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Using a systematic approach to synthesize existing knowledge on *Gymnopus fusipes* (syn. *Collybia fusipes*), the cause of *Collybia* root rot

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Abstract

Gymnopus fusipes (syn. *Collybia fusipes*; syn. *Agaricus fusipes*) is an agaricomycete fungus known to cause root rot on a number of economically important tree species, including oak, where it has been linked to the development of chronic oak decline. Due to lack of correlation between above-ground decline symptoms and *G. fusipes* infection, its presence can often go undiagnosed until mortality. Although *G. fusipes* was first described over 200 years ago, there is still a paucity of information on the biology and ecology of this species, which represents a barrier to understanding its impacts on tree health. The aim of this review was to synthesize existing knowledge on the biology, ecology, host range and host interactions of *G. fusipes*. Using a systematic search, five online databases were used to obtain published literature resulting from the search terms '*Gymnopus fusipes*', '*Collybia fusipes*' and '*Agaricus fusipes*'. After a strict filtering process, the papers were examined for data pertaining to the biochemistry, distribution, ecology, genomic information, host range, infection biology, morphology and phylogeny of the species. The results reveal that there is a large amount of ambiguous and sometimes spurious citation of *G. fusipes* in the literature. However, it can be confirmed that *G. fusipes* is a facultative saproparasite, found in several countries, mainly in Europe, and is associated with several socioeconomically important host species, including oak, chestnut, and fir. *Gymnopus fusipes* has repeatedly been investigated with regard to oak decline in Europe, where it is believed to play a crucial role in the early stage of decline development. Key knowledge gaps highlighted in this review include a lack of information on the basic biology of the species, including its life cycle, which is crucial to fully understanding *G. fusipes* infection and epidemiology. Further work is needed to assess *G. fusipes* distribution, phylogeny and host range through molecular identification. There is also a need to characterize the pathogen–host interaction at a molecular level, with identification of active genes and therefore the mechanisms of infection. A combination of culture-based and molecular techniques should be utilized in order to close these key knowledge gaps.

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KEYWORDS

chronic oak decline, *Collybia fusipes*, distribution, *Gymnopus fusipes*, host range, infection biology

1 | INTRODUCTION

Gymnopus fusipes (Bull.:Fr.) Grey (syn. *Collybia fusipes*) is a mushroom-forming agaricomycete fungus from the family Omphalotaceae (Ványolós et al., 2016). The species *G. fusipes*, first appeared in the literature under the name *Agaricus fusipes*, in Volume III of Pierre Bulliard's 'Herbier de la France' (1783), a descriptive collection of plants and fungi native to France, complete with hand-drawn images, anatomical description and details on properties and uses. *Gymnopus fusipes*, or *Agaricus fusipes*, was described as a mushroom, common in French woodlands, with a morphological description mentioning the stipe which decreases in thickness from the top to a point at the base (Bulliard, 1783; Campbell, 1939). In 1821, the species was reclassified as *Gymnopus fusipes* (Gray, 1821); however, in 1872, the species was again reclassified, placing it in the genus *Collybia* (Quelet, 1872). This nomenclature remained for 125 years, when a more rigorous classification system was developed (Antonin et al., 1997). The new classification included a more in-depth morphological analysis including spore-print typing, the study of stipe shape and measurements of fruiting bodies at full maturity. This work along with the advent of molecular phylogeny, providing greater phylogenetic resolution, supported previous claims that the genus *Collybia* should be divided into three genera, *Collybia*, *Rhodocollybia* and *Gymnopus*, with *Rhodocollybia* and *Gymnopus* being more closely related (Antonin et al., 1997; Mata et al., 2004; Mata & Petersen, 2003).

Current analysis describes species within the genus *Gymnopus* as fungi with fruiting bodies that grow on substrates from basal mycelia, forming a non-insititious or pseudoinstititious stipe, a cap with a pileipellis made up of smooth or irregular hyphae and a white to cream coloured spore print (Antonin et al., 1997). The genus *Gymnopus* contains approximately 300 plant-associated saprotrophic, mushroom-forming species with an almost global distribution (Jang et al., 2016).

Gymnopus fusipes fruiting bodies, have typical agaricomycete morphology (Figure 1), are often brown to reddish-brown in colour, and can appear individually, but more often form in small groups at the base of trees and stumps (Marçais et al., 2000b). The distinctive tapering stipe of the species has led to the common name of the spindle-shank mushroom (Ványolós et al., 2019).

