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Neofusicoccum and *Phytophthora* Species: An Emerging Threat to Fig Trees (*Ficus carica*) in Italy, With the Description of *Phytophthora messapica* sp. nov.

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ABSTRACT

Monitoring surveys, conducted in four Italian regions (Apulia, Marche, Sardinia and Veneto), revealed the widespread occurrence of young and mature fig trees (*Ficus carica*) showing sudden death, crown thinning, shoot blight, branch dieback, cankers and root rot symptoms. Given the widespread distribution and severity of these symptoms, a study was conducted to identify the main causal agents. To achieve this goal, 86 samples including fine roots with rhizosphere (11) and branches with bleeding and sunken cankers (75) were collected from 11 symptomatic fig trees. Isolations performed on universal and selective growth medium yielded colonies belonging to three families: *Botryosphaeriaceae*, *Diaporthaceae* (Ascomycetes) and *Peronosporaceae* (Oomycetes). Based on morphobiometric data and DNA nucleotide sequences, seven species, namely *Botryosphaeria dothidea* (14 isolates), *Diaporthe cinerascens* (10), *Neofusicoccum australe* (9), *Neofusicoccum mediterraneaum* (10), *Neofusicoccum parvum* (28), *Phytophthora citricola* (3) and *Phytophthora plurivora* (6) were identified. In addition, two isolates of a new putative *Phytophthora* species obtained from the rhizosphere including symptomatic fine roots of fig trees in Apulia region are described here as *Phytophthora messapica* sp. nov. For *Phytophthora* species, *N. australe* and *N. mediterraneaum* (reported here for the first time on fig trees worldwide), Koch's postulates were satisfied by inoculating 5-year-old fig trees under controlled conditions. Sixty days after inoculation, all inoculated plants showed the same symptoms as those observed in the field. Overall, the data obtained highlights the involvement of multiple *Botryosphaeriaceae* and *Phytophthora* species in the aetiology of the emerging diseases affecting fig trees in Italy.

1 | Introduction

The genus *Ficus* (*Moraceae*) represents one of the largest groups of angiosperms, comprising around 800 species of woody plants worldwide (Falistocco 2024). *Ficus* species have a broad distribution across subtropical and tropical regions, especially in Asia and Australia (Berg 1989; Shi et al. 2018). The common fig (*Ficus carica*) is the only species of this genus with a Mediterranean distribution. It is among the earliest of domesticated fruit trees, with archaeobotanical evidence of cultivation dating back to around 9400 B.C. in Asia (Falistocco 2024; Stover et al. 2007). Originating in the Middle East, its cultivation spread through ancient Egypt, Greece and Rome, where it gained both economic and symbolic importance (Falistocco 2024). From the

17th century, the species expanded beyond the Mediterranean establishing in America through Spanish missions (Flaishman et al. 2008).

In addition to its agronomic relevance, *F. carica* has played a central role in religious, cultural and symbolic traditions, embodying fertility, abundance and knowledge. During the Middle Ages, figs remained a key dietary resource, while the Renaissance consolidated varietal selection and horticultural practices (Badgujar et al. 2014). Its historical trajectory illustrates the intersection of agriculture, culture and human subsistence across millennia (Dueñas et al. 2008; Kislev et al. 2006).

Among Mediterranean-producing countries, Turkey, Algeria, Egypt, Morocco, Greece, Italy and Spain account for approximately 70% of global fig production, with Turkey (about 350,000 t) being the leading producer (ISTAT 2024; Melgarejo et al. 2017; Sadder and Ateyyeh 2006; Sarkhosh et al. 2022). In Italy, as in other Mediterranean countries, wild forms and landraces of fig persist because of long-term acclimatisation and environmental adaptation processes. Specialised fig orchards have become increasingly common only in recent decades, particularly in southern regions, with a total cultivated area of approximately 2700 ha, about 30% of which is located in Apulia, followed by Calabria, Campania and Sicily (ISTAT 2024). However, the area cultivated with fig trees in Italy has drastically declined over past decades; in the 1970s it exceeded 40,000 ha. In 2023, annual fig production in Italy amounted to around 13,000 t, showing a slow increase compared with previous years (Mazzeo et al. 2024).

For decades, the fig tree has been regarded as a hardy species with a high level of resistance to diseases. Historically, the main diseases associated with fig have a fungal origin and include fig rust caused by *Cerotelium fici*, Cercospora leaf spot caused by *Pseudocercospora fici* and leaf and fruit anthracnose due to *Colletotrichum* spp. (Avasthi et al. 2023; Michailides 2003; Nur-Shakirah et al. 2023; Schubert et al. 1999). Moreover, several soilborne fungi, such as *Rosellinia necatrix* and *Armillaria mellea*, are known to cause root and collar rot of fig, leading to decline and death of adult trees in poorly drained soils (Michailides 2003).

In Italy, starting from the 1930s, a new viral disease called fig mosaic disease (FMD) emerged, and it has been associated with a viral complex of emaraviruses (Preising et al. 2021). Infected fig trees exhibit stunted growth and a reduction in yield ranging from 10% to 50%, depending on the severity of the infection, cultivar and environmental conditions (Preising et al. 2021).

In recent years, extensive decline and dieback of fig trees have been observed in different countries characterised by a Mediterranean climate. The associated symptoms include a loss of vegetative vigour, branch cankers and dieback, with sudden death of young and adult trees (Aiello et al. 2020; Habib et al. 2023; Mellal et al. 2023). Several pathogens have been isolated from trees with these symptoms, including *Ceratocystis ficicola*, *Neocosmospora caricae*, *Peroneutypa scoparia*, *Neofusicoccum parvum* and *Diaporthe cinerascens* (Bolboli et al. 2025; Çeliker and Michailides 2012; Ghaedi et al. 2023; Gusella et al. 2021, 2024; Habib et al. 2023; Michailides 2003; Tsopelas et al. 2021). In Italy, *Botryosphaeria dothidea* and *N. parvum* are the main species associated with branch cankers and dieback, as well as loss of fig production (Aiello et al. 2020, 2023; Gusella et al. 2024).

Some members of the *Botryosphaeriaceae* family have also been found to be involved in the aetiology of diseases affecting leaves, stem and fruits (Gusella et al. 2021; Habib et al. 2025; Wang et al. 2020). To date, eight species of *Botryosphaeriaceae* belonging to the genera *Botryosphaeria*, *Diplodia*, *Lasiodiplodia*, *Neofusicoccum* and *Neoscytalidium* have been reported as fig pathogens worldwide (Chen et al. 2018; Güney et al. 2022; Gusella et al. 2021, 2024; Jabnoun-Khiareddine et al. 2022; Li et al. 2024; Nur-Shakirah et al. 2022; Ray et al. 2010; Seo et al. 2019; Wang et al. 2020).

