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Invasive forest pathogens affect the characteristics, microbial colonisation, and decomposition of leaf litter in streams

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Abstract

1. Invasive tree pathogens threaten forests worldwide, but their effects on streams are poorly understood. Nevertheless, tree infections that lead to changes in the characteristics of litter inputs to streams may affect stream communities and ecosystem processes.
2. We studied cross-ecosystem effects derived from *Phytophthora cinnamomi*, *Phytophthora ×alni*, and *Ophiostoma novo-ulmi* infection on *Castanea sativa* (chestnut), *Alnus lusitanica* (alder), and *Ulmus minor* (elm) trees, respectively, by assessing physical and chemical characteristics of senescent leaves from healthy, symptomatic, and highly symptomatic individuals. Leaf litter from the three health statuses per tree species was then incubated in laboratory microcosms and the effects of tree infection on microbial decomposers and leaf litter decomposition were assessed.
3. Tree infection significantly affected leaf litter characteristics, microbial decomposers and leaf litter decomposition, and the health status of trees conditioned these effects differently depending on the tree species. In *C. sativa*, leaf litter of highly symptomatic trees had higher toughness, higher polyphenolic concentration and slower decomposition than leaf litter of symptomatic and healthy trees. In *A. lusitanica*, leaf litter of highly symptomatic trees had higher phosphorus concentration, lower carbon:phosphorus ratio and faster decomposition than leaf litter of symptomatic and healthy trees. Finally, in *U. minor*, leaf litter of highly symptomatic trees had higher nitrogen concentration and lower carbon:nitrogen ratio than leaf litter of healthy trees, and faster decomposition than leaf litter of symptomatic and healthy trees. Effects of changes in litter characteristics on litter decomposition were mediated by changes in microbial decomposer colonisation and activity.
4. The composition of the aquatic hyphomycetes communities associated with *C. sativa* and *U. minor* litter varied depending on the tree health status. Most striking was the two-fold higher aquatic hyphomycetes species richness in litter of *U. minor* trees infected with *O. novo-ulmi* than in litter of healthy *U. minor* trees.
5. Tree infection alters the nutritional quality of leaf litter, potentially affecting the functioning of aquatic ecosystems strongly dependent on riparian litter inputs.

KEYWORD
microbial decomposers, *Ophiostoma novo-ulmi*, pathosystem, *Phytophthora cinnamomi*, *Phytophthora ×alni*,

1 | INTRODUCTION

Biological invasions are major threats to biodiversity and ecosystem functioning worldwide (Gallardo et al., 2016; Vitousek et al., 1997). Forests are particularly threatened by invasive pathogens due to globalisation that facilitates pathogen transportation over long distances, forestry activities that often use nursery-infected plants and facilitate pathogen propagation across large areas, climate change that leads to pathogen establishment in areas that were previously unsuitable, and lack of pathogen-host co-evolution that makes trees highly susceptible to infectious diseases (Jung et al., 2016; Stenlid & Oliva, 2016).

Tree infection by invasive pathogens can cause devastating diseases and extensive diebacks (Basiewicz et al., 2007; Hansen, 2015; Loo, 2008). Pathogen-induced tree mortality can lead to changes in tree community composition, with consequences on the amount and dynamics of litter fall, and on litter quality, potentially affecting detrital pathways and nutrient cycling (Smock & MacGregor, 1988; Cobb & Rizzo, 2016). Moreover, inoculum build-up and disease development in mature trees can last for years to decades before tree death (Gea-Izquierdo et al., 2021; Jung et al., 2018). For example, infection of oaks by the soil-borne pathogen *Phytophthora* spp. often results in a slow process of tree decline characterised by non-specific symptoms of drought and malnutrition observed in leaves (Encinas-Valero et al., 2021; Jung et al., 2018; Solla et al., 2021). Because of biotic and abiotic stress, there can be changes in leaf quality, although the effects are not consistent across pathosystems. For example, the concentration of leaf litter lignin, leaf and leaf litter nitrogen, and leaf phosphorus have been found to significantly change or not after tree infection (Cobb & Rizzo, 2016; Fleischmann et al., 2010; Maurel et al., 2001; Milanović et al., 2015). Therefore, ecosystem effects of tree infection may result first from non-specific changes induced by the pathogen, and only at later stages from tree species replacement. Effects of tree infection on the detrital pathway may be noticed in the infested forest and in adjacent ecosystems, but cross-ecosystem effects derived from tree infection have been seldom assessed (but see Smock & MacGregor, 1988; Pazianoto et al., 2019; Alonso et al., 2021).

Forests and their streams are tightly connected by the bidirectional transfer of matter and energy (Marks, 2019; Tolkkinen et al., 2020). In particular, forest streams strongly depend on terrestrial organic matter for their functioning (Marks, 2019; Wallace et al., 1997), and are thus potentially susceptible to changes in the forest ecosystem that lead to altered litter inputs (Ferreira et al., 2021; Hladyz et al., 2011; Larrañaga et al., 2021; Mineau et al., 2012). The incorporation of litter inputs into aquatic food webs is mediated by microbial decomposers, mostly aquatic hyphomycetes (Gulis & Suberkropp, 2003; Hieber & Gessner, 2002). Microbes boost litter mass loss directly through carbon mineralisation and incorporation into their biomass, and indirectly by promoting litter maceration and by increasing litter nutrient concentration, which makes it more appealing for invertebrate consumers (Graça, 2001; Gulis & Suberkropp, 2003). The rate at which litter decomposes and carbon and nutrients are cycled depends on litter characteristics. Litter that is soft, is poor in defensive compounds (e.g., low polyphenol concentration) and in refractory carbon compounds (e.g., low lignin concentration), and is rich in nutrients (e.g., high nitrogen and phosphorus concentrations), generally sustains higher microbial activity and decomposes faster than more recalcitrant litter (Gessner & Chauvet, 1994; Lecerf & Chauvet, 2008; LeRoy et al., 2012; Ramos et al., 2021; Schindler & Gessner, 2009), thus entering the food web faster.

We studied cross-ecosystem effects of tree infection by invasive pathogens on stream ecosystems by assessing changes in the characteristics, colonisation by stream microbial decomposers and decomposition of leaf litter. We collected senescent leaves from healthy, symptomatic, and highly symptomatic *Castanea sativa* Mill. (sweet chestnut), *Alnus lusitanica* Vít, Douda and Mandák (alder), and *Ulmus minor* Mill. (field elm) trees to test the following hypothesis: (1) the health status of trees affects the physico-chemical characteristics of leaf litter, with more recalcitrant leaf litter being obtained from infected than from healthy trees, and from highly symptomatic than symptomatic trees. We then assessed the microbial colonisation and processing of leaf litter from trees of different health status in laboratory microcosms to test the following hypothesis: (2) microbial activity, decomposition, and aquatic hyphomycete communities of leaf litter respond to differences in litter characteristics induced by tree infection, with higher activity on less recalcitrant leaf litter.

2 | METHODS

2.1 | Study area and leaf litter collection

To test whether infection caused by invasive pathogens affects leaf litter characteristics and, consequently, microbial-driven leaf litter decomposition in streams, we used leaf litter from: (1) *C. sativa*, highly susceptible to the oomycete *Phytophthora cinnamomi* Rands; (2) *A. lusitanica* (previously *A. glutinosa* (L.) Gaertn.), highly susceptible to the oomycete *Phytophthora ×*alni Brasier & S. A. Kirk; and (3) *U. minor*, highly susceptible to the ascomycete *Ophiostoma novo-ulmi* Brasier. These three pathosystems were selected as they are widespread and have resulted in extensive dieback and tree mortality in southern Europe (Alcaide et al., 2020; Ghelardini et al., 2017; Jung et al., 2018; Solla et al., 2010; Zamora-Ballesteros et al., 2016).