Gymnopus fusipes was first noted to cause root rot in oak (*Quercus* L.) trees in France in the early 1980s (Delatour & Guillaumin, 1984; Guillaumin et al., 1985), prior to which, there was no established link between the presence of *G. fusipes* and an impact on tree health (Marçais et al., 2000b). Since this time, *G. fusipes* has been established as a primary pathogen capable of infecting both young and mature oak trees (Marçais et al., 2000b; Marçais & Delatour, 1996), as well as suggested associations with tree species in other genera including beech (*Fagus* L.), chestnut (*Castanea* Mill.) and hornbeam

(*Carpinus* L.; Marçais & Caël, 2000; Piou et al., 2002). Infection by *G. fusipes* typically causes deterioration of host health, vigour and root condition, which can occur over several decades (Camy, Delatour, Caël, & Marçais, 2003). Symptoms of infection include distinctive orange lesions on main roots below ground level, with small white mycelial fans dispersed within the necrotic tissues, as well as hypertrophy of host cells, in which bark can increase in thickness up to 4 cm (Guillaumin et al., 1985; Marçais et al., 2000b). There is little information regarding the exact mechanisms used by *G. fusipes* when causing infection; however, it is thought that this pathogen may kill large lateral and collar roots, and central sections of the root system where the deep anchoring roots are found, which in turn leads to impaired water uptake and in some cases higher rates of wind failure (Marçais et al., 1999).

Gymnopus fusipes, as well as other fungal or oomycete pathogens, such as those in the genera *Armillaria* and *Phytophthora*, have been associated with oak decline in Europe (Ragazzi et al., 1995; Thomas, 2008; Thomas et al., 2002). In the UK specifically, *G. fusipes* has been linked to two oak decline syndromes, acute oak decline (AOD) and chronic oak decline, otherwise known as COD (Denman & Webber, 2009; Gagen et al., 2019). Whilst AOD is a rapidly progressing decline caused by a combination of bacterial and insect elements and is characterized by vertical cracks and stem bleeding (Brown et al., 2015; Denman et al., 2012, 2014), COD is a slowly progressing decline disease, linked primarily to fungal infection, poor root health and prolonged weakening of host condition (Denman & Webber, 2009; Gagen et al., 2019; Lonsdale, 2015). Both forms of



FIGURE 1 Photograph of *Gymnopus fusipes* fruiting bodies (basidiocarps), after being pulled from beneath the tree host. The stipe clearly decreases in width from the cap to the base, the tapered section is darker in colour due to being buried beneath the groundline. These features can make it difficult to identify without specialist knowledge. Photo credit: David Humphries.

decline are caused by interactions between biotic and abiotic factors and ultimately lead to deterioration of the host and eventually tree mortality (Finch et al., 2021; Marçais et al., 2011).

COD, as with other decline syndromes, can be conceptualized using Manion's decline spiral (Manion, 1981). In this process, numerous biotic and abiotic factors are grouped into different levels representing their contribution to the decline. In the first phase of decline, predisposing factors are biotic factors such as host age, genetic potential and host susceptibility to infection, along with abiotic factors such as soil compaction and air pollution. The next stage of the decline spiral, the inciting factors, include major tipping events such as severe insect defoliation (biotic) and environmental factors such as drought and frost. In the final stage of the spiral, the contributing factors take hold and ultimately lead to death of the host. These are mainly biotic factors, such as canker fungi, viruses, and root rot fungi, including species from the genus *Armillaria*. *Gymnopus fusipes* may therefore also represent a major contributing factor to tree declines, but its specific role and impacts on the decline process currently represents a major knowledge gap.

The overarching aim of this review is to synthesize existing knowledge on the distribution, ecology and infection biology of *Gymnopus fusipes*. This resource will provide key insights into the activities of *G. fusipes*, which will help inform future research priorities and guide management of the species.

2 | MATERIALS AND METHODS

The specific objectives of this review were to firstly conduct a systematic literature search to identify published literature concerning *Gymnopus fusipes*; secondly, to filter the published works through a strict selection process, to collate information on key topics and finally to synthesize a resource on the current state of *Gymnopus fusipes* research and identify key knowledge gaps.