Recently, in addition to the typical symptoms caused by *Botryosphaeriaceae* species in some Italian orchards the onset of new disease symptoms has been observed, suggesting a more complex aetiology (Habib et al. 2025). These symptoms were similar to those detected in different Mediterranean regions on both woody agricultural crops (pomegranate and olive) and forest trees such as beech, ash and oaks (Benigno et al. 2023; Bregant, Marcolongo, Montecchio, et al. 2024; Bregant et al. 2025; Linaldeddu et al. 2020, 2023). In all of these cases a plethora of *Botryosphaeriaceae* and *Phytophthora* species have been found to be involved simultaneously (Linaldeddu et al. 2023; Bregant, Rossetto, Montecchio, et al. 2024; Bregant et al. 2025).

Therefore, given the rapid and extensive diffusion of these new symptoms on fig trees across Italian regions and the limited information about the aetiology, a study was conducted in four Italian regions in order to isolate and characterise the main causal agents.

2 | Materials and Methods

2.1 | Field Surveys and Sampling Procedure

The study was conducted from 2022 to 2025 in five sites located in four Italian regions: Veneto, Marche, Apulia and Sardinia (Table 1). These included semi-naturalised fig formations as well as orchards. Phytosanitary monitoring was performed to assess the health status of the plants, evaluate the nature and severity of the symptoms and collect symptomatic samples for diagnostic analysis. In sites 1, 4 and 5 three 50-m linear transects were randomly established to assess disease incidence and mortality rates, as reported in Bregant et al. (2023). In sites 2 and 3, single plants were sampled (there were no rows). A total of 86 representative samples including branches and twigs with cankers (75 samples) and fine roots with rhizosphere (11 samples) were collected from symptomatic plants (Table 1).

2.2 | Pathogen Isolation

In the laboratory, branch samples were first surface-sterilised with 70% ethanol and the outer bark was then removed using a sterile scalpel. Both longitudinal and cross sections were performed to examine the internal disease symptoms. For fungal isolation 10 small fragments (3 × 3 mm) of inner bark and xylem

TABLE 1 | Details of sampling sites and number of samples of fig (*Ficus carica*) collected.

Study site	Italian region	Coordinates	Number of samples	
			Root/rhizosphere	Branch cankers
1	Veneto	45°15′27.6″ N, 12°12′05.4″ E	2	30
2	Marche	43°49′13.8″ N, 13°01′33.6″ E	1	10
3	Marche	43°18′10.7″ N, 13°40′54.9″ E	1	5
4	Apulia	40°43′44.0″ N, 17°34′37.9″ E	5	15
5	Sardinia	39°27′18.0″ N, 08°45′03.0″ E	2	15

from the margin of the necrotic lesions were aseptically cut and placed onto 90 mm Petri dishes containing potato dextrose agar (PDA, Oxoid).

Phytophthora isolation from fine roots and rhizosphere samples was performed by the zoospore trap method proposed by Linderman and Zeitoun (1977) with the changes reported by Bregant et al. (2020). More specifically, the root samples including the rhizosphere (100 g) were placed in 1 L conical shape beakers and these were flooded with 800 mL of distilled water. Young *Quercus suber* leaves, obtained from cork oak seed-grown seedlings cultivated under greenhouse conditions, were used as baits on the water surface. Beakers were kept at 20°C under natural daylight and checked every 12–24 h for 3–5 days. Leaves showing dark spots were cut in to small fragments of 5 mm^2 and placed on 90 mm Petri dishes containing the *Phytophthora* selective medium PDA+ (Bregant et al. 2020).

All plates were incubated in the dark at 20°C and examined every 12 h. Hyphal tips from the emerging colonies were subcultured on PDA, carrot agar (CA), V8 agar (V8A) and malt extract agar (MEA, Oxoid; 20 $g\,L^{-1}$) and incubated at 20°C in the dark (Erwin and Ribeiro 1996) for subsequent assessment.

2.3 | Morphological Identification of Pathogens

All fungal and oomycetes isolates were initially grouped into morphotypes based on colony appearance, growth and morphobiometric data of asexual and sexual structures including conidia, ascospores, sporangia and oogonia. The morphological features of the fungal colonies were evaluated after 7 days of incubation at 25°C in the dark on PDA and MEA, while those of the oomycetes were evaluated on PDA, CA, MEA and V8A at 20°C.

For *Phytophthora* species, the formation of chlamydospores, hyphal swellings and sporangia was evaluated on CA and V8A (Erwin and Ribeiro 1996). To stimulate sporangial production, ten 5-mm mycelial plugs excised from the margin of 4-day-old CA cultures were placed in Petri dishes containing filtered non-sterile pond water supplemented with three 1-cm long *Q. suber* roots taken from seedlings obtained in the laboratory and washed in distilled water to remove soil. Petri dishes were incubated in the dark at temperatures ranging from 15°C to 28°C, and sporangia formation was monitored at 12-h intervals over 4 days. The production of gametangia in single culture was investigated on 90 mm CA and V8A plates incubated in the dark at 25°C for 21 days.

For the new putative *Phytophthora* species, mating behaviour was evaluated in dual cultures on CA by pairing isolates of the same species with each other and with heterothallic tester strains of known mating types: *Phytophthora cambivora* (CB11 [A1]), CB406 ([A2]), *Phytophthora citrophthora* (CB314 [A1]) and *Phytophthora cinnamomi* (CBS144.22 [A2]), following the protocol described by Brasier (1972). Additionally, gametangia induction was assessed by placing 5-mm mycelial plugs, taken from the margins of actively growing colonies on CA incubated at 15°C and 25°C in the dark for 5 days, in Petri dishes containing 5 mL of unsterile pond water.

In addition, for the new putative *Phytophthora* species the influence of temperature on mycelial growth was evaluated in vitro using 90 mm V8A Petri dishes incubated in the dark at 2°C, 5°C, 8°C, 10°C, 12°C, 15°C, 18°C, 20°C, 23°C, 25°C, 28°C, 30°C, 33°C and 35°C (±0.5°C). Five replicate plates were prepared by placing 5-mm agar plugs—excised from the actively growing margins of 4-day-old colonies on V8A plates incubated at 25°C ± 0.5°C—centrally on fresh V8A plates, with the mycelium side in contact with the medium. After 7 days of incubation, colony diameters were measured in two perpendicular directions per colony. Final growth values were obtained by averaging the measurements after subtracting the initial plug diameter.