The soil-borne *P. cinnamomi* is a generalist pathogen that infects close to 5,000 plant species and causes devastating diseases in agriculture, horticulture, and forest ecosystems (Hansen, 2015; Hardham & Blackman, 2018; Jung et al., 2018). Infection of *C. sativa* by *P. cinnamomi* causes the chestnut ink disease (Jung et al., 2018), which is widespread in Europe (Vannini & Vettraino, 2001); chestnut ink disease was also a major problem for *Castanea dentata* (Marsh.) Borkh. forests in North America before the emergence of the chestnut blight caused by the ascomycete *Cryphonectria parasitica* (Murrill) M. E. Barr, which functionally eradicated this tree species (Hansen, 2015). The oomycete *P. cinnamomi* attacks the fine feeder roots and the root collar, which affects tree nutrition and leads to the formation of abnormally small and chlorotic leaves, defoliation, and dieback of the canopy (Camisón, Martín, Sánchez-Bel, et al., 2019). At advanced stages of the disease, root cankers and collar rot usually lead to tree death, which can occur years after the first symptoms were visible in the canopy (Jung et al., 2018). Ink disease in chestnut can have serious ecological consequences on streams because *C. sativa* is a dominant tree species in northern temperate forests, contributing substantial litter inputs to forest streams during autumn (Lecerf et al., 2005; Molinero & Pozo, 2006).

The oomycete *P. ×alni* is a specialist pathogen that infects *Alnus* trees, with all species in the genus being potential hosts, causing decline and mortality of alders (Jung et al., 2018). The pathogen was first described in 1993 in the U.K., and it is now widespread across Europe (Bjelke et al., 2016; Jung et al., 2018). Zoospores infect the collar region usually via the non-suberised adventitious roots and through the large lenticels, and affected trees show small-sized, sparse, and often chlorotic foliage, a thinning and dieback of the crown, early and often excessive fructification, and eventually death (Jung et al., 2018). Young trees die within a few months while mature trees with large stem diameters take several years before they die (Jung et al., 2018). Decline and mortality of alders may have severe consequences on riparian ecosystems, since alders are often the most abundant trees in riverbanks, associate with nitrogen-fixing bacteria, and contribute large amounts of nitrogen-rich litter to streams in autumn (Bjelke et al., 2016; Lecerf et al., 2005; Molinero & Pozo, 2006).

Finally, the ascomycete *O. novo-ulmi* is responsible for Dutch elm disease (Santini & Faccoli, 2015). This vascular pathogen is vectored by elm bark beetles (Coleoptera: Curculionidae, Scolytinae), and is widespread across Europe and North America where it has devastated most *U. minor* and *Ulmus americana* L. populations, respectively (Brasier & Webber, 2019; Ghelardini et al., 2017). External symptoms of Dutch elm disease include crown discoloration and leaf wilting (Solla et al., 2014). Vessel obstruction drastically reduces the hydraulic conductivity in the functional xylem, resulting in a severe wilt syndrome, which kills the tree rapidly (Martín et al., 2021). In dry areas of southern Europe, where *U. minor* is considered a riparian species (López-Almansa, 2004; Martín et al., 2019), the impact of Dutch elm disease on stream ecosystems has not been assessed.

Senescent leaves (i.e., leaves that were gently removed from trees after undergoing natural senescence in autumn; *leaf litter* hereafter) from five healthy (≤ 5% crown transparency; estimated visually), five symptomatic (21%–40%), and five highly symptomatic (≥60%) trees of each species were collected in November 2017 (Pazianoto et al., 2019). Healthy and *P. cinnamomi*-symptomatic chestnuts were located in Hervás forest, Extremadura, Spain (40°15′11.8″N 5°52′44.3″W; 805 m above sea level [a.s.l.]). This riparian forest has a Mediterranean climate, with mean air temperature of 14.9°C and mean annual precipitation of 1005 mm. Isolations of *P. cinnamomi* from the rhizosphere of symptomatic trees suggested that they were infected, whereas no *P. cinnamomi* was isolated from the rhizosphere of healthy trees (Camisón et al., 2019). Healthy and declining alders were located along the river Jerte, Plasencia, Spain (40°01′51.2″N 6°04′46.0″W; 329 m a.s.l.; Marques et al., 2021). Isolations of *P. ×alni* from bark samples, including the cambium, confirmed infection of the ten symptomatic trees selected. Finally, healthy and diseased elms were located at 20–60 m from the river Jerte, Plasencia, Spain (40°02′04.0″N 6°04′20.3″W; 332 m a.s.l.). Isolations of *O. novo-ulmi* from the xylem of symptomatic trees confirmed that they were infected, whereas no *O. novo-ulmi* was isolated from the xylem of healthy trees. Senescent leaves were air-dried at room temperature, sent to the University of Coimbra and stored in the dark until used. All collection sites were within 30 km of each other.

2.2 | Leaf litter characterisation

Three leaf litter subsamples per tree were ground to powder (Retsch MM 400, Haan, Germany), oven-dried at 105°C, and used for initial chemical characterisation. Carbon (C) and nitrogen (N) concentrations were determined using an autoanalyser (IRMS Thermo Delta V advantage with a Flash EA-1112 series; Thermo Fisher Scientific Inc.), and phosphorous (P) concentrations were determined by the ascorbic acid method after alkaline digestion with sodium hydroxide and sodium persulfate (Bärlocher et al., 2020). Concentrations of total polyphenols were determined by the Folin-Ciocalteu method (Bärlocher et al., 2020) and lignin concentrations by the Goering-van Soest method (Goering & van Soest, 1970). Concentrations were expressed as percentage of dry mass (% DM). Carbon:nutrient (i.e., C:N and C:P) molar ratios were also calculated. Physical characteristics of leaf litter were also determined after moistening leaf litter with distilled water for 1 hr and cutting leaf litter discs with a cork borer 12 mm in diameter. Initial leaf litter toughness was estimated with a penetrometer as the mass (g) required to punch an iron rod, 1.55 mm in diameter, through the disc ($n = 9$ discs per tree) (Bärlocher et al., 2020). Specific leaf area was determined on the same leaf litter discs as the ratio of disc area (mm^2) to disc dry mass (mg) after drying for 24 hr at 105°C.

2.3 | Leaf litter conditioning

Before the microcosm experiment started, leaf litter of all 45 trees was moistened with distilled water and leaf litter discs 12 mm in diameter were obtained with a cork borer, avoiding the central

vein of leaves. Discs were air-dried for 72 hr, weighed in sets of 20 units, and each set was enclosed in a 0.5-mm mesh bag (5 × 7 cm). Three mesh bags per tree were incubated in a 15-L tank filled with filtered stream water, continuously aerated, and supplied with *c*. 4.5 L of a leaf litter mixture composed of leaves at different degradation stages as a source of microbial inoculum. Both water and leaf litter were collected from a local oligotrophic stream (Ribeira da Sardeira, Lousã Mountain, central Portugal; 40°5′21″N, 8°12′6″W; 683 m a.s.l.) that flows through a broadleaf deciduous forest (for more details see Ferreira et al., 2016; Gulis et al., 2006; Pereira et al., 2021). This stream has been used as a reference stream by the research team owing to the low human activity in the catchment and low dissolved nutrient concentration (36–76 μg dissolved inorganic N/L, 5–7 μg P/L; Gulis et al., 2006; Ferreira et al., 2016; Pereira et al., 2021). Incubation took place in a temperature-controlled room set at 13°C, with a 12-hr light: 12-hr dark photoperiod, and lasted 5 days. The water in the tank was renewed after 3 days to avoid inhibition of microbial conditioning of leaf litter discs by accumulation of polyphenols and tannins leached from the leaf litter mixture.