A systematic literature search was conducted to identify peer-reviewed published works on *Gymnopus fusipes* (syn. *Collybia fusipes* or *Agaricus fusipes*). For this analysis, five publication databases were selected (based on relevance to biological/environmental sciences and microbial ecology) to obtain literature, which was then analysed (Figure 2). These databases were BioOne, CAB Direct, ProQuest, Bangor University Library Catalogue and Google Scholar.

The exact phrases '*Gymnopus fusipes*', '*Collybia fusipes*' and '*Agaricus fusipes*' were searched in all five databases, and all search results were compiled into a spreadsheet using Microsoft Excel. The filtering process for the review was as follows: firstly, any publication with occurrence in two or more databases was retained only once as a single copy. Secondly, any works that were published in a language other than English were removed. Many of these publications were not relevant and were collated by the search due to the word '*fusipes*' being mentioned in the reference list and not the main text. Consequently, translation of these sources (across numerous languages) was deemed unfeasible. Thirdly, due to a large amount of grey literature and anecdotal mentions of *G. fusipes*, any publications

that were not considered primary peer-reviewed research were also removed from the collection. Numerous publications were found to mention *G. fusipes* only in the reference list, therefore the next stage of the filtering process was to only preserve publications which made mention of '*Gymnopus fusipes*' '*Collybia fusipes*' and '*Agaricus fusipes*' in the main body of the text. This process was inclusive of the abstract, any figures and tables, but excluded the reference list. These publications were compiled into a separate spreadsheet for analysis (Appendix S1).

The publications obtained from this systematic search were then reviewed for their accuracy and relatedness to the topic and the purpose of this review. Publications which were deemed appropriate to the subject included novel information on *G. fusipes* or clear results associated with the species. These publications were given a coded letter (Table 1) to highlight the key topics covered by the existing literature.

Graphics were produced to depict the breadth of topics covered in the existing literature on *G. fusipes* and information collated to form an up-to-date resource on current literature and knowledge on *G. fusipes*.

3 | RESULTS AND DISCUSSION

3.1 | Systematic literature search and data analysis

The results from each stage of the systematic literature search are detailed in Table 2.

The number of publications found across the five databases regarding *G. fusipes* was 1000, however, after applying the strict selection criteria, few remained, including only 15 publications with '*fusipes*' in the title. Almost a quarter of the original 1000 publications were lost after removing duplicates, and of the 765 publications that remained, approximately 48% were lost after removing works published in a language other than English. Although some information may have been lost in this step, it was deemed as appropriate, as after the final stages of analysis, <25% of the English language publications were considered relevant. Further to this, the majority of the key publications cited in the research were already included in the analysis, indicating that few important publications had been missed.

After removing any works not considered to be primary research, only 25.7% of the original 1000 works remained and after selecting for works where the species name '*fusipes*' appeared in the main body of text (inclusive of figures and tables but excluding the reference list) the number of publications suitable for analysis was 184, 18.4% of the original 1000 publications. These publications were then reviewed and assessed for their accuracy and relatedness to *G. fusipes*. This process included removing any publications not containing novel information or results without a clear link to *G. fusipes* (Figure 3).

Just over half of the 184 publications from the systematic search were deemed relevant for the purpose of this review (Appendix S1),