Morphobiometric *Botryosphaeriaceae* data was evaluated according to Phillips et al. (2013). For both fungi and oomycetes, the size and shape of asexual and sexual structures was measured and recorded at 400× and 600× magnification with the software Motic Images Plus 3.0 paired with a Moticam 10+ camera connected to a Motic BA410E microscope. For each structure data were presented as mean values ± standard deviation of 50 measurements.

Representative isolates of each species were preserved on PDA and CA slopes under mineral oil and maintained in the culture collection of the Department of Land, Environment, Agriculture and Forestry (TESAF), University of Padova. The ex-type culture of the newly described species was deposited in the Westerdijk Fungal Biodiversity Institute (Utrecht, Netherlands), and the associated nomenclatural information was registered in MycoBank (www.MycoBank.org). The holotype specimen, consisting of a dried culture on CA, was deposited in the herbarium of the Westerdijk Fungal Biodiversity Institute.

2.4 | DNA Extraction, PCR Amplification and Sequencing

Molecular analysis was performed to confirm the identity of all isolates at the species level. Genomic DNA was extracted from the mycelium of 5-day-old cultures grown on PDA at 20°C using Instagene Matrix (Bio-Rad). The primers ITS1 and ITS4 (White et al. 1990) were used to amplify and sequence the rRNA internal transcribed spacer (ITS) regions of fungi and oomycetes, including the complete 5.8S rRNA gene. For four *Phytophthora* isolates including those of the new species, two other additional DNA regions, namely β-tubulin (*tub*) and mitochondrial cytochrome c oxidase subunit I (*cox1*), were amplified and sequenced using the primer pairs TUBUF2/TUBUR1 and FM84/FM83 (Kroon et al. 2004; Martin and Tooley 2003), whereas for four *Botryosphaeriaceae* isolates a portion of the translation elongation factor 1α gene (*tef1-α*) was amplified and sequenced with the primers EF446f and EF1035r (Inderbitzin et al. 2010). PCR mixtures and amplification conditions were performed as described by Bregant et al. (2023) and Linaldeddu et al. (2013).

The PCR products were purified using the Monarch PCR & DNA Cleanup Kit according to the manufacturer's instructions (New England Biolabs) and sequenced by the BMR Genomics DNA sequencing service (www.bmr-genomics.it). The nucleotide sequences were read and edited with FinchTV v. 1.4.0 (Geospiza Inc. http://www.geospiza.com/finchtv) and then compared with reference sequences (ex-type material) retrieved from GenBank using the BLASTn algorithm. ITS, *tub* and *cox1* sequences from representative isolates obtained in this study were deposited in GenBank (www.ncbi.nlm.nih.gov/genbank) (Table S1).

2.5 | Phylogeny

A concatenated phylogenetic analysis based on ITS, *tub* and *cox1* sequences was used to reconstruct the evolutionary relationships among the *Phytophthora* species obtained in this study into the major clades of the genus (Abad et al. 2023; Yang et al. 2017).

Nucleotide sequences were compiled into a dataset including representative sequences of the three taxa obtained in this study, including the two isolates of the new species and other 144 sequences from ex-type or representative isolates of the 13 major clades available in GenBank (Table S1). Sequences were aligned with ClustalX v. 1.83 (Thompson et al. 1997), using the parameters reported by Bregant et al. (2020).

Phylogenetic reconstructions were performed with MEGA-X 10.1.8, including all gaps in the analyses and by determining the best model of DNA sequence evolution automatically by the software (Kumar et al. 2018). Maximum-likelihood (ML) analysis was performed with a neighbour-joining (NJ) starting tree generated by the software. A bootstrap analysis (1000 replicates) was used to estimate the robustness of nodes. Alignments and trees are available in TreeBase (study ID 32495).

2.6 | Pathogenicity Test

To fulfil Koch's postulates, the pathogenicity of five isolates obtained in this study representing new host–pathogen associations (*Neofusicoccum australe* CB1281, *N. mediterraneum* CB1438, *Phytophthora citricola* CB1437, *Phytophthora messapica* CBS153930 and *Phytophthora plurivora* CB1274) was evaluated against 5-year-old fig trees cultivated in plastic pots (1.5 L volume). Fifteen replications were tested for each isolate with 10 for the control treatment.

For the collar inoculations, a 5 mm diameter hole was made through the bark using a cork borer and replaced with an agar plug of the same size taken from the margin of 5-day-old cultures grown on PDA. The inoculation wounds were wrapped with sterile damp cotton wool and covered with an aluminium foil. The plants were kept under greenhouse conditions, with natural light and temperatures ranging from 20°C to 30°C and were watered regularly every 3 days for 2 months (March/May 2025). Control plants were inoculated with a sterile PDA plug.

At the end of the experimental period, symptoms were examined and the extent of both external and internal lesions was measured. Pathogenicity assay data were tested for normality and then subjected to ANOVA. Significant differences among mean values were determined using Fisher's least significant difference multiple range test ($p = 0.05$) after one-way ANOVA, with the analysis conducted using XLSTAT 2008 software (Addinsoft). Reisolation was performed from small pieces of inner bark samples taken from the margin of necrosis and placed onto PDA and PDA+ medium. Growing colonies were subcultured onto CA and PDA, incubated in the dark at 20°C and identified by morphological and molecular (ITS sequence) analysis.

3 | Results

3.1 | Field Survey

Severe disease symptoms (Figure 1) affecting both tree vitality and productivity were consistently detected in all surveyed fig orchards. Affected figs showed root and collar rot, shoot blight (Figure 1b,c), cankers (Figure 1d–f), some with orange exudation, often seen on the lower part of the stem (Figure 1i), dieback (Figure 1a) and eventually sudden death. Extensive sunken cankers showing the characteristic wedge-shaped necrotic sector in cross section (Figure 1g,h) were frequently observed on stems and branches. Necrotic lesions gradually girdling the branches causing severe dieback (Figure 1a). Bleeding cankers with orange exudation were often visible on the lower part of the stem. Disease incidence ranged from 40% to 80%, with an average tree mortality rate of 15%.

3.2 | Aetiology

The isolation performed on 86 fig tree samples collected in different Italian regions yielded a total of 61 fungal and 11 oomycetes isolates in pure culture. The isolates were representative of three families, namely *Botryosphaeriaceae*, *Diaporthaceae* (ascomycetes) and *Peronosporaceae* (oomycetes).

Based on morphological and DNA sequences data seven known species were identified, including *B. dothidea* (14 isolates), *Diaporthe cinerascens* (10), *N. australe* (9), *N. mediterraneaum* (10), *N. parvum* (28), *P. citricola* (3) and *P. plurivora* (6) (Table 2, Figure 2). In addition, two *Phytophthora* isolates could not be assigned to any formally described species and shared the same ITS and *tub* sequences with an isolate (SCVWD302) available in GenBank with the *nomen nudum Phytophthora* taxon 'mugwort'. Therefore, to accommodate these isolates a new species was described here as *P. messapica* sp. nov.