Dry mass (DM) of leaf litter discs at day 0 (i.e., after the conditioning period) was estimated by multiplying air-dry mass before microbial conditioning by a conversion factor derived from additional sets of leaf litter discs for each tree. The additional sets of discs were air-dried and weighed (DM_1), conditioned as described, oven-dried at 105°C for 24 hr, and weighed after conditioning (DM_2). The conversion factor was estimated as DM_2/DM_1.

2.4 | Microcosms

After conditioning, leaf litter discs were used in a laboratory microcosm experiment to test the effects of tree infection on microbial-driven decomposition of *C. sativa*, *A. lusitanica*, and *U. minor* leaf litter. Microcosms comprised 100-mL Erlenmeyer flasks filled with 40 mL of filtered water (glass microfibre filters, 0.7 μm pore size; Whatman GF/F, GE Healthcare UK Limited) from the same stream as above, renewed twice a week. Each microcosm received one set of conditioned leaf litter discs and was assembled on an orbital shaker (100–120 rpm; GLF 3017), kept at 13°C and under a 12-hr light: 12-hr dark photoperiod.

For each tree species (*C. sativa*, *A. lusitanica*, and *U. minor*) and health statuses (healthy, symptomatic, and highly symptomatic trees), 15 microcosms were prepared (i.e., three per tree). One microcosm per tree was sacrificed at days 11, 32 and 57 after incubation to determine conidial production by aquatic hyphomycetes, microbial respiration rates, leaf litter toughness, fungal biomass, and leaf litter mass. In total, 135 microcosms were used (three species × three tree health statuses × five trees × three sampling dates).

2.5 | Conidial production by aquatic hyphomycetes

On each sampling date, the conidial suspensions were transferred into 50-mL Falcon tubes, fixed with 2 mL of formalin (37% formaldehyde in water) and stored in the dark until used. For conidia identification and counting, 150 μL of Triton X-100 (0.5%) were added to each suspension, mixed with a magnetic stirrer to guarantee uniform distribution of conidia, and an aliquot of 10–20 mL, according to conidia density, was passed through cellulose filters (25-mm diameter, 5-μm pore size; Fioroni). Filters were stained using 0.05% cotton blue in 60% lactic acid and conidia were identified and counted using a microscope at 400× magnification (Nikon Eclipse E200, Nikon Corporation), according to Bärlocher et al. (2020). Sporulation rates by aquatic hyphomycetes were expressed as the number of conidia released per mg of leaf litter DM and day, and species richness was expressed as the number of species per sample.

2.6 | Microbial respiration rates

Microbial respiration rates, a proxy of overall microbial metabolism, were determined using a closed six-channel dissolved oxygen measuring system (Strathkelvin 929 System, North Lanarkshire, U.K.; Bärlocher et al., 2020). The oxygen electrodes were calibrated at 13°C with a 0% O_2 solution (sodium sulfite in 0.01 M sodium borate) and a 100% O_2 saturated stream water. Subsets of five discs from each sacrificed microcosm were incubated at 13°C for *c*. 1 hr in 3-mL chambers containing 100% O_2 saturated stream water. Additional chambers without leaf litter discs were used as controls. Respiration rates were determined as the difference between the oxygen concentration in the sample and the control over a 20-min interval during which oxygen consumption was linear. Results were expressed as mg O_2 consumed per g leaf litter DM per hour.

2.7 | Leaf litter toughness

The same discs used for microbial respiration rates were used to determine leaf litter toughness, as a surrogate for enzymatic maceration of leaf litter. The same penetrometer and method described above was applied. Results were expressed as leaf litter toughness in g and as leaf litter toughness remaining in percentage of leaf litter toughness relative to initial toughness (at day 0), estimated as (toughness/initial toughness) × 100. Leaf litter discs were then oven-dried for 24 hr at 105°C and weighed for determination of DM.

2.8 | Fungal biomass

An additional subset of five leaf litter discs from each microcosm was promptly frozen at −20°C, lyophilised overnight, weighed for determination of DM, and used to determine ergosterol concentration as a proxy for fungal biomass (Bärlocher et al., 2020; Gessner & Chauvet, 1993). Ergosterol was extracted in 10 mL of alkaline methanol (8 g KOH/L) for 30 min at 80°C. The extract was then purified by solid phase extraction (Waters Sep-Pak® Vac RC, 500 mg, Tc18

cartridges; Waters Corp) and quantified with high-performance liquid chromatography (Dionex DX-120) by measuring absorbance at 282 nm. The chromatography system was equipped with the Thermo Scientific Syncronis C18 column (250 × 4 mm, 5-μm particle size; Thermo) and the Thermo Universal Uniguard holder 4/4.6 mm ID3 + Syncronis C18 (10 × 4 mm, 5-μm particle size) drop in guard pre-column (Thermo), which was set at 33°C. The mobile phase was 100% methanol, flowing at a rate of 1.4 mL/min. Because on day 32 ergosterol recovery rates were extremely low for *A. lusitanica* leaf litter, data are not shown. Ergosterol concentration was converted into fungal biomass assuming 5.5 μg ergosterol per mg fungal DM (Gessner & Chauvet, 1993), and the results were expressed as mg fungal DM per g leaf litter DM.

2.9 | Leaf litter mass remaining

The remaining 10 leaf litter discs from each microcosm were oven-dried for 24 hr at 105°C and weighed for determination of DM. This DM was added to that of the discs used for determination of microbial respiration and fungal biomass to allow estimation of total DM remaining. Results were expressed as percentage of initial DM (total DM remaining/initial DM × 100).

2.10 | Data analysis

Physical and chemical leaf litter characteristics were compared among the three health statuses (healthy, symptomatic, and highly symptomatic) for each tree species separately by one-way analysis of variance (ANOVA; using the average of three subsamples for each tree). Decomposition rates (k, day^{-1}) were calculated for each tree health status assuming an exponential decay model, by linear regression of ln-transformed fraction of DM remaining over time, considering the intercept fixed at ln(1) = 0. Leaf litter DM and toughness remaining (fraction, ln-transformed) over time were compared among the three health statuses for each tree species separately by analysis of covariance (ANCOVA), with tree health status as categorical factor and time as covariate. Leaf litter toughness, microbial respiration rates, fungal biomass and aquatic hyphomycetes sporulation rates and species richness were compared among the three tree health statuses for each tree species separately by repeated measures (RM) ANOVA. Tukey's tests were used for multiple comparisons when significant effects were detected in ANCOVA or RM ANOVA. Aquatic hyphomycete communities were compared among the three health statuses for each tree species by analysis of similarity (ANOSIM) based on a Bray–Curtis dissimilarity matrix of conidial production by aquatic hyphomycetes (log(x + 1)-transformed).

