread of the pathogens through nursery stock (Jung and Blaschke, 2004). In riparian ecosystems, difficulty in isolating the pathogen(s) indicates limitations in detection methods, which can hinder accurate epidemic assessments (Thoirain *et al*., 2007). Ioos *et al*. (2005) noted that direct isolation of the pathogen is often unsatisfactory, and developed SCAR-based PCR primers and an Internal Amplification Control to create molecular tools for detection and discrimination of *P.* ×*alni* and *P.* ×*multiformis* in environmental substrates (water, soil, bark), addressing the need for improved pathogen detection.

In Europe, a variety of resistant clones is required to sustain riparian alder stands, since coppicing of infected trees is only a short-term control measure (Jung and Blaschke, 2004; 2006). Jung and Blaschke (2006) and Chandelier *et al*. (2016) reported considerable variation in susceptibility to *P.* ×*alni* between different genotypes of *A. glutinosa*, and a tendency for increased resistance in surviving healthy trees in affected riparian alder stands, which could be the basis for resistance screening programmes. Martin *et al*., (2024) proposed a tree breeding programme to gain understanding of existing genetic variability of alders in the Iberian Peninsula, and the need to study stability of inherited resistance responses over time and host generations. For this purpose, a reliable and repeatable inoculation method is required to effectively screen alder genotypes for resistance to *Phytophthora* ×*alni* species (Jung and Blaschke, 2006; Chandelier *et al*., 2016). Stem wound inoculations on excised shoots are unreliable for evaluating resistance levels, due to lack of repeatability between successive years or different inoculation periods (Chandelier *et al*., 2016). Soil infestation tests with seedlings have been efficient in the resistance screening programme of *Chamaecyparis lawsoniana* to *P. lateralis* (Sniezko *et al*., 2019). With *P.* ×*alni* and *A. glutinosa*, zoospore inoculations of cuttings could be efficient and rapid for early screening of field trees (Jung and Blaschke, 2006). Limited studies have compared pathogenicity of *Phytophthora* pathogens in parallel, in underbark inoculation and soil infestation tests, highlighting a need for further research. Resist-

ance breeding programmes require, after the first period of screening, subsequent assessments for resistance of F1 and F2 generations under controlled conditions, and long-term trials in naturally infested stands to assess the field resistance of selected genotypes (Sniezko *et al*., 2020; Sniezko and Liu, 2023).

A knowledge gap exists for understanding possible synergies between different *Phytophthora* species within the *P.* ×*alni* complex, regarding the reported damage caused to alders (Cordeiro *et al*., 2024). Empirical understanding is required of *P.* ×*alni* impacts at multiple levels of ecological organization (Ferreira *et al*., 2022), particularly considering the potential for climate change to facilitate future disease spread (Bjelke *et al*., 2016). Macháčová *et al* (2024) and Gomes Marques *et al.* (2025) reported that research is urgently required on the interactions between *Phytophthora* pathogens, root and collar rot of alders, and climate change, particularly on effects of increasing frequency of climatic extremes such as droughts, floodings and heat waves.

Knowledge gaps on emerging diseases in Mediterranean crops

Phytophthora diseases of olive

Despite the increasing number of *Phytophthora* species reported from olive and wild olive, significant knowledge gaps remain regarding their introduction pathways, epidemiology, pathogenicity, and ecological impacts in Mediterranean agroecosystems (Deidda *et al*., 2025).