Among the species isolated, *B. dothidea* and *N. parvum* were the most frequent on stem and branches with sunken cankers, with a wide geographical distribution (Table 2). *P. plurivora* was

FIGURE 1 | Overview of the symptoms observed on fig trees: progressive canopy dieback (a), shoot blight (b, c), sunken cankers (d–f), cross sections of branches showing the characteristic wedge-shaped necrotic sector in correspondence to the sunken canker (g, h), bleeding cankers on the lower part of the stem (i).

TABLE 2 | Number of isolates obtained from fig (*Ficus carica*) trees monitored at the study sites.

	Gen Bank accession no.			Number of isolates		
Species	**ITS**	***tef1-α***	***cox1***	**Root and rhizosphere**	**Branches**	**Sites[a]**
Botryosphaeria dothidea	PX928709	PX967079	—	—	14	1, 3, 4, 5
Diaporthe cinerascens	PX928710	—	—	—	10	1
Neofusicoccum australe	PX928711	PX967080	—	—	9	5
Neofusicoccum mediterraneum	PX928712	PX967081	—	—	10	4
Neofusicoccum parvum	PX928713	PX967082	—	—	28	1, 2, 3, 5
Phytophthora citricola	PX928714	—	PX967074	3	—	4
Phytophthora messapica	PX928715	—	PX967075	2	—	4
Phytophthora plurivora	PX928717	—	PX967077	6	—	1, 2, 3, 5

[a]Site locations are provided in Table 1.

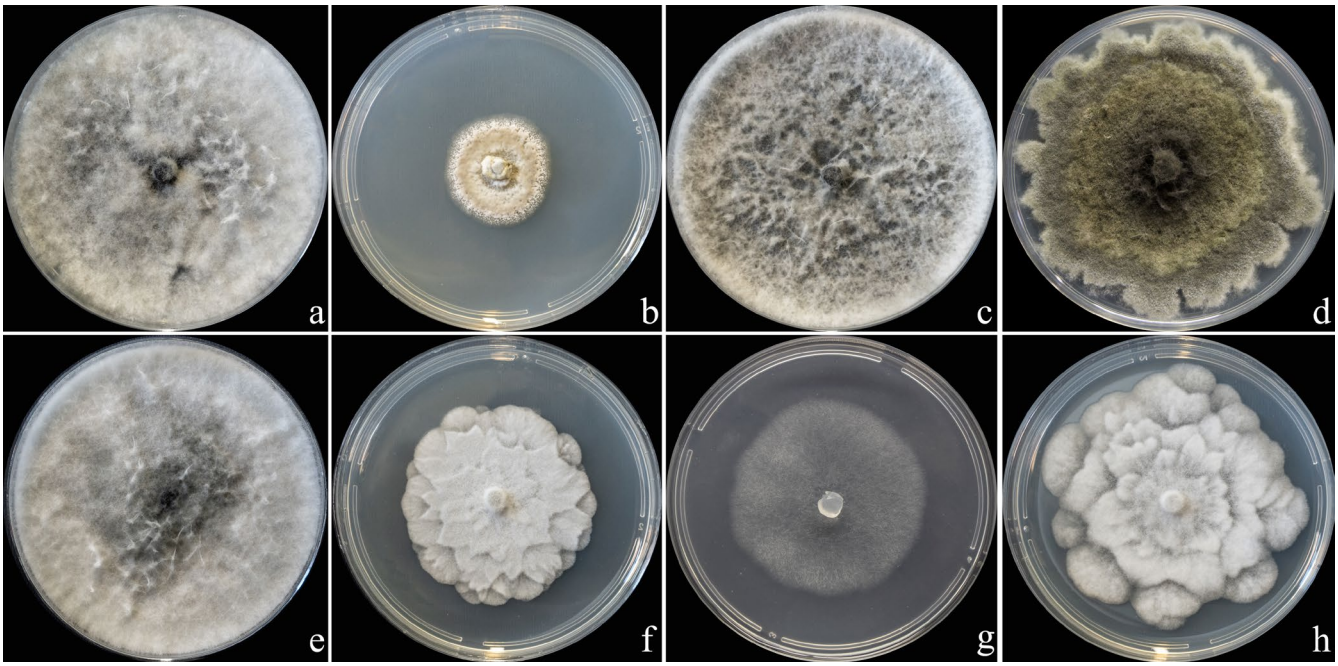

FIGURE 2 | Colony morphology of *Botryosphaeria dothidea* (a), *Diaporthe cinerascens* (b), *Neofusicoccum australe* (c), *Neofusicoccum mediterraneum* (d), *Neofusicoccum parvum* (e), *Phytophthora citricola* (f), *Phytophthora messapica* (g) and *Phytophthora plurivora* (h) on potato dextrose agar after 7 days at 25°C in the dark.

isolated from the root/rhizosphere samples in four sites from six out of the 11 trees monitored showing bleeding canker and root rot symptoms. The other *Phytophthora* species (*P. citricola* and *P. messapica*) appeared to be less common being only found at one site (Table 2). *N. australe*, *N. mediterraneum*, *P. citricola*, *P. messapica* and *P. plurivora* had never been previously isolated from fig trees worldwide.

Diaporthe cinerascens, an emerging pathogen recognised chiefly in Iran, in this study was isolated from sunken branch cankers at one site in the same cankers as *N. parvum*.

3.3 | Phylogeny of *Phytophthora* Species

PCR amplification of *Phytophthora* isolates yielded fragments of approximately 800 bp for the ITS region, 920 bp for *tub* and 1070 bp for *cox1*. Phylogenetic analyses of individual genes showed no significant incongruences, supporting the concatenation of the three loci for further analysis (data not shown).

The phylogenetic relationships among the *Phytophthora* isolates obtained in this study were evaluated using concatenated ITS, *tub* and *cox1* sequences (Figure 3). In particular, two representative isolates included in the phylogenetic analysis clustered into the clade 2c together with the ex-type strain of *P. citricola* and *P. plurivora*, respectively (Figure 3).

The other two *Phytophthora* isolates clustered together in a well-supported final clade (ML bootstrap = 100%) and were considered to represent a new *Phytophthora* species. These isolates share identical ITS and *tub* sequences with the strain SCVWD302 deposited in GenBank with the *nomen nudum* *Phytophthora* taxon 'mugwort', whereas they differ by one nucleotide in the *cox1* sequences.

The isolates of this new species form a distinct lineage within the newly formally designated clade 13 (Bourret, Choudhury, et al. 2018; Bourret, Mehl, et al. 2018), together with *Phytophthora transitoria* (Figure 3) (Abad et al. 2023).