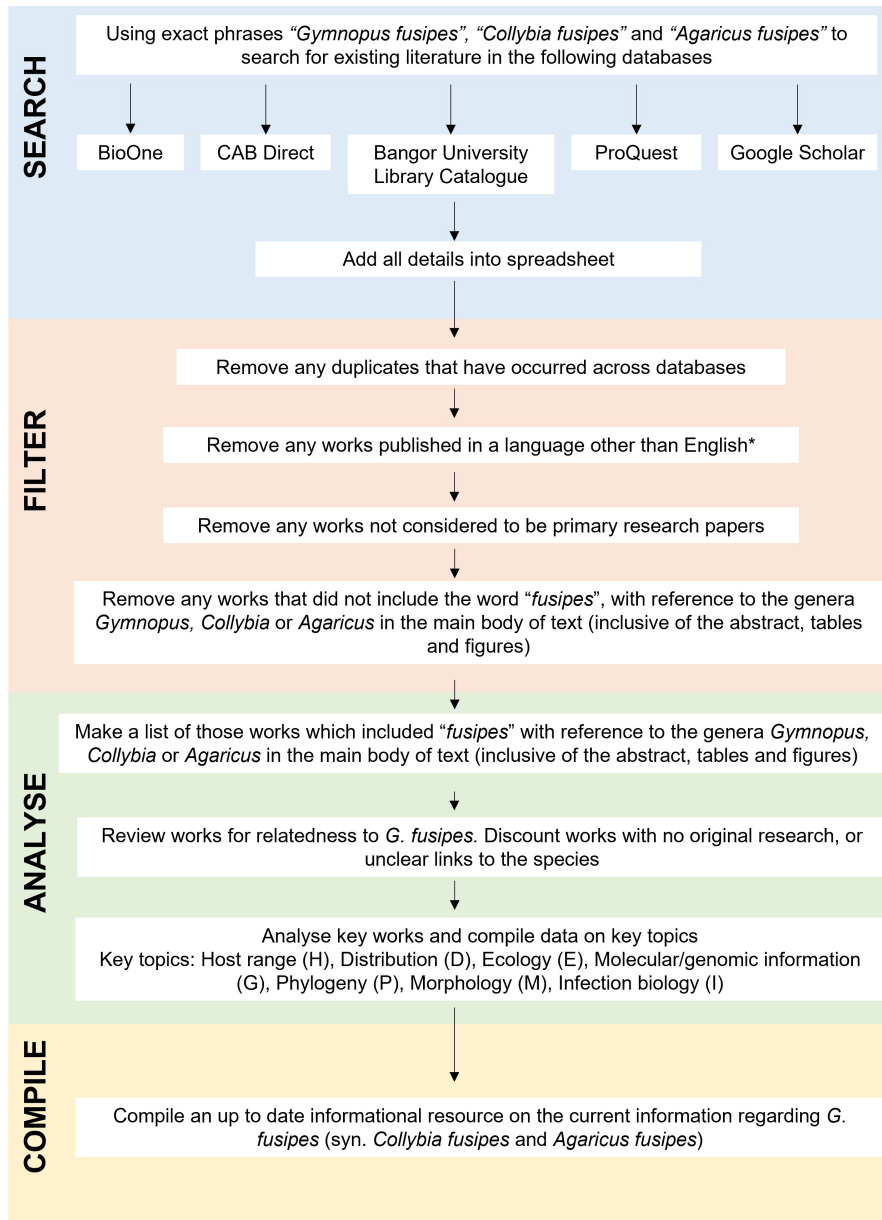


FIGURE 2 Schematic of the methods used in this review, from the literature search to obtain literature through the filtering of non-target works, analysis of content, and finally to compilation of an up-to-date informational resource on *G. fusipes*. *There were a high number of non-English publications in the collection at this stage, and it was considered unfeasible to obtain accurate translations for this number of publications; therefore, this filtering step was added to the methods.

Key topic	Coded letter
Host range of <i>G. fusipes</i>	H
Distribution of <i>G. fusipes</i>	D
Ecology of <i>G. fusipes</i> and ecological strategy	E
Genomic analysis of <i>G. fusipes</i>	G
Phylogeny and taxonomy of <i>G. fusipes</i>	P
Morphology of <i>G. fusipes</i> and any information on the life cycle of the species	L
Infection biology of <i>G. fusipes</i> and its links with Chronic Oak Decline (COD)	I
Biochemistry of <i>Gymnopus fusipes</i>	B

TABLE 1 Coded letters assigned to publications when each of the particular topics was mentioned with reference to *Gymnopus fusipes*.

<25% of the English language publications and just 9.6% of the original 1000 search results.

At the time of writing, search results from Google Scholar returned 227 results for *G. fusipes*. The same database returned

approximately 1690 results for *Dothistroma septosporum*, a causal agent of *Dothistroma* needle blight in pine species (Mccarthy et al., 2022) and 3820 results for *Fusarium circinatum*, the causal agent of pitch canker in pine species (Wingfield et al., 2008). These

TABLE 2 Number of search results from each stage of the systematic literature review.