Data were checked for normality by Shapiro–Wilk's test and homoscedasticity by Levene's test, and transformed when necessary before analysis (details are provided in the statistical tables). Analyses were performed using Statistica 7.0 (StatSoft, Inc.), except ANOSIM, which was performed using Primer 6 v6.1.11 (Primer-E Ltd; Clarke & Gorley, 2001).

3 | RESULTS

3.1 | Leaf litter characteristics

Tree infection significantly affected initial physical and chemical characteristics of leaf litter, although not in a consistent way across species (Table 1). In leaf litter of *C. sativa*, toughness and polyphenols concentration were significantly higher in highly symptomatic than in healthy or symptomatic trees (Table 1). There was also a marginal tendency (one-way ANOVA, $p = 0.052–0.087$) for specific area and P concentration to decrease, and for lignin concentration, C concentration and C:P molar ratio to increase as *C. sativa* trees were more symptomatic (Table 1). In leaf litter of *A. lusitanica*, P concentration was significantly higher and C:P molar ratio was significantly lower in highly symptomatic than in healthy or symptomatic trees, while N concentration was significantly lower and C:N molar ratio was significantly higher in symptomatic than in healthy trees (Table 1). Finally, in leaf litter of *U. minor*, polyphenols concentration was significantly higher in symptomatic than in healthy or highly symptomatic trees, N concentration was significantly higher and C:N molar ratio was significantly lower in infected than in healthy trees (Table 1). There was also a marginal tendency (one-way ANOVA, $p = 0.059–0.093$) for lower specific area and higher leaf litter lignin concentration in symptomatic than in healthy and highly symptomatic *U. minor* trees, and for higher leaf litter P concentration in infected than in healthy trees (Table 1).

3.2 | Leaf litter decomposition

Remaining leaf litter mass significantly decreased over the incubation period, and after 57 days it varied between 54% and 67%, 48% and 63%, and 39% and 59% for *C. sativa*, *A. lusitanica*, and *U. minor*, respectively (Figure 1a–c). Leaf litter decomposition rates were significantly affected by tree health status (ANCOVA, $p < 0.001$; Table 2, Table S1), although not in the same way across tree species. In *C. sativa*, decomposition rates were significantly lower for leaf litter of highly symptomatic than of healthy or symptomatic trees (Tukey's test, $p \leq 0.003$; Table 2). On the contrary, in *A. lusitanica* and *U. minor*, decomposition rates were significantly higher for leaf litter of highly symptomatic than of healthy or symptomatic trees (Tukey's test, $p \leq 0.002$; Table 2).

3.3 | Leaf litter toughness

Leaf litter toughness significantly decreased over the incubation period (Figure 1d–f), and after 57 days toughness remaining varied between 33% and 51%, 14% and 40%, and 25% and 35% for *C. sativa*, *A. lusitanica*, and *U. minor*, respectively (Figure 1g–i). Leaf litter

TABLE 1 Physical and chemical characteristics (mean ± *SE*) of leaf litter of healthy, symptomatic, and highly symptomatic *Castanea sativa*, *Alnus lusitanica*, and *Ulmus minor* trees ($n = 5$)

Leaf litter characteristics	Tree health status			
	Healthy	Symptomatic	Highly symptomatic	*p* value
Castanea sativa				
Toughness (g)	114 ± 9[a]	113 ± 10[a]	150 ± 6[b]	**0.014**
SLA (mm^2/mg)	29.6 ± 3.3	28.6 ± 2.3	21.5 ± 1.5	0.079
Polyphenols (%DM)	9.8 ± 1.0[a]	10.0 ± 0.9[a]	15.4 ± 1.1[b]	**0.003**
Lignin (%DM)†	25.1 ± 1.5	28.5 ± 0.6	29.3 ± 1.4	0.072
Carbon (%DM)	48.6 ± 0.5	49.3 ± 0.4	50.2 ± 0.3	0.052
Nitrogen (%DM)	0.61 ± 0.03	0.67 ± 0.09	0.90 ± 0.20	0.255
Phosphorus (%DM)	0.087 ± 0.010	0.068 ± 0.011	0.054 ± 0.006	0.070
Carbon:nitrogen	94.8 ± 5.3	93.8 ± 12.2	87.4 ± 28.6	0.953
Carbon:phosphorus	1525 ± 250	2055 ± 320	2456 ± 228	0.087
Alnus lusitanica				
Toughness (g)	113 ± 11	140 ± 11	121 ± 16	0.354
SLA (mm^2/mg)	20.3 ± 1.8	16.4 ± 1.2	18.9 ± 1.6	0.243
Polyphenols (%DM)	6.5 ± 1.1	7.3 ± 0.7	8.5 ± 0.9	0.326
Lignin (%DM)	36.6 ± 1.9	36.2 ± 0.8	37.4 ± 1.5	0.847
Carbon (%DM)†	47.8 ± 0.9	47.3 ± 0.4	46.9 ± 0.4	0.641
Nitrogen (%DM)	2.16 ± 0.07[a]	1.76 ± 0.14[b]	1.96 ± 0.06[ab]	**0.035**
Phosphorus (%DM)	0.016 ± 0.002[a]	0.017 ± 0.002[a]	0.047 ± 0.004[b]	**<0.001**
Carbon:nitrogen	26.0 ± 0.7[a]	32.3 ± 2.5[b]	28.1 ± 0.9[ab]	**0.046**
Carbon:phosphorus	8,417 ± 1,059[b]	7,631 ± 937[b]	1,717 ± 247[a]	**<0.001**
Ulmus minor				
Toughness (g)	100 ± 12	104 ± 5	86 ± 4	0.247
SLA (mm^2/mg)	13.4 ± 1.1	11.9 ± 1.5	16.8 ± 1.5	0.067
Polyphenols (%DM)	10.6 ± 1.0[a]	13.8 ± 0.8[b]	10.46 ± 0.9[a]	**0.042**
Lignin (%DM)	28.6 ± 2.2	33.7 ± 1.9	27.6 ± 0.9	0.059
Carbon (%DM)	42.9 ± 1.4	45.8 ± 2.9	44.2 ± 1.9	0.644
Nitrogen (%DM)	0.79 ± 0.11[a]	1.35 ± 0.14[b]	1.67 ± 0.17[b]	**<0.001**
Phosphorus (%DM)	0.032 ± 0.003	0.048 ± 0.009	0.064 ± 0.013	0.093
Carbon:nitrogen	74.4 ± 8.8[b]	41.1 ± 1.9[a]	32.1 ± 2.8[a]	**<0.001**
Carbon:phosphorus	1547 ± 173	1774 ± 697	2177 ± 581	0.706

Note: Comparisons among health statuses for each tree species were made by one-way ANOVA and significant *p* values are highlighted in bold. Different letters indicate significant differences between means according to Tukey's tests ($p < 0.050$).

Abbreviations: DM, dry mass; SLA, specific leaf litter area.

†These variables were transformed for the analyses (arcsine(x)).

toughness was significantly affected by the health status only in *C. sativa* trees (RM ANOVA, $p = 0.009$; Table S2), with higher values in leaf litter of highly symptomatic than of healthy or symptomatic trees (Tukey's test, $p \leq 0.010$).