3.4 | Taxonomy

***Phytophthora messapica* Bregant, Bourret and Linaldeddu sp. nov.**

MycoBank: MB862342.

Etymology: the epithet refers to the Messapia, an ancient region of pre-Roman Apulia, corresponding to the current Salento (south-eastern part of Apulia).

Holotype: CBS H- 25759.

Host/distribution: On rhizosphere of declining *Ficus carica* in Italy and *Artemisia douglasiana* in California.

Description: non-papillate sporangia were produced on CA plugs flooded in unsterile pond water after 36–48 h of incubation at 25°C. Sporangia were mostly persistent (90%), occasionally caducous (10%) with a short pedicel (av. 2.7 ± 0.7 μm, $n = 50$), from ovoid to pyriform, rarely obovoid (Figure 4d–h). Sporangia size ranged from 43.0 to 69.6 μm in length (av. 58.6 ± 5.5 μm) and from 32.8.1 to 48.6 μm in breadth (av. 39.9 ± 3.0 μm) with a length/breadth ratio of 1.5 ± 0.2 ($n = 50$). Typically, sporangia were borne terminally on unbranched

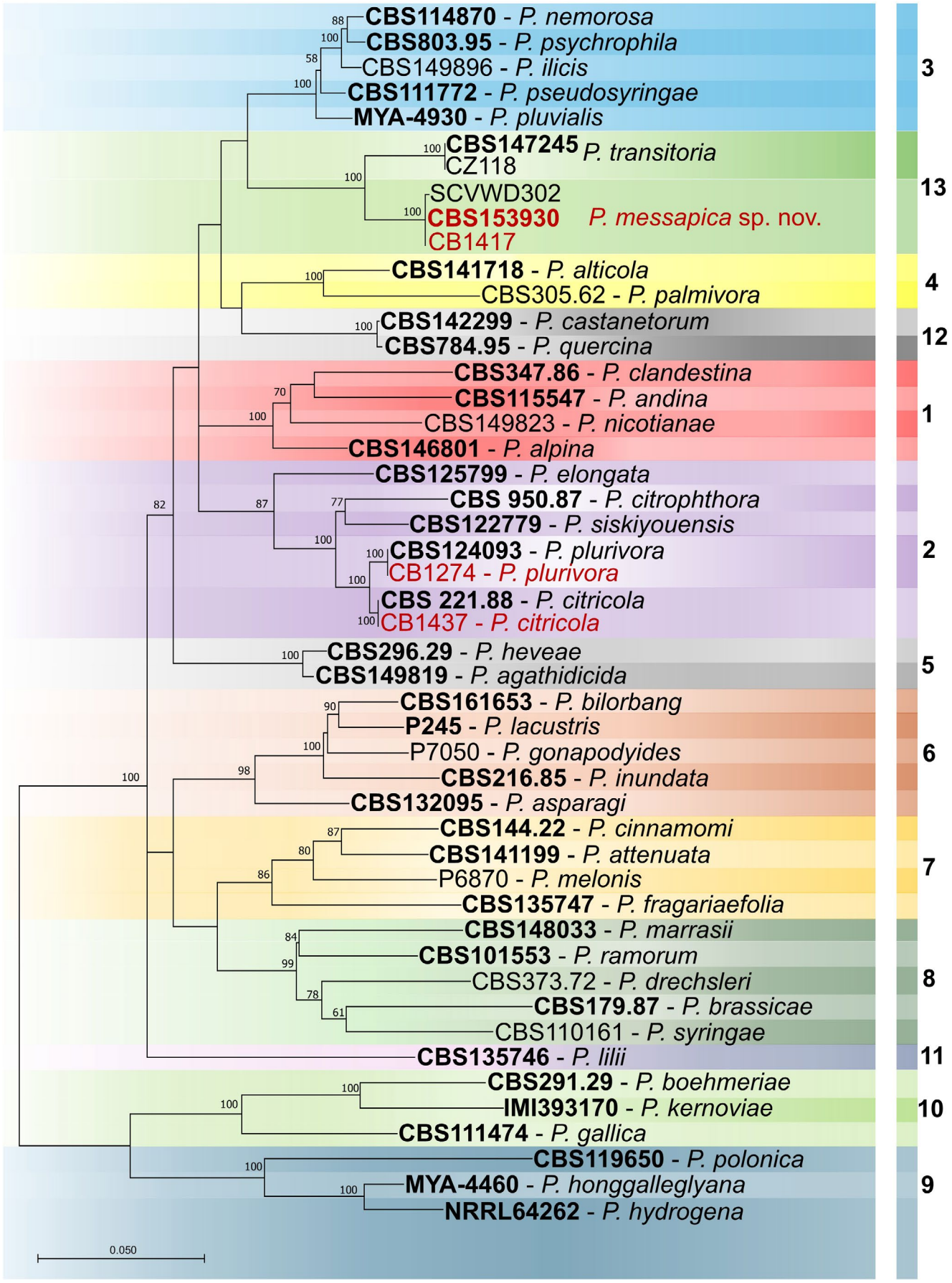

FIGURE 3 | Legend on next page.

FIGURE 3 | Maximum-likelihood tree obtained from concatenated ITS, *tub* and *cox1* sequences of *Phytophthora* species representative of the 13 major clades. Data are based on the general time reversible model. A discrete gamma distribution was used to model evolutionary rate differences among sites. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Bootstrap support values in percentage (1000 replicates) are given at the nodes. Ex-type cultures are in bold, and isolates obtained in this study in red.