Search/selection criteria	Total no. of publications
Number of initial search results across all five databases	1000 ' <i>Gymnopus fusipes</i> ' - 252 ' <i>Collybia fusipes</i> ' - 706 ' <i>Agaricus fusipes</i> ' - 42
Number of publications after removing duplicates	765
Number of publications after removing non-English language works	396
Number of publications when filtered for primary, peer-reviewed research papers only	257
Number of publications where ' <i>fusipes</i> ' (with reference to the genera <i>Gymnopus</i> , <i>Collybia</i> or <i>Agaricus</i>) appears in the main body of text (inclusive of figures and tables)	184
Number of publications containing novel information or clear results directly associated to <i>Gymnopus fusipes</i> (or its synonyms)	96

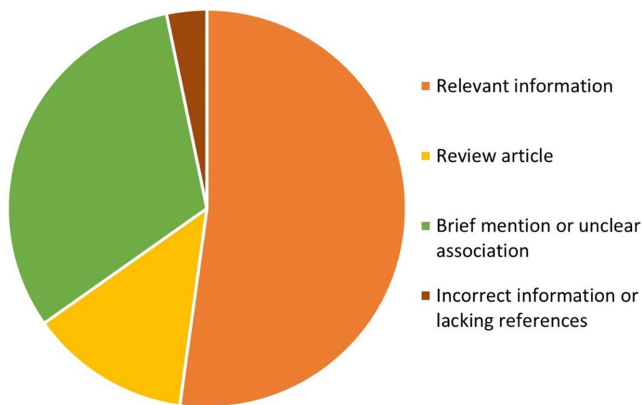


FIGURE 3 Chart depicting the status of available information on *G. fusipes*. Only 96 out of the original 184 publications could be considered relevant and appropriate to provide information for the up-to-date resource.

results indicate a clear lack of research on *G. fusipes*, in comparison with other fungal forest pathogens.

Figure 4 indicates how many times the species name '*fusipes*' was mentioned in the 96 publications. The majority of the publications, even with the inclusion of research with direct and clear links to *G. fusipes*, mentioned the species name '*fusipes*' only once, indicating how *G. fusipes*, although seemingly well-known, is understudied as a focus organism.

The 96 published works were analysed, and the literature examined to identify any information on *G. fusipes* pertaining to its biochemistry (B), distribution (D), ecology (E), molecular information and genomic analysis (G), host range (H), infection biology and its links to chronic oak decline (I), morphology including links to the life-cycle of the species (M) and the phylogeny and taxonomy of *G. fusipes* (P); the information was coded based on the topics referenced (Figure 5).

3.2 | Distribution of *Gymnopus fusipes*

Analysis of the existing literature on *G. fusipes* revealed that distribution is the most extensively reported aspect of the species, with 62

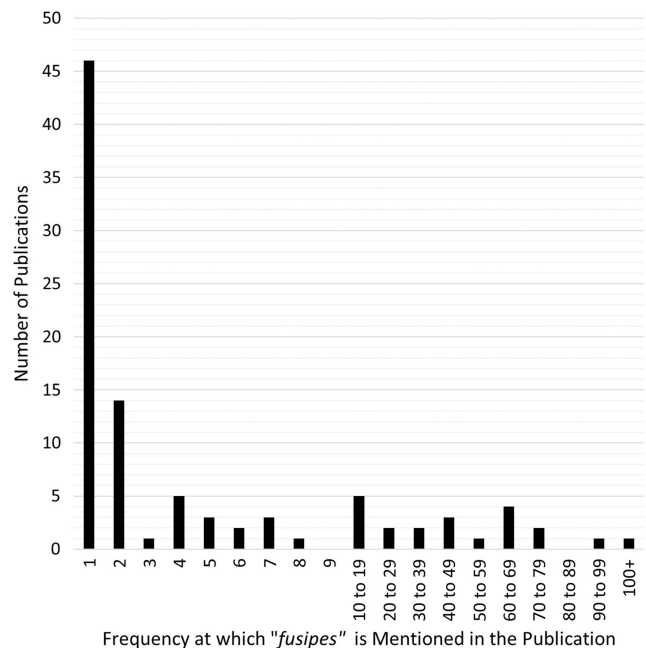


FIGURE 4 Frequency with which the species name '*fusipes*' is mentioned in the 96 analysed publications.

publications indicating a location of presence (Figure 6). Of these 62 publications, 49 used only macroscopic or microscopic analysis to confirm species presence, often in the field. This process requires high levels of skills in fungal identification and is often subject to seasonal sampling and environmental conditions. Ten publications reported isolation of *G. fusipes* from fruiting bodies or infected wood tissues as an identification method, which is reasonably reliable, but only three publications used molecular analysis to confirm species identification. Molecular identification is the gold standard for species identification, as once a new species evolves, gene sequences change and can be identified before changes to morphology or mating behaviours occur (Taylor et al., 2000).