Leaf litter toughness remaining in relation to initial values was significantly affected by the health status in *C. sativa* and *A. lusitanica* trees (ANCOVA, $p = 0.033$ and $p < 0.001$, respectively; Table S1). Toughness was higher in leaf litter of symptomatic than of healthy *C. sativa* trees (Tukey's test, $p = 0.031$), and lower in leaf litter of infected than of healthy *A. lusitanica* trees ($p \leq 0.008$).

3.4 | Microbial respiration rates

Microbial respiration rates were generally stable over the incubation period, and after 57 days they ranged from 0.31 to 0.53, 0.20 to 0.53, and 0.29 to 0.35 mg O_2 g^{-1} DM h^{-1} in leaf litter of *C. sativa*, *A. lusitanica*, and *U. minor* trees, respectively (Figure 2a–c). Respiration rates were significantly affected by the health status of trees in *A. lusitanica* (RM ANOVA, $p < 0.001$; Table S2), with higher values in leaf litter of infected than of healthy trees (Tukey's test, $p < 0.001$). In *U. minor*, respiration rates were significantly affected by

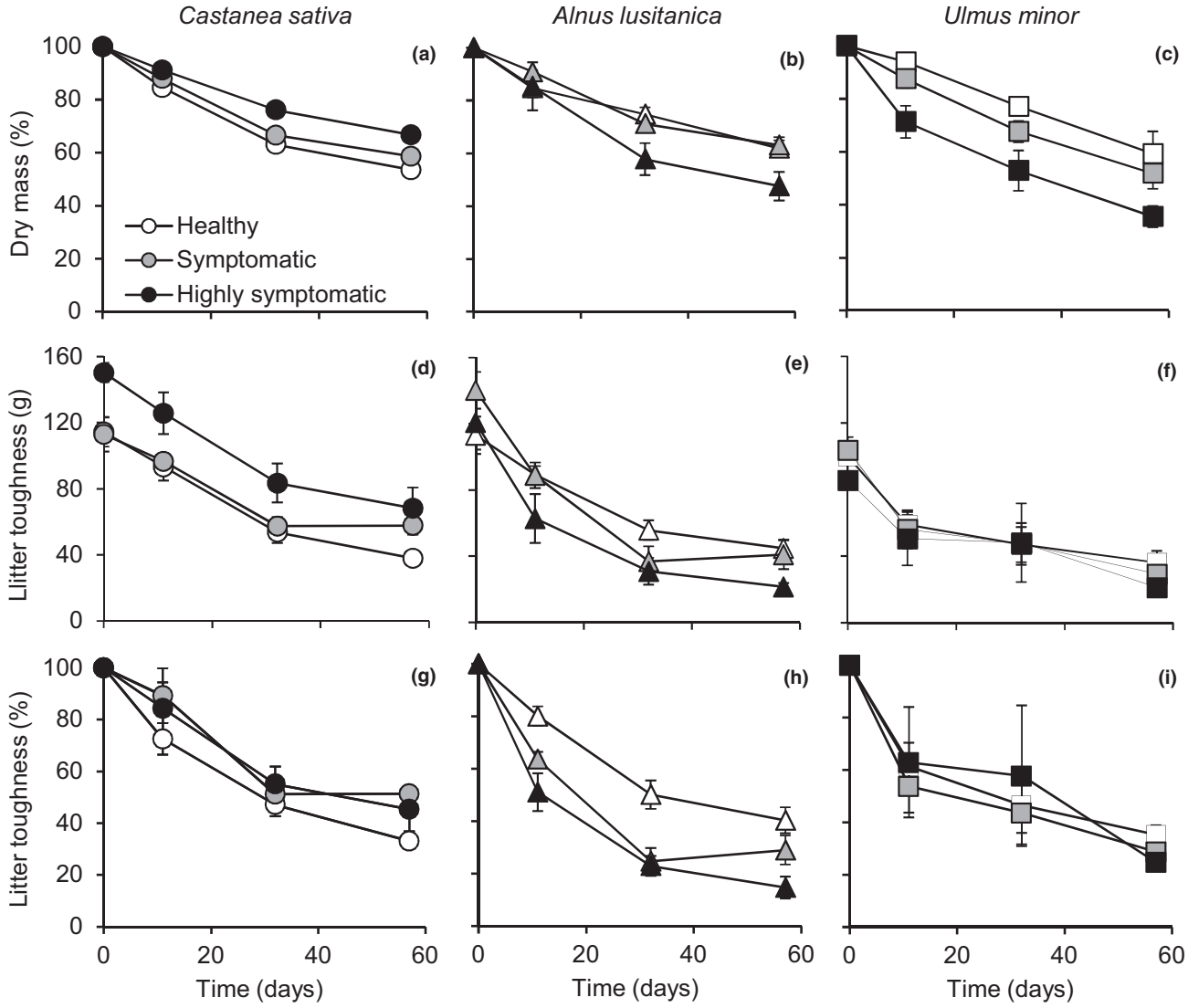

FIGURE 1 Dry-mass remaining (a–c), toughness (d–f), and toughness remaining (g–i) of leaf litter of healthy, symptomatic, and highly symptomatic *Castanea sativa*, *Alnus lusitanica*, and *Ulmus minor* trees incubated in laboratory microcosms for 11, 32, and 57 days. Values are means ± *SE* ($n = 5$)

tree health status and by the interaction between tree health status and time (RM ANOVA, $p \leq 0.043$; Table S2), with higher values in leaf litter of highly symptomatic than of healthy trees on day 11 only (Tukey's test, $p = 0.019$).

3.5 | Fungal biomass

Fungal biomass reached peak values ranging from 48 to 147 and from 40 to 119 mg/g DM in leaf litter of *C. sativa* and *U. minor* trees, respectively (Figure 2d,f); technical problems prevented the detection of peak values in leaf litter of *A. lusitanica* (Figure 2e). Fungal biomass was significantly affected by the health status of *A. lusitanica* trees (RM ANOVA, $p = 0.008$; Table S2), with higher values in leaf litter of highly symptomatic than of healthy and symptomatic trees (Tukey's test, $p \leq 0.029$). A significant interaction occurred between tree health status and time for *C. sativa* and *U. minor* (RM ANOVA, $p < 0.001$ and $p = 0.004$, respectively; Table S2). On day 11, fungal biomass attained a significant peak in leaf litter of symptomatic *C. sativa* trees (Tukey's test, $p < 0.001$) and in leaf litter of highly symptomatic *U. minor* trees ($p = 0.048$), but not in leaf litter of any other health status.