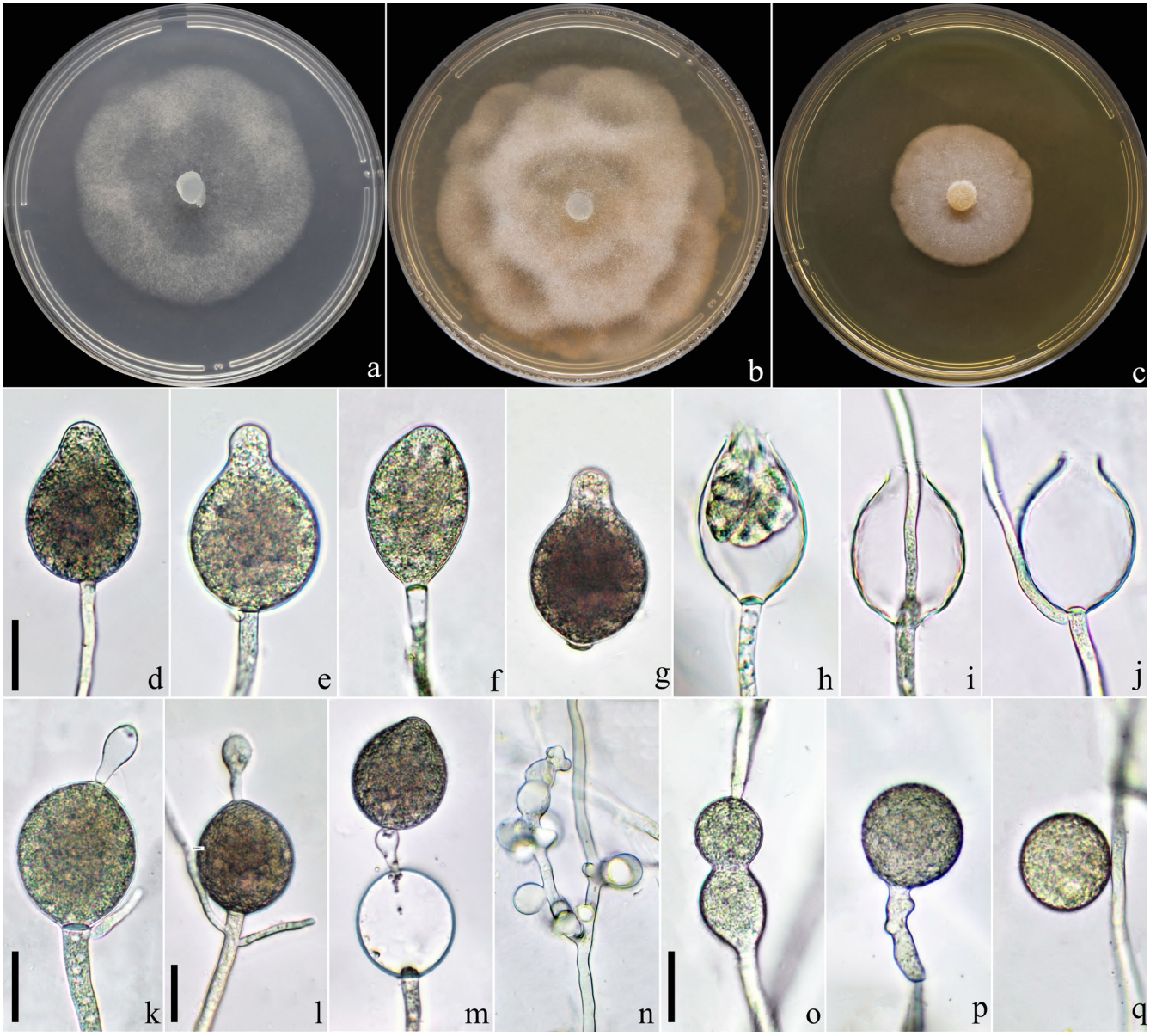

FIGURE 4 | Colony morphology of *Phytophthora messapica* (CBS153930) after 7 days growth at 20°C on potato dextrose agar (PDA) (a), carrot agar (CA) (b) and malt extract agar (MEA) (c). Non-papillate sporangia on CA after 36–48 h flooding in nonsterile pond water: Persistent (d–f), pyriform (d, e) to obovoid (f); caducous with a very short pedicel (g); sporangium releasing zoospores (h); internal extended (i) and external (j) proliferations; primary sporangia in different stages of development of secondary sporangia (k, l); empty primary sporangia and secondary mature sporangia after completion of cytoplasm transfer (m); subglobose catenulated hyphal swelling (n, o); globose terminal (p) and lateral chlamydospores (q). Scale bars = 20 μm.

sporangiophores and only occasionally on compound sporangiophores. Sporangial proliferation was usually external and very rarely internal (extended) (Figure 4i,j). Sporangia can directly release zoospores or sometimes exhibit transitional behaviour, progressively releasing their undifferentiated cytoplasm into secondary non-papillate sporangia (Figure 4k–m). Zoospores were produced in liquid cultures after 36–48 h (Figure 4h). Globose to subglobose, irregular and catenulate hyphal swellings were produced on CA flooded in unsterile pond water (Figure 4n,o). Spherical chlamydospores were mostly terminal and only occasionally intercalary or lateral (Figure 4p,q). Chlamydospores ranged from 17.7 to 40.2 μm in diameter (av. 31.5 ± 6.2 μm). Gametangia not observed in pure culture and in mating tests (dual culture) with *P. cambivora*