Much of the research concerning *G. fusipes* has been focused in Europe, with molecular-based identification confirming the presence in France (Aguayo et al., 2021), Germany (Schmidt et al., 2012) and Belgium (Chandelier et al., 2021). Studies that isolated *G. fusipes*

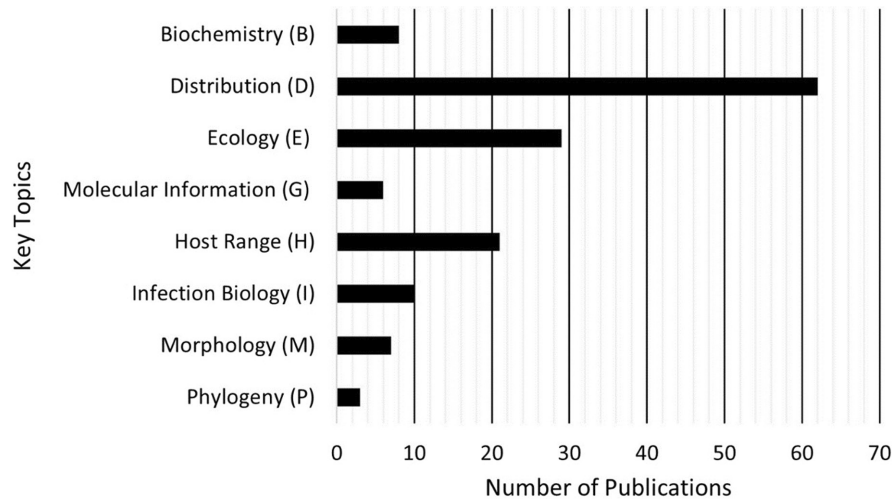


FIGURE 5 Number of publications mentioning each of the identified key topics in the analysed publications. Some publications covered more than one topic and were counted for each topic covered.