3.6 | Conidial production

Sporulation rates by aquatic hyphomycetes were relatively low over time across tree species and health statuses, with maximum sporulation rates ranging from 3 to 21, 2 to 4, and 1 to 16 conidia mg^{-1} DM day^{-1} in leaf litter of *C. sativa*, *A. lusitanica*, and *U. minor*, respectively (Figure 2g–i). Sporulation rates on *C. sativa* leaf litter were significantly affected by the interaction between tree health status and

TABLE 2 Exponential decomposition rates (k; mean ± SE) of leaf litter of healthy, symptomatic, and highly symptomatic *Castanea sativa*, *Alnus lusitanica*, and *Ulmus minor* trees incubated in laboratory microcosms for up to 57 days (n = 15 microcosms per health status and tree species)

Tree health status	k (day^{-1})	r^2
Castanea sativa		
Healthy	0.0119 ± 0.0005^{b}	0.92
Symptomatic	0.0103 ± 0.0007^{b}	0.85
Highly symptomatic	0.0075 ± 0.0004^{a}	0.90
Alnus lusitanica		
Healthy	0.0088 ± 0.0007^{a}	0.78
Symptomatic	0.0088 ± 0.0006^{a}	0.88
Highly symptomatic	0.0148 ± 0.0016^{b}	0.61
Ulmus minor		
Healthy	0.0095 ± 0.0015^{a}	0.70
Symptomatic	0.0122 ± 0.0012^{a}	0.79
Highly symptomatic	0.0196 ± 0.0017^{b}	0.74

Note: Regression determination coefficients are shown (r^2; $p <$ 0.001 in all cases). Comparisons among health statuses for each tree species were made by ANCOVA. Different letters indicate significant differences between means according to Tukey's tests ($p < 0.050$).

time (RM ANOVA, $p = 0.012$; Table S2), with peaks on leaf litter of healthy and symptomatic but not of highly symptomatic trees on day 11 (Tukey's test, $p \leq 0.049$). Sporulation rates on *A. lusitanica* leaf litter were significantly affected by tree health status and by the interaction between tree health status and time (RM ANOVA, $p = 0.028$ and $p = 0.045$, respectively; Table S2), with higher values in leaf litter of highly symptomatic than of healthy or symptomatic trees on day 11 (Tukey's test, $p \leq 0.043$), and higher values on leaf litter of healthy and symptomatic trees, but not of highly symptomatic trees, on day 57 than on days 11 and 32 (Tukey's test, $p \leq 0.043$). Sporulation rates on *U. minor* leaf litter were also significantly affected by tree health status and by the interaction between tree health status and time (RM ANOVA, $p = 0.014$ and $p = 0.045$, respectively; Table S2), with higher values in leaf litter of highly symptomatic than of healthy trees on day 11 (Tukey's test, $p = 0.010$).

3.7 | Aquatic hyphomycete communities

In total, 15, 9, and 14 aquatic hyphomycete species were identified in leaf litter of *C. sativa*, *A. lusitanica*, and *U. minor*, respectively (Table S3). Throughout the incubation period, species richness ranged from 11 to 12, 5 to 7, and 6 to 12 species in leaf litter of *C. sativa*, *A. lusitanica*, and *U. minor*, respectively (Table S3). Aquatic hyphomycete species richness per sampling date was significantly affected by tree health status in *U. minor* (RM ANOVA, $p = 0.002$; Table S2), being higher in leaf litter of infected than of healthy trees (Tukey's test, $p \leq 0.010$; Table S3). *Tetrachaetum elegans* Ingold and *Anguillospora longissima* (Sacc. & P. Syd.) Ingold were the aquatic hyphomycete species contributing most to conidial production (Table S3; Figure 3). The structure of aquatic hyphomycete community in leaf litter was significantly affected by health status of *C. sativa* ($r = 0.12$, $p = 0.029$) and *U. minor* trees ($r = 0.32$, $p = 0.001$; Table S4). Communities of aquatic hyphomycetes in leaf litter significantly differed between healthy and highly symptomatic *C. sativa* trees ($r = 0.26$, $p = 0.003$), and between all health statuses for *U. minor* trees ($r = 0.19$–0.47, $p \leq 0.017$) (Figure 3). It was especially relevant to observe that the aquatic hyphomycete species richness in leaf litter of infected *U. minor* trees doubled that of healthy trees (10–12 vs. 6, respectively; Table S3). Time was an important factor structuring aquatic hyphomycete communities in leaf litter of all tree species (ANOSIM, $R = 0.43$–0.57, $p = 0.001$; Table S4).

4 | DISCUSSION

Tree infection by invasive pathogens has the potential to affect detrital pathways in terrestrial and aquatic ecosystems, with consequences on food webs and nutrient cycling. We found that tree infection affected leaf litter characteristics, and consequently leaf litter colonisation and decomposition by stream decomposers. However, effects of tree infection were not consistent across pathosystems, preventing generalisations.

4.1 | Characteristics of leaf litter vary across different pathosystems

We expected leaf litter quality to be lower in infected than in healthy trees because of cell death and leaf chlorosis induced by tree pathogens (Camisón, Martín, Sánchez-Bel, et al., 2019; Jung et al., 2018; Milanović et al., 2015). Indeed, infection of *C. sativa* trees by *P. cinnamomi* resulted in a decrease in leaf litter quality, with tougher and more recalcitrant leaf litter in highly symptomatic than in healthy trees. Higher toughness in leaf litter of highly symptomatic trees probably resulted from the tendency towards a lower specific area and a higher lignin concentration in leaf litter of these trees. Trees that grow in water- and nutrient-limiting conditions are known to invest in structural and defensive compounds as a strategy to optimise resource uptake and avoid herbivory (Coley et al., 1985; Solla et al., 2016), and it could be feasible that trees stressed by infection would use the same strategy. Additionally, polyphenols have antimicrobial properties (Daglia, 2012), and the increase of polyphenol concentration in leaf tissues of highly symptomatic chestnuts was probably mediated by tree infection (Camisón, Martín, Sánchez-Bel, et al., 2019). There was also a tendency towards lower P concentration (but not N) in leaf litter of highly symptomatic than of healthy trees, in partial agreement with previous studies. Lower concentration of macro- and micronutrients was found in leaves of *P. cinnamomi*-infected than of healthy *C. sativa* trees (Portela et al., 1998), and lower P concentration was found in *P. cinnamomi*-inoculated than in non-inoculated *Quercus ilex* L. saplings (Maurel et al., 2001).