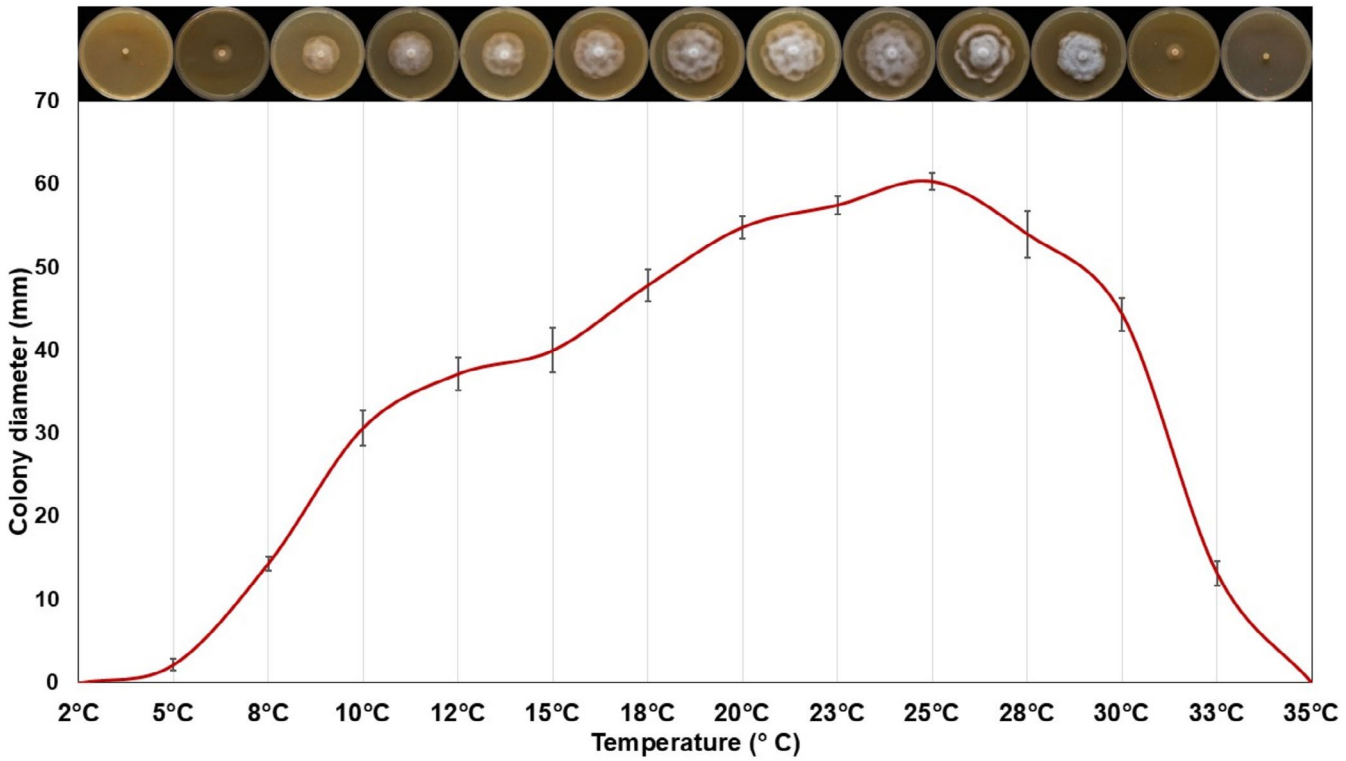

FIGURE 5 | Colony growth of *Phytophthora messapica* (isolate CBS153930) on V8A medium at different temperatures in the dark. The colony diameters were measured after 7 days of incubation. Data are presented as mean ± standard deviation.

(A1, A2), *P. citrophthora* (A1) and *P. cinnamomi* (A2) tester strains.

Cultural characteristics: colonies without a distinct pattern and a regular border on PDA (Figure 4a) and MEA (Figure 4c), petaloid and with irregular margin on CA (Figure 4b). On MEA colony growth was slow, whereas on PDA and CA colony reached 55 mm and 70 mm diameter in 7 days at 25°C, respectively.

Cardinal temperatures for growth: minimum 5°C, maximum 33°C and optimum 25°C. Isolates failed to grow at 35°C, and mycelium did not resume growth when V8A plates were moved to 25°C (Figure 5).

Material examined: ITALY: Ostuni, isolated from rhizosphere of a symptomatic *F. carica* tree, 12 November 2024, collected and isolated by Carlo Bregant, HOLOTYPE CBS H-25759, a dried culture on CA, culture ex-holotype CB1211 = CBS153930. ITALY: Ostuni, isolated from rhizosphere of a symptomatic *F. carica* tree, 12 November 2024, collected and isolated by C. Bregant (isolate CB1417).

Additional isolates studied: USA: California, baited with green pear from rhizosphere soil collected under nursery-origin *A. douglasiana*, 2 November 2015, collected and isolated by Heather Mehl (isolate SCVWD302 = CBS 149408) (Bourret, Mehl, et al. 2018).

Notes: *P. messapica* differs from the closely related species *P. transitoria* with a combination of unique morphological and molecular features, such as sporangia shape and size, the production of caducous sporangia and hyphal swellings, maximum cardinal temperature value, as well as a total of 84 fixed nucleotide differences in the ITS (29 bp), *tub* (30 bp) and *cox1* (25 bp) sequences. It shares the inability to differentiate gametangia in culture and the transient behaviours of the primary sporangia.

3.5 | Pathogenicity

All five species tested were shown to be pathogenic to *F. carica* and they were reisolated from all inoculated trees (Table 3), thereby fulfilling Koch's postulates. At the end of the experimental period, inoculated 5-year-old trees exhibited dark brown inner bark lesions that extended longitudinally above and below the inoculation site on the stem (Figure 6).

Statistical analysis of internal lesion length revealed significant differences among the species (Table 3). *N. australe* and *N. mediterraneum* on branches caused the most extensive cankers, characterised by dark inner bark necrosis (Figure 6). Lesions caused by these two species were significantly larger than those caused by the three *Phytophthora* spp. Among the *Phytophthora* species, *P. plurivora* was shown to be the most virulent, causing necrotic lesions significantly longer than those caused by *P. citricola* and *P. messapica*. Control seedlings remained asymptomatic showing a small wood discolouration at the inoculation point (Figure 6f,l).

Positive reisolation was achieved for all seedlings artificially inoculated with the five pathogens (Table 3).

TABLE 3 | Mean internal lesion length ± standard deviation caused by inoculation of 5-year-old fig (*Ficus carica*) trees with *Neofusicoccum* and *Phytophthora* species.

Species	Isolate	Mean lesion length (mm)	Reisolation (%)
Neofusicoccum australe	CB1281	44 ± 7 a	100
Neofusicoccum mediterraneum	CB1438	34 ± 3 b	100
Phytophthora citricola	CB1437	21 ± 3 d	100
Phytophthora messapica	CBS153930	18 ± 3 d	100
Phytophthora plurivora	CB1274	27 ± 4 c	100

Note: Values with the same letter do not differ significantly at $\alpha = 0.05$, according to LSD multiple range test.

FIGURE 6 | Symptoms observed on 5-year-old trees of *Ficus carica* 2 months after inoculation with *Neofusicoccum australe* (a, g), *Neofusicoccum mediterraneum* (b, h), *Phytophthora citricola* (c, i), *Phytophthora messapica* (d, j) and *Phytophthora plurivora* (e, k). Control seedling (f, l).

4 | Discussion

This study clarified the complex symptomatology and aetiology of the emerging diseases affecting fig trees in four Italian regions, achieving new insights into the role of *Botryosphaeriaceae* and *Phytophthora* infections. Specifically, the symptoms caused by the main isolated species often overlapped on the same tree, making a clear separation difficult. The synergic attack of *Botryosphaeriaceae* and *Phytophthora* species causes sudden death of young and mature trees.

Based on DNA sequence data and morphological features, five fungal species were identified: *B. dothidea*, *N. australe, N. mediterraneum, N. parvum* (*Botryosphaeriaceae*) and *D. cinerascens* (*Diaporthaceae*).

The genera *Botryosphaeria* and *Neofusicoccum* include polyphagous pathogens already widely known on fig and other woody hosts in Italy and worldwide (Batista et al. 2021; Bregant, Rossetto, Montecchio, et al. 2024; Li et al. 2024; Wang et al. 2020). In particular, *B. dothidea* and *N. parvum*

were previously reported as cankers and dieback agents of fig in southern Italy (Aiello et al. 2020, 2023). Recently, fig decline was redefined in the Salento peninsula (southern Italy) as a multifactorial disease relating to *Botryosphaeriaceae*, *Fusarium solani* species complex and *Ceratocystis ficicola* (Habib et al. 2025).