Assessment of pathogenic roles and aggressiveness of the different *Phytophthora* taxa detected in association with olive decline is a research priority. Although several species have been isolated from symptomatic plants, their individual contributions to disease development often remain unclear. Comparative pathogenicity studies under controlled and field conditions are required to determine pathogen virulence, host range, and possible interactions with climate stressors (Cacciola *et al*., 2011; Legrifi *et al*., 2024). Origins and introduction pathways of *Phytophthora* species associated with olive are further knowledge gaps. Their frequent detection in nurseries and young plantations highlights the role of infected planting material as an important pathway for dissemination (Jung *et al*., 2016; Scanu *et al*., 2021; Brasier *et al*., 2022), and the relative importance of other dispersal routes, such as irrigation water, soil movement, and agricultural machinery, remains little quantified. Integrating molecular epidemiology and population genetics could clarify these pathways and improve phytosanitary management strategies (Jung *et al*., 2016). Olive orchards may also be reservoirs of *Phytophthora* species that could spread to surrounding natural ecosystems. In Mediterranean landscapes, where olive groves often coexist with semi-natural habitats, pathogen spread from cultivated systems to native vegetation is a potential phytosanitary risk (González *et al*., 2017; González and Sánchez, 2020; Deidda *et al*., 2025). Long-term monitoring programmes combining traditional isolation methods with eDNA metabarcoding could provide insights into the diversity and dynamics of *Phytophthora* populations across agricultural and natural ecosystems (Jung *et al*., 2019; La Spada *et al*., 2022; Seddaiu *et al*., 2025).

Further research is also required on host resistance and disease management. Wild olive populations are important sources of genetic diversity, that could be exploited to identify tolerant genotypes for breeding programmes. However, the genetic basis of resistance to *Phytophthora*-induced root and collar rot remains largely unexplored (Cacciola *et al*., 2011; Jung *et al*., 2016; Legrifi *et al*., 2024). In parallel, additional field studies are required to evaluate effectiveness of integrated disease management strategies, including improved nursery hygiene, use of pathogen-free planting material, and optimized water management (Jung *et al*., 2016; Morales-Rodríguez *et al*., 2025).

Addressing these knowledge gaps is essential for increased understanding of the role of *Phytophthora* species in olive decline, and for development of sustainable strategies to protect olive production and Mediterranean ecosystems.

Decline of avocado caused by *Phytophthora*

As with *Phytophthora* problems on other hosts in the Mediterranean region, there are outstanding issues with the disease in avocado production that require investigation for optimum disease management. Although *P. cinnamomi* is the most commonly reported cause of avocado root rot, other *Phytophthora* spp. may also cause significant damage to this host. Therefore, it is necessary to assess the virulence of different *Phytophthora* spp., particularly when considering the use of resistant root stocks as an important major management technique.

In many avocado-growing regions, resistant rootstocks are used as a powerful disease management tool. Performance of resistant rootstocks under growing conditions in the different avocado-producing Mediterranean regions must be fully evaluated, including interactions with local environmental conditions and under climate change. It would also be useful if novel resistant rootstocks were selected with suitable adaptations to Mediterranean conditions.

For the existing problems that occur with *Phytophthora* root rot of avocado in Mediterranean countries, improved methods for sustainable disease management are required, including strong focus on the avocado holobiome and soil microbial communities that inhibit disease development. For effective future disease management, research is required to develop holistic strategies to reduce temptation to apply xenobiotic agrochemicals. This will likely maximize biological and cultural disease management, along with host resistance approaches (Pérez-Jiménez, 2005).

Citrus diseases caused by *Phytophthora*

Two major and interrelated knowledge gaps limit understanding and risk governance of citrus diseases caused by *Phytophthora* spp. in the Mediterranean Basin. The first is methodological and translational: a standardized, operational framework is lacking to convert heterogeneous detection outputs into comparable, decision-relevant estimates of inoculum pressure and disease risk at orchard scales. Culture-based isolation and baiting preferentially recover viable, often aggressive taxa, whereas metabarcoding can provide broad community snapshots that are sensitive to marker choice, bioinformatic processing, and the imperfect relationship between sequence reads, organism biomass, and viability. Partially discordant pictures of dominance and prevalence can emerge from the same production systems, and robust quantitative thresholds that integrate method outputs with epidemiological meaning remain insufficiently defined (La Spada *et al*., 2022; Conti Taguali *et al*., 2025). In export-oriented citrus industries, the need to estimate risks of moving quarantine-relevant *Phytophthora* taxa has stimulated quantitative assessments of species occurrence, niche preference, and seasonal windows of risk. This has provided examples of how surveillance outputs can be linked to trade-affecting risk interpretation (Hao *et al*., 2018, 2023).