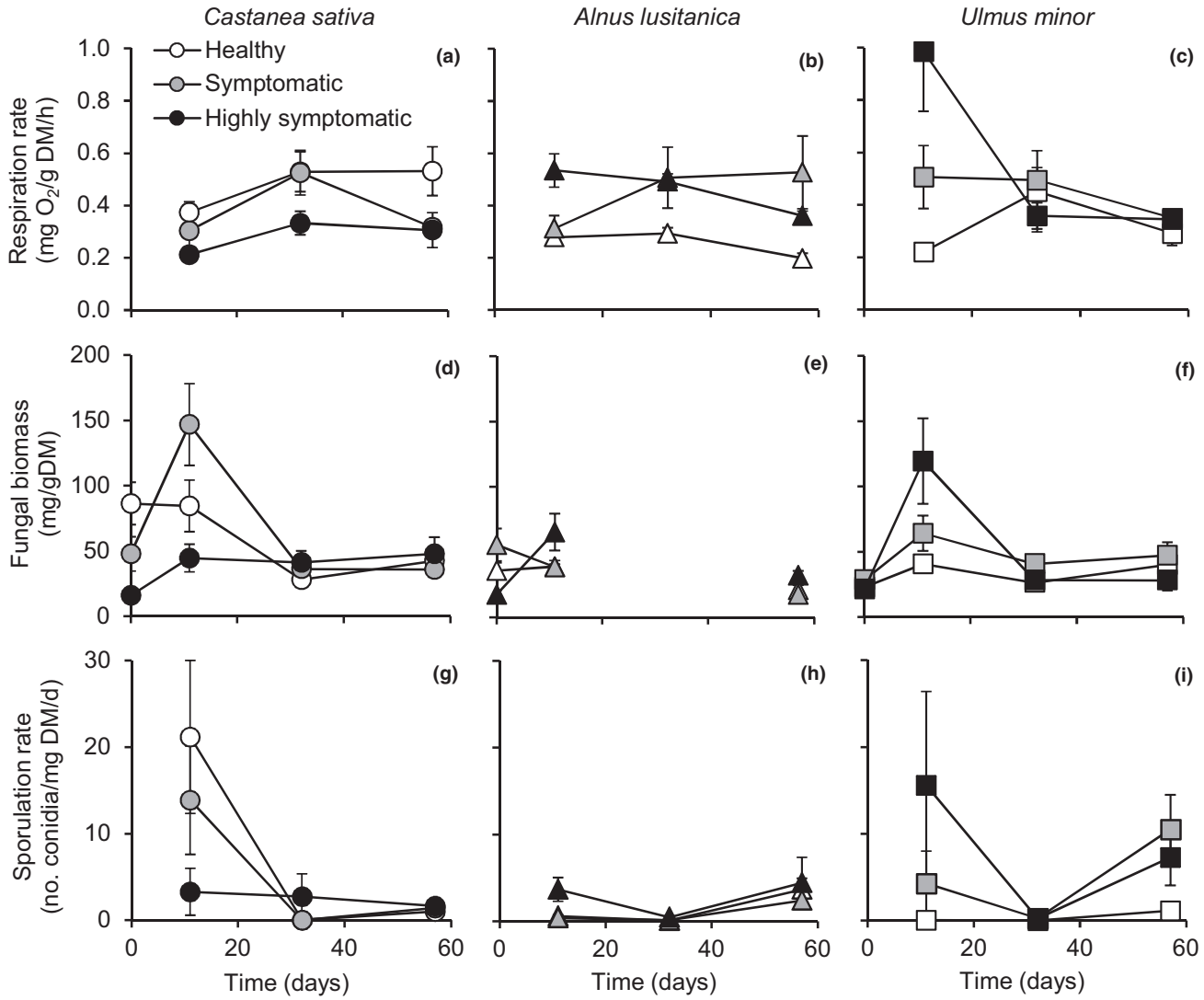

FIGURE 2 Microbial respiration rates (a–c), fungal biomass (d–f), and sporulation rates by aquatic hyphomycetes (g–i) on leaf litter of healthy, symptomatic, and highly symptomatic *Castanea sativa*, *Alnus lusitanica*, and *Ulmus minor* trees incubated in laboratory microcosms for 11, 32, and 57 days. No fungal biomass values are shown for *A. lusitanica* on day 32 due to technical problems during ergosterol extraction. Values are means ± *SE* ($n = 5$)

However, the opposite pattern was found in *A. lusitanica*–*P. ×alni* and *U. minor*–*O. novo-ulmi* pathosystems, with leaf litter of highly symptomatic trees being of higher quality than leaf litter of healthy trees. The high nutrient concentration in leaf litter of infected *A. lusitanica* and *U. minor* trees could be explained by nutrient resorption from chlorotic (damaged) leaves to neighbouring leaves remaining in the tree (Gortari et al., 2021). The high nutrient concentration in leaf litter of infected trees could also be explained by the accumulation of nutrients in the leaves induced by infection (Milanović et al., 2015), or by a lower resorption efficiency of nutrients from senescent leaves, before abscission, due to infection (Cao et al., 2015). Therefore, effects of tree infection by invasive pathogens on leaf litter characteristics cannot be generalised across tree species and need to consider the specific pathosystem.

4.2 | Infection of *C. sativa* by *P. cinnamomi* inhibits microbial activity and leaf litter decomposition

Decomposition of leaf litter of highly symptomatic *C. sativa* trees was slower than that of symptomatic or healthy trees, because of the lower microbial activity in the former litter type. The lower microbial activity in leaf litter of highly symptomatic trees probably resulted from its higher toughness and polyphenols concentration compared with leaf litter of symptomatic and healthy trees. High concentrations of structural and secondary compounds hinder microbial colonisation and activity on leaf litter (Bärlocher et al., 1995; Canhoto & Graça, 1999). In consequence, negative relationships between leaf litter decomposition and leaf litter concentrations of structural and secondary compounds are common (Frainer et al., 2015; Gessner & Chauvet, 1994; Lecerf & Chauvet, 2008; Schindler & Gessner, 2009).

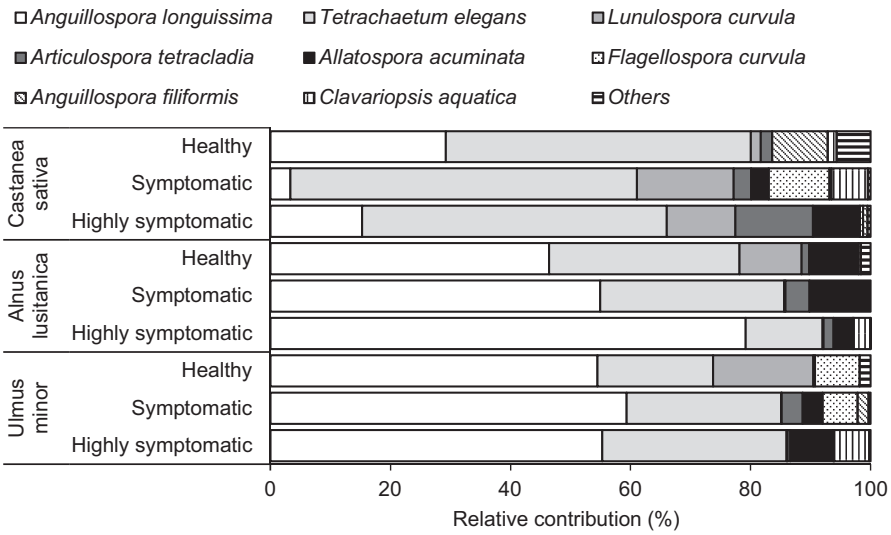

FIGURE 3 Relative contribution (average across sampling dates) of aquatic hyphomycete species to conidial production in leaf litter of healthy, symptomatic, and highly symptomatic *Castanea sativa*, *Alnus lusitanica*, and *Ulmus minor* trees incubated in laboratory microcosms. Others include species contributing less than 1% to total conidial production

There was also a tendency for lower P concentration in leaf litter of highly symptomatic *C. sativa* trees, which may have limited microbial activity and leaf litter decomposition (Lecerf & Chauvet, 2008).

Castanea sativa is an abundant tree species in temperate forests, which contributes large amounts of leaf litter to streams during autumn (Lecerf et al., 2005; Molinero & Pozo, 2006). The observed reduction by 37% in the decomposition rate of leaf litter of highly symptomatic *C. sativa* trees may impair secondary production in aquatic food webs. In this study, we only addressed microbial-driven leaf litter decomposition, but it is expected that the more recalcitrant nature of leaf litter of highly symptomatic trees, and the lower microbial activity they support, will hinder detritivore colonisation and feeding on this litter type (Graça & Cressa, 2010; Graça et al., 2001).

Chestnut ink disease is widespread in Europe (Alcaide et al., 2020; Vannini & Vettraino, 2001) and it will likely expand to new areas and increase its severity in a global warming context (Jung et al., 2018). In fact, the disease has already expanded to northern France (Cécile Robin, INRAE, Univ. Bordeaux, personal communication). Therefore, more streams will be at risk of receiving *C. sativa* leaf litter of impoverished quality in the future.