The complexity of fig decline aetiology is confirmed by the data obtained in this study with the discovery for the first time of the involvement of two more *Neofusicoccum* species (*N. australe* and *N. mediterraneum*) in Sardinia and Apulia, respectively; *N. australe* is an invasive pathogen originally described in Australia, and currently reported in Italy on several agricultural hosts such as avocado, grapevine, mango and olive (Aiello et al. 2023; Linaldeddu et al. 2011, 2023, 2026). *N. mediterraneum* is widespread across Mediterranean countries on different ornamental and crop plants (Aiello et al. 2023; Batista et al. 2021; Phillips et al. 2013). In Apulia it is currently considered to be one of the key agents involved in the olive quick decline syndrome (Brunetti et al. 2022; Scortichini et al. 2023). The proximity to other crops such as olive, grapevine and eucalyptus may have facilitated the host jump of these species onto fig. The diversity of *Neofusicoccum* species associated with branch dieback of fig trees suggest that no one single agent is involved in the aetiology but that it is the result of single or multiple infections of different pathogenic species able to induce the same symptoms.

In this study, *D. cinerascens* was detected in association with *N. parvum* from sunken cankers. Various canker types have been described in susceptible Iranian fig cultivars, including trunk lesions with zonation, sunken lesions and discoloured necrotic areas (Bolboli et al. 2022). *D. cinerascens* has been isolated from fig plants in Iran, California, Canada and Bulgaria (Banihashemi and Javadi 2009; Ferguson et al. 1990; Gomes et al. 2013; Hampson 1981). A defining characteristic of *D. cinerascens* is its narrow host range; indeed, *F. carica* remains the only host documented to date (Bolboli et al. 2022; Gomes et al. 2013). Our findings represent, to the best of our knowledge, the first report of this species in Italy.

The results obtained demonstrated for the first time the susceptibility of fig tree to *Phytophthora* infections. Two known species from clade 2c, *P. citricola* and *P. plurivora*, were isolated from the rhizosphere and symptomatic fine roots of fig. *P. citricola* was detected only in Apulia, whereas *P. plurivora* was found in all investigated regions except Apulia, suggesting a key role of this polyphagous pathogen in the mortality of figs. These two species were once considered to be a single taxon, belonging to the *P. citricola* complex. Morphological studies made it possible to separate the two cryptic species into *P. plurivora* and *P. citricola sensu strictu* (Jung and Burgess 2009). *P. plurivora* is an emerging pathogen now reported across Europe on several hosts in nursery, crop and forest systems (Bregant et al. 2021; Bregant, Rossetto, Sasso, et al. 2024; Schoebel et al. 2014). The adaptability of this species to different environmental conditions makes it a highly invasive organism, able to cause extensive mortality on various hosts and ecosystems spanning from agricultural to forest sectors, often in association with members of the *Botryosphaeriaceae* family (Benigno et al. 2023; Bregant et al. 2020; Bregant, Marcolongo, Montecchio, et al. 2024; Linaldeddu et al. 2026).

Furthermore, two *Phytophthora* isolates could not be assigned to any known species and are therefore described here as *P. messapica* sp. nov. The multilocus phylogeny placed *P. messapica* in the *Phytophthora* major clade 13 together with *P. transitoria* (Chen et al. 2022). *P. messapica* differs from its sister species *P. transitoria* based on 84 fixed polymorphisms in the ITS, *tub* and *cox1* sequence data. Both species produce primary transient sporangia and secondary sporangia. This feature represents a distinctive feature within the genus *Phytophthora*. This morphological trait together with the paraphyletic nature of the genus *Phytophthora* highlights the need for a taxonomic revision of the genus as recently suggested by Runge et al. (2011) and Thines et al. (2023). In the phylogenetic analysis one isolate (SCVWD302) available in GenBank as *Phytophthora* taxon 'mugwort' clustered together with *P. messapica*. *P. messapica* shows identical ITS and *tub* sequences with the strain SCVWD302, whereas one fixed polymorphism is present in the *cox1* region. The *nomen nudum Phytophthora* taxon 'mugwort', was established by Bourret, Mehl, et al. (2018) and Bourret, Choudhury, et al. (2018) to accommodate an isolate obtained from soil collected beneath a nursery-reared California mugwort shrub (*A. douglasiana*) planted for ecological restoration purposes in Santa Clara, California (USA). The plant was of moderate health with few above-ground symptoms and was included as part of a larger survey of restoration outplantings. This record, together with the findings obtained in this study, suggests that *P. messapica* is capable of attacking the root system of woody plants in areas with Mediterranean and semi-arid climates. Whether the species is native to Italy, California or introduced to both areas cannot be determined until more isolates are found. A genome assembly of the Californian isolate is available with accession GCA_033558025.1.

In the pathogenicity tests, all *Phytophthora* species caused necrotic lesions on the artificially inoculated plants and all were reisolated, thus fulfilling Koch's postulates and demonstrating for the first time their pathogenicity on *F. carica*.

Field surveys conducted in four Italian regions over a 3-year period showed a complex of pathogenic *Botryosphaeriaceae* and *Phytophthora* species associated with shoot blights, cankers and root rot symptoms on fig trees. Co-infection of native and exotic *Botryosphaeriaceae* and *Phytophthora* species on fruit trees such as fig (this study), olive (Linaldeddu et al. 2023) and pomegranate (Bregant, Rossetto, Montecchio, et al. 2024) are becoming more frequent in Mediterranean areas. Given the limited number of registered fungicides for these pathogens on agricultural crops, early diagnosis is crucial for understanding and managing these emerging diseases.

To date, knowledge on *Phytophthora*-related diseases on fig was very limited. Given the occurrence in all sites of the same symptoms observed on fig trees, also on other fruit trees such as almond and orange (authors' unpublished observations), further studies are in progress to evaluate the potential host jump of these pathogens from fig to other hosts, as well as the potential host range and geographic distribution of *P. messapica*.

Author Contributions

Benedetto T. Linaldeddu: conceptualization, investigation, funding acquisition, writing – review and editing, methodology, validation, supervision, data curation, formal analysis. **Sergio Murolo:** investigation, funding acquisition, writing – review and editing, supervision, formal analysis. **Francesca Carloni:** writing – review and editing, formal analysis, data curation, investigation. **Lucio Montecchio:** funding acquisition, writing – review and editing, supervision. **Carlo Bregant:** conceptualization, investigation, writing – original draft, funding acquisition, methodology, writing – review and editing, formal analysis, data curation. **Tyler B. Bourret:** investigation, funding acquisition, writing – review and editing, methodology.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Sequence data has been submitted to GenBank with accession numbers provided in Table 2 and Table S1. Other data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Details of *Phytophthora* isolates included in the phylogenetic analyses. Newly generated sequences are indicated in italics. [T]ex-type material.