The second gap is eco-epidemiological, and concerns the increasing role of climatic extremes as non-linear drivers of disease outbreaks. The epidemiology of citrus Phytophthora diseases is shaped by water availability, because zoospore release and dispersal depend on free water, and infections of subterranean and aerial organs are strongly modulated by soil moisture and canopy wetness duration (Judelson and Blanco, 2005; Cacciola and Magnano di San Lio, 2008). However, the increasing frequency and intensity of short-duration, high-impact rainfall events in the Mediterranean, including medicane-like storms, may episodically amplify dispersal, redistribute inoculum via splash and runoff, and prolong wetting windows in ways that depart from risk assumptions based on seasonal averages. Experimental evidence from non-Mediterranean citrus systems further indicates that flooding conditions can exacerbate host functional damage associated with *Phytophthora* infections, indicating that extreme wetness episodes act as disproportionate drivers of decline-risk beyond what is captured by mean seasonal patterns (Chaudhary *et al*., 2016). Quantitative understanding remains limited regarding how such events reshape within-orchard spatial patterns, timing, and severity of epidemics, and how these shock-like meteorological drivers propagate into the pre-harvest and post-harvest continuum of citrus production (Cacciola and Gullino, 2019; Rovetto *et al*., 2024a). The role of *Phytophthora* in exacerbating citrus tree decline caused by the lethal citrus diseases Huanglongbing and Citrus tristeza virus requires further research.

Prunus disease caused by *Phytophthora*

Several *Phytophthora* species have been reported infecting *Prunus* hosts across the Mediterranean Basin (Pérez-Sierra *et al*., 2010; Çiftçi *et al*., 2016; Jung *et al*., 2016; Kurbetli and Yilmaz, 2016; Türkölmez *et al*., 2016b; Kurbetli *et al*., 2025). Nevertheless, substantial gaps remain for this region in understanding of pathogen diversity, epidemiology, and disease dynamics. Existing surveys are typically restricted to individual host species, or are confined to specific localities, resulting in a fragmented overall view of *Phytophthora* incidence (Pérez-Sierra *et al*., 2010; Kurbetli and Deĝirmenci, 2011; Beluzán *et al*., 2022). To date, no comprehensive, region-wide assessments of root or stem rot caused by *Phytophthora* spp. on different *Prunus* species have been conducted, so emerging pathogen species are often documented only through isolated reports. A coordinated survey encompassing a broad geographical range is therefore essential to determine which *Phytophthora* species constitute significant threats to *Prunus* production systems. Furthermore, the potential impacts of these pathogens in nurseries remain insufficiently characterized, despite the critical role of nursery plants in pathogen dissemination.

Deeper understanding of the biology and pathogenicity of the *Phytophthora* species associated with *Prunus* is required to identify the most aggressive taxa, and to clarify host–pathogen interactions. In parallel, the susceptibility of commonly used rootstocks and commercially important cultivars should be systematically evaluated (Browne, 2017; Beluzán *et al.,* 2023). This information is pivotal for guiding *Prunus* breeding programmes aimed at developing tolerant or resistant rootstocks and cultivars.

Despite advances in sequencing techniques, limited understanding of *Phytophthora* infection processes and virulence factors, together with gaps in knowledge of host immune responses, are bottlenecks for the development of next-generation molecular tools. These are necessary for early diagnoses and to distinguish between the presence of pathogens and active, virulent infections.

Studies have focused on forecasting risks of *P. cinnamomi* infections of *Prunus* hosts (Brasier and Scott, 1994; Burgess *et al*., 2017; Cidre-González *et al.,* 2025). However, predictive models addressing climate-driven shifts in *Phytophthora* behaviour specifically affecting these plants are currently lacking.

Integrated disease management strategies tailored to Mediterranean *Prunus* orchards and nurseries are urgently needed to reduce/eliminate pathogen spread. Such strategies must be based on region-specific epidemiological data, and supported by robust, standardized diagnostic protocols. Addressing these research gaps will require coordinated, international efforts that use harmonized methods and advanced molecular diagnostics, as well as interdisciplinary collaboration among agronomists, plant breeders, plant pathologists, and modellers.