4.3 | Infection of *A. lusitanica* by *P.* ×alni stimulates microbial activity and leaf litter decomposition

Decomposition of leaf litter of highly symptomatic *A. lusitanica* trees was faster than that of symptomatic or healthy trees, because of higher microbial activity in the former litter type. The higher microbial activity in leaf litter of highly symptomatic trees probably resulted from its higher P concentration compared with leaf litter of symptomatic and healthy trees. Phosphorus concentration in stream water was low, and therefore an increase in P availability in leaf litter by *c.* 3× may have relaxed P limitation and stimulated microbial activity and leaf litter decomposition (Lecerf & Chauvet, 2008). Changes in elemental stoichiometry (i.e., decrease in C:P molar ratio) may have also contributed to reduce the elemental imbalance between leaf litter and microbial consumers (Danger et al., 2016), making leaf litter of highly symptomatic trees more appealing. The lower N concentration in leaf litter of symptomatic than of healthy trees did not result in lower microbial colonisation or slower decomposition of the former leaf litter type, maybe because N concentration was still reasonably high in leaf litter of symptomatic trees (1.76% DM).

Alnus lusitanica is a dominant riparian tree species (Marques et al., 2021), which produces soft, N-rich leaf litter that decomposes quickly (Ferreira et al., 2012; Pereira et al., 2016). The stimulation by 68% of decomposition rates for leaf litter of highly symptomatic trees may lead to an early disappearance of high-quality leaf litter from the stream bed. Decomposition rates of leaf litter of highly symptomatic trees may further increase in the presence of detritivores, as they generally prefer to feed on leaf litter that is well conditioned, i.e., enzymatically macerated, soft, and supporting high microbial biomass (Cornut et al., 2015; Graça & Cressa, 2010).

Infection of *Alnus* spp. trees by the *Phytophthora alni* complex occur frequently along streams in Europe and North America (Bjelke et al., 2016; Jung et al., 2018). For example, in northeastern France, dieback of alder occurs in 78%–90% of the *A. glutinosa* plots examined and there is a 16% incidence (Aguayo et al., 2014; Thoirain et al., 2007). In Bavaria, Germany, tree mortality was reported to be 70% in some locations (Downing et al., 2010). Although the full distribution of dieback of alder is presently unknown, *c.* 27 million km^2 of the world's land surface is suitable for alders and the *P. alni* complex, with maximum disease hazards at low distances from the streams (Downing et al., 2010). The restoration of degraded riparian areas using infected nursery plants may contribute to pathogen spread as nursery stands are frequently infected by *Phytophthora* species (Jung et al., 2016). Global warming may also affect the pathogen's distribution. The optimal temperature range for *P.* ×alni growth is 22.5–25.0°C (Brasier et al., 1999), which explains the increased occurrence of alder dieback with rising mean summer water temperature (Thoirain et al., 2007). In light of the climatic predictions for the Iberian Peninsula where temperatures are expected to rise, with higher frequency and longer duration of heat waves (Carvalho

et al., 2021; Viceto et al., 2019), the area suitable for *P.* ×alni may increase in some regions where winter temperature is presently unfavourable for sporulation (<10°C; Chandelier et al., 2006), while it may decrease in regions where summer temperatures may exceed the optimal temperature for *P.* ×alni to grow (Aguayo et al., 2014; Downing et al., 2010). However, fast flowing mountain streams are less favourable for the establishment of *P.* ×alni (Thoirain et al., 2007).

4.4 | Infection of *U. minor* by *O. novo-ulmi* stimulates microbial activity and leaf litter decomposition

Decomposition of leaf litter of highly symptomatic *U. minor* trees was faster than that of symptomatic or healthy trees, because of the higher microbial activity in the former litter type. This high microbial activity probably occurred because N and P concentrations in leaf litter of highly symptomatic trees doubled those in leaf litter of healthy trees. The C:N ratio also decreased in leaf litter of highly symptomatic trees, contributing to improve the stoichiometric balance between microbial decomposers and leaf litter (Danger et al., 2016).

Ulmus spp. populations have been devastated in Europe and North America, and *Ulmus minor* is no longer a typical riparian tree. Therefore, effects of *U. minor* infection on stream ecosystem are likely to be small. However, many trees survive as sprouts and root suckers suffering recurrent Dutch elm disease symptoms (Brasier & Webber, 2019), and elm breeding programmes have permitted selection of resistant elm varieties currently used for reforestation of riparian areas (Martín, Domínguez, et al., 2021; Martín et al., 2019).

4.5 | Aquatic hyphomycete communities on leaf litter differ depending on the health status of trees

Infection of trees by invasive pathogens also affected the structure of aquatic hyphomycete communities, major microbial decomposers in streams (Gulis & Suberkropp, 2003; Hieber & Gessner, 2002). The most striking effect was the two-fold higher aquatic hyphomycete species richness associated with leaf litter of infected *U. minor* trees compared with healthy trees. This high species richness could be explained by the high N and P concentrations in leaf litter of infected trees. According to the productivity hypothesis (Srivastava & Lawton, 1998), higher nutrient availability, i.e., more resources, allows the coexistence of a higher number of species, so the increased nutrient concentration of leaves infected by certain pathogens might promote conditions that support greater richness of decomposers.

4.6 | Ecological consequences of tree infection on stream ecosystems

For toughness and polyphenolics, intraspecific differences resulting from tree infection were as large as interspecific differences within healthy trees. Leaf litter decomposition also varied more among health statuses of trees than among species within healthy trees. This suggests that changes in leaf litter characteristics induced by tree infection may have relevant consequences on stream functioning to be added to those derived from changes in tree community composition that may result from tree mortality and replacement by plant species tolerant to the pathogen (Smock & MacGregor, 1988).

Leaf litter decomposition was significantly affected in highly symptomatic trees across all pathosystems, because of altered microbial activity. However, altered microbial activity in leaf litter of symptomatic compared with healthy trees did not result in significant differences in leaf litter decomposition. This suggests that there is some buffering capacity of stream ecosystems to early stages of tree infection. Therefore, during periods in which trees could recover from infection or when conditions are non-favourable for disease development, stream functioning may be maintained.

Impacts of pathogens on stream functioning will also depend on the abundance and role of the host tree species on the tree community, and are likely to be higher when the host tree is a dominant species or when it represents a unique functional group in the ecosystem (Cobb & Rizzo, 2016; Ellison et al., 2005). *Castanea sativa* is an often (co)dominant species in northern temperate forests and *A. lusitanica* is a N-fixing species; therefore, infection of these two tree species by pathogens has a great potential to affect stream ecosystems. *Ulmus minor* is not present as a dominant species in riparian forests anymore and the impact of Dutch elm disease on stream ecosystems probably peaked during the 1960s and 1970s, coinciding with pandemic events (Brasier & Webber, 2019; Santini & Faccoli, 2015).

The potential for cross-ecosystem effects of tree infection on stream ecosystems is high (Pazianoto et al., 2019; Smock & MacGregor, 1988), and therefore close collaboration between forest pathologists and stream ecologists is needed. Impacts on litter inputs and litter processing in streams should consider intraspecific changes induced by tree infection, and interspecific changes caused by the replacement of susceptible by tolerant trees (Cobb & Rizzo, 2016). Moreover, litter inputs should be characterised quantitatively and year round. Finally, effects of tree infection need to be addressed under field conditions in order to also consider altered stream shading resulting from crown transparency, and altered nutrient leaching from soils if root rot occurs.

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DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request.

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