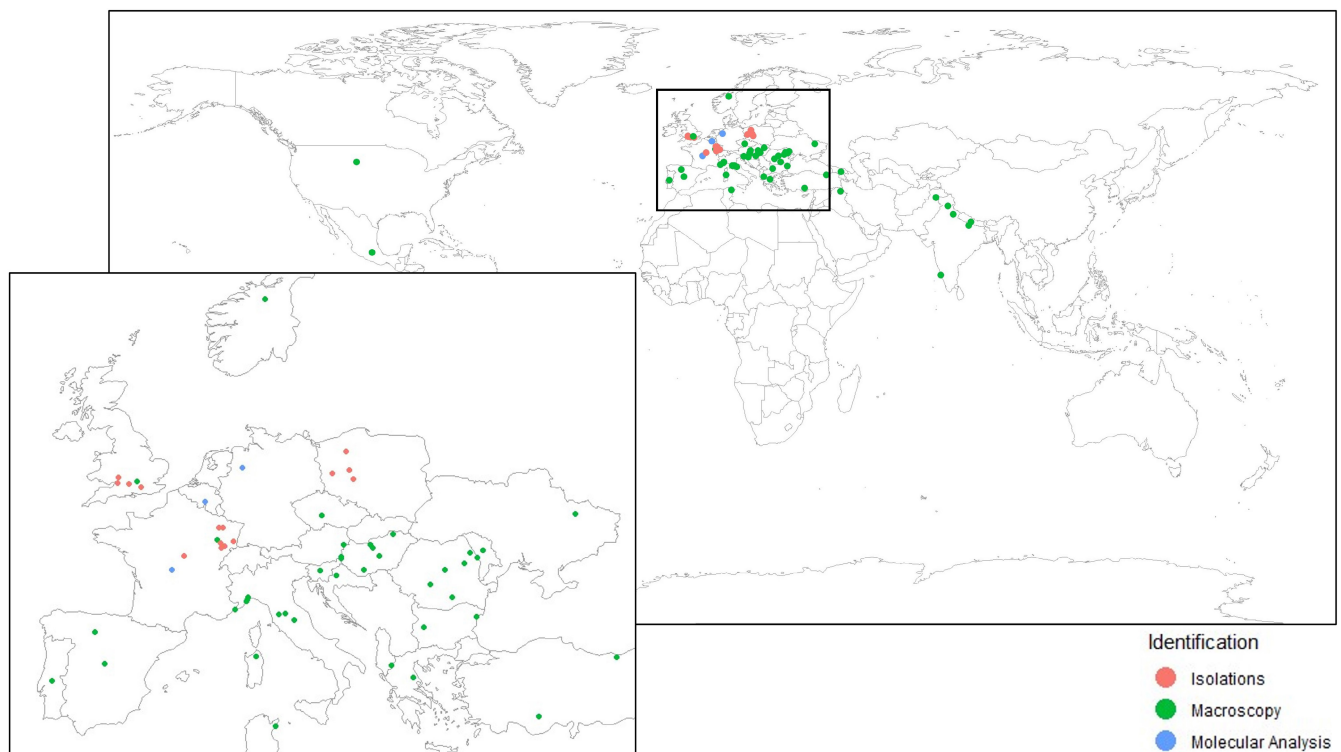


FIGURE 6 Currently known distribution of *Gymnopus fusipes*, created using data from the published literature (Appendix S1). Molecular based identifications depicted in red, isolation-based identifications in green and macroscopic-based identifications in blue.

have been concentrated in France (Marçais et al., 1998, 1999, 2000b; Marçais & Caël, 2001), the UK (Boddy & Thompson, 1983; Campbell, 1939; Denman et al., 2017; Gibbs & Greig, 1990) and Poland (Przybyl, 1994). The presence of *G. fusipes* in these areas can therefore be considered with confidence. If macroscopic analysis is taken into account (with the aforementioned caveats), *G. fusipes* is suggested to have a distribution covering most of Europe (Piou et al., 2002), areas in the USA (Gabel et al., 2004), Mexico (Reverchon et al., 2010), northern Africa (Ben et al., 2013) and parts of Asia (Semwal & Bhatt, 2019).

3.3 | Ecology of *Gymnopus fusipes* in Forest environments

Gymnopus fusipes is widespread where the environment is suitable, and although sometimes documented as a typical member of the oak associated fungal community (Watling, 2014), *G. fusipes* is actually categorized as a forest pathogen (Aguayo et al., 2021; Chandelier et al., 2021). *Gymnopus fusipes* is most often found on tree stumps or at the base of living trees (Sardariu, 2013; Tortic & Lisiewska, 1978); however, macroscopic identifications have suggested that *G. fusipes*

may also occur in soil (Ambrosio et al., 2018) and leaf litter (Diamandis & Perlerou, 2001), although this finding may result from the stipe of the fruiting body being attached to a suitable organic matter substrate below the ground level, such as decaying wood or root tissue (Campbell, 1939).

Species in the genus *Gymnopus* are generally saprotrophic organisms, with some parasitic species, which utilize leaf litter and other forms of vegetation as nutrient sources (Arenal et al., 2006). It has been suggested that *G. fusipes* has two different ecological strategies (Przybyl, 1994). Firstly, as a parasitic biotroph, obtaining nutrients from the tissues of living hosts (Tortici & Lisiewska, 1978), and secondly, as a saprotroph, obtaining nutrients from dead tissues (Reis et al., 2011).

As a saprotroph, *G. fusipes* obtains nutrients from decaying wood (Chandrawati & Narendra Kumar, 2014; Murvanishvili et al., 2010; Vishwakarma et al., 2017). As a biotrophic parasite, *G. fusipes* obtains nutrients from the roots of the living host (Angelini et al., 2012; Thomas et al., 2002). The mechanisms utilized by *G. fusipes* in these scenarios are currently unknown.

Gymnopus fusipes is thought to be lignicolous (Laganà et al., 2002), suggesting it produces extracellular enzymes capable of degrading lignin, cellulose and xylans (Petre & Tanase, 2013). Lignicolous fungi are crucial for wood decay and carbon cycling and can be saprotrophic, when metabolizing dead organic matter, or saproparasitic, when obtaining nutrients from the roots of the living host, therefore, referred to as a 'saproparasite' (Sardariu, 2013; Sardariu & Mititiuc, 2009).