Knowledge gaps on *Phytophthora* pathways and drivers

Further spread of *Phytophthora* pathogens is inevitable due to increasing international trade (Jung *et al*., 2016; Horta Jung *et al*., 2025), revealing requirements for research into effective biosecurity measures along trade pathways. International regulations and protocols must be established, including an EU-wide nursery accreditation scheme with high biosecurity standards, to prevent the spread of *Phytophthora* species to new sites, which will require coordinated policy measures and management-focused research within countries (Jung *et al*., 2016; Contreras-Cornejo *et al*., 2023; Horta Jung *et al*., 2025).

Major gaps persist in national reporting of *Phytophthora* species. For example, Scott *et al*. (2019) highlighted that two-thirds of trading nations have lower-than-predicted species numbers, indicating knowledge gaps regarding the true global distribution of the genus. Barwell *et al*. (2021, 2025) stressed the need for increased knowledge about geographic ranges and host associations of *Phytophthora* species, and Guegan *et al*. (2023) highlighted that macroecology and biogeography research on plant pathogens and pests, including oomycetes like *Phytophthora*, remains limited. Surveys of natural ecosystems in previously unexplored regions of Asia, Africa and the Americas have unveiled unprecedented diversity of known and unknown *Phytophthora* species and, with population genetic and population genomic studies, have helped to clarify the geographic origins of major international *Phytophthora* pathogens, including *P. cactorum*, *P. cinnamomi*, *P. kernoviae*, *P. lateralis*, *P. multivora*, *P. plurivora*, *P. ramorum* and *P.* ×*cambivora* (Brasier *et al*., 2012; Jung *et al*., 2017b, 2017c, 2018b, 2020, 2021, 2022, 2024; Shakya *et al*., 2021; Bourret *et al*., 2022; Tsykun *et al*., 2022; Mullett *et al*., 2023). In a soil infestation test, the new hybrid species from Taiwan *P.* ×*heterohybrida* and *P.* ×*incrassata* caused severe root and collar rot and mortality of *C. sativa*. This highlighted the potential threats posed by new *Phytophthora* species not yet introduced to Europe (Jung *et al*., 2017b). Therefore, host range testing under controlled and biosecure conditions of this plethora of new *Phytophthora* species on major forest trees and crop species, including those in Mediterranean countries, and further surveys in previously unsurveyed regions of the world, are urgently required to assess the magnitude of threats posed by unknown *Phytophthora* pathogens (Jung *et al*., 2024). It is unlikely that only one *Phytophthora* species, *P. quercina*, occurs in Moroccan forests (Dorado *et al*., 2023a). Therefore, Mediterranean countries in North Africa require modern diagnostic methods, training of staff, and adequate research infrastructures. In these settings, risk assessments are constrained by under-reporting and limited surveillance, as several high-impact forest pathogens may remain undetected. International and cross-sectoral collaborations between Europe and the Maghreb region are essential for developing centralized databases that integrate pathogen distributions, environmental drivers, and invasion histories. This knowledge will support plant health horizon scanning. Robust legislative measures are needed to improve plant health protocols, together with development of an international best practice certification scheme (Green *et al*., 2021). Adopting best practice diagnostics and enhancing resource and data sharing are crucial for co-ordinated international pathogen surveillance and biosecurity.

Surveillance, detection and diagnosis of Phytophthora

Early and accurate detection is essential to prevent outbreaks and reduce immediate and long-term impacts of *Phytophthora* pathogens. Despite technological advances in surveillance, detection and diagnosis of *Phytophthora*, critical challenges remain. These include:

(i) Developing practical, affordable, and sensitive diagnostic methods (O'Brien *et al*., 2009; Keriö *et al*., 2020),
(ii) Portable tools for early and rapid pathogen detection by using molecular tools, including pyrosequenc-

ing for surveillance of forests and plantation crops (Clement *et al*., 2025);

(iii) Quantification and detection of multiple *Phytophthora* species by using a single genus-specific method (Cooke *et al*., 2007; Bilodeau *et al*., 2014);

(iv) Implementing surveillance schemes that encompass a broader range of *Phytophthora* species than previously targeted, reflecting the greater-than-expected diversity of the genus (Martin *et al*., 2012), and incorporating molecular validation to ensure taxonomic consistency and enable robust comparisons of pathogen impacts across studies (Geiser *et al*., 2023).

Complexes of closely related species (morphospecies) need to be taxonomically studied, and, if necessary, new species should be segregated and officially described. This will allow correct and exact disease diagnostics (Jung *et al*., 2003b, 2011, 2022, 2024; Jung and Burgess, 2009; Rea *et al*., 2010; Ginetti *et al*., 2014; Henricot *et al*., 2014; Scanu *et al*., 2014, 2021). Most molecular techniques used for detection are not designed to identify hybrid *Phytophthora* species. Bilodeau *et al*. (2014) underscored the importance of reproducible and accurate detection across different operators and equipment, because variations in annealing temperatures or thermal cyclers can lead to false-positive or false-negative results, and reduced reproducibility between different diagnostic facilities.

The limitations of traditional pathogen detection methods have been highlighted, including baiting or direct isolations, which are incapable of handling large volumes of material that need to be analysed (O'Brien *et al*., 2009; Shamoun *et al*., 2018). Avila-Quezada and Rai (2023) discussed the potential of nanomaterials and the application of mass spectrometry techniques, such as MALDI-MS, GC–MS, and LC-MS, for rapid and precise analysis of metabolites and identification of *Phytophthora* species. They suggested new ways for disease diagnoses. Use of bioelectronic noses is being assessed to detect and differentiate *Phytophthora* species through their volatile compounds (Borowik *et al*., 2021; Santonocito *et al*., 2023; Favaro *et al*., 2024). This would probably offer time-saving alternatives or additions to traditional detection methods. Groth-Helms *et al*. (2023) mentioned the development of isothermal diagnostic assays, that are accurate and sensitive for detecting some *Phytophthora* species (Hieno *et al*., 2021; Siegieda *et al*., 2021; Mainello-Land *et al*., 2025). The review by Papini *et al*. (2026) reported innovations focussed on sensor technology and point-of-care (POC) devices for fast, highly sensitive, and low-cost *Phytophthora* species detection in plant matrices, water and soil.

Knowledge gaps for *Phytophthora* management

A major challenge regarding *Phytophthora* in Mediterranean ecosystems is the management of *Phytophthora* species and the diseases they cause across the region. Although several *Phytophthora* species have been intensively studied, and are widely recognized as major pathogens causing root rot syndromes in chestnut, oak, alder, beech and horticultural woody species, there is incomplete knowledge about their management in most of Mediterranean environmental contexts, particularly before the appearance of disease symptoms (López-García *et al*., 2024). Detection and surveillance tools for *Phytophthora* in soil and plant tissues are currently limited in sensitivity and scalability. Traditional diagnostic methods often fail to detect the pathogens until trees show advanced disease symptoms (Encinas-Valero *et al*., 2022), restricting opportunities for early intervention (Keriö *et al*., 2020). There is a pressing need for development and validation of rapid, sensitive molecular diagnostics, and integrated surveillance systems that can track pathogen presence and spread over time and space (Ioos *et al*., 2005; Thoirain *et al*., 2007). Use of trained sniffer dogs to improve *Phytophthora* species detection has been suggested (Swiecki *et al.,* 2018; Morales-Rodríguez *et al*., 2025).

Evidence for effective direct control strategies in agriculture and natural forest settings remains scarce, likely because the broad host ranges of many *Phytophthora* species and the high susceptibility of naïve hosts (Jung and Burgess, 2009; Hardham and Blackman, 2018; Jung *et al.* 2018a, 2024; Brasier *et al*., 2022) often make disease management impractical or ineffective (Keriö *et al*., 2020). The diversity of pathogens and the impossibility of eradicating them also make management difficult (Moricca *et al*., 2016; Brasier *et al*., 2022). Many current detection and control methods are expensive, require considerable expertise, and can be used under controlled conditions, but they are technically non-applicable under field conditions (e.g., methyl jasmonate spray) (Dorado *et al*., 2025). A systematic mapping review by López-García *et al*. (2024) found that while biological and bio-based approaches (such as soil amendments or microbial antagonists) and genetic strategies (e.g., breeding for resistance) are relatively well studied, chemical and silvicultural measures at landscape scales have been less explored. This review also highlighted a general lack of holistic, long-term assessments of management interventions, underscoring the need for field trials that integrate ecological, biological, and operational dimensions for disease management. There have been, for example, no trials aimed

at reverting the lack of natural regeneration caused by *Phytophthora* (Domínguez-Begines *et al*., 2020).

Future research should also focus on implementing current tools and solutions for integrated management protocols, by developing holistic management strategies including the use of helper microorganisms and antagonists (Berger *et al*., 2015; Ruiz-Gómez *et al*., 2019; Morales-Rodríguez *et al*., 2025). Data generated in disease control trials carried out in laboratories and greenhouses must be transferred to the field, but under the different environmental stress conditions that prevail in the Mediterranean region (Solla *et al*., 2009; Tundo *et al*., 2025). Studying the resistance mechanisms of plants that are resistant to *Phytophthora* may aid in development of resistant tree varieties (Santos *et al*., 2017; de Andrade Lourenço *et al*., 2020, 2022; Saiz- Fernández *et al*., 2022).

In addition, risk assessment and decision-support tools for proactive management of diseases caused by *Phytophthora* are underdeveloped. Without spatially explicit risk maps or models that combine environmental data with pathogen occurrence and host vulnerability, as developed for *P. ramorum* and *P.* ×*alni* (Gomes Marques *et al*., 2024; Kartakis *et al*., 2026), forest managers face challenges for prioritizing areas for intervention or disease prevention. Integrating diverse datasets into accessible frameworks that support early warning and adaptive planning is an important research and operational need (Cidre-González *et al*., 2025).

There are gaps in knowledge transfer and stakeholder engagement. Many research outputs remain confined to academic circles, with limited translation into practical guidance tailored for forest managers, landowners, and policymakers. Strengthening participatory research and co-developing management guidelines with practitioners would help bridge science and disease management practice, improving the uptake of evidence-based strategies for *Phytophthora* management in Mediterranean agriculture, horticulture and forests (López-García *et al*., 2024). Bayesian Belief Networks have proven to be useful in integrating published research, unpublished data and expert knowledge (Gomes Marques *et al*., 2024).

CONCLUSIONS

Many species of *Phytophthora* cause major problems in a wide range of ecosystems across the Mediterranean region, in food crops, ornamental horticulture, urban plantings, forests, and natural environments. The wide variety of ecosystems in the Mediterranean region, coupled with high crop diversity, diverse endemic flora, and complex trade networks are compounded by climatic conditions favouring pathogen establishment and spread.

The severity of many diseases caused by *Phytophthora* species on a range of host plant species could increase driven by climatic changes. Yet, despite long awareness of these major problems in Mediterranean agricultural, horticultural and natural ecosystems, and the considerable research effort that has gone into understanding and managing them, many open questions remain. Concerted research effort is required, and could lead to improved disease control and management.

By reviewing the many important problems caused by these oomycetes in Europe, it becomes clear that methods used in one host-*Phytophthora* combination are likely to be useful for other host-*Phytophthora* systems, despite many differences in disease aetiologies. The processes for different pathogens, however, may differ based on types of land use system involved. It is essential that applied research aims to develop integrated, holistic protocols for disease management in nurseries, trade pathways, and all affected environments, while taking maximum advantage of developments in state-of-the-art methods for biosecurity, detection, resilience, and understanding of the molecular basis for infections and host resistance. These advances, must be utilised as widely as possible, and not confined to wealthy Mediterranean nations, as the pathogens are not confined by national boundaries.

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