Aspects of *G. fusipes* ecology are linked very closely to its distribution, as geographical factors and climate have a considerable influence on the success of many species. *Gymnopus fusipes* thrives in soils with a low pH, low nutrient availability and a high sand content, a coarse soil texture is also preferred, presumably for the increased drainage provided (Camy, Dreyer, Delatour, & Marçais, 2003). These conditions are crucial to the survival of *G. fusipes* as well as many other species of plants and fungi (Camy, Dreyer, Delatour, & Marçais, 2003), as waterlogging can lead to hypoxia, a condition

whereby gas exchange between the organism and the atmosphere is drastically reduced, leading to build-up of toxic compounds such as metal ions and organic and volatile acids (Bourgeade et al., 2018). It has been demonstrated that there is increased presence of *G. fusipes* in non-waterlogged soils, and the fitness and survival of *G. fusipes* is negatively affected when waterlogging occurs (Camy, Delatour, Caël, & Marçais, 2003; Camy, Dreyer, Delatour, & Marçais, 2003), or groundwater levels are high (Piou et al., 2002).

It was confirmed, through somatic incompatibility tests (Marçais et al., 2000a), that *G. fusipes* spreads via basidiospores, which germinate on the root collar of potential host trees, resulting in a scattered distribution of the pathogen throughout a forest ecosystem (Marçais et al., 1998).

3.4 | Host range of *Gymnopus fusipes*

The host range of *G. fusipes* has a strong influence on distribution and ecology, and the species has been reported in association with 13 genera of host species, including both angiosperms and gymnosperms (information from the literature in Appendix S1). Unfortunately, the majority of these reports do not demonstrate a clear and direct link between *G. fusipes* and a specific host, and it is merely noted to be associated with a forest dominated by a particular host species. From the literature in this analysis (Appendix S1), direct associations between *G. fusipes* and three tree genera were made, *Quercus*, *Castanea* and *Abies*, with *Quercus* spp. making up the majority of associations. Molecular identifications have been made only from *Quercus robur*, and isolations have been made only from other *Quercus* species (Figure 7). Different *Quercus* species appear to vary in susceptibility to *G. fusipes* infection (Marçais & Caël, 2000), with *Q. rubra* (red oak) being more susceptible than *Q. robur* (pedunculate oak) which is more susceptible than *Q. petraea* (sessile oak). This observation further highlights the importance of both fungal isolation studies and molecular identification to improve our understanding of the distribution and host range of *G. fusipes*.

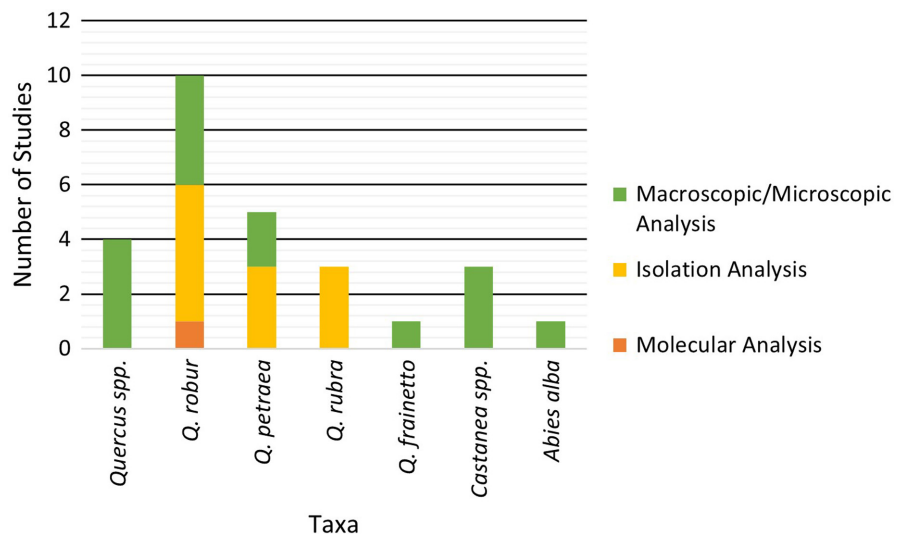


FIGURE 7 Number of studies that have focussed on *Gymnopus fusipes* association with different tree host genera. Colour is indicative of methods used for identification (macroscopy, isolations or molecular analysis).

3.5 | Infection biology of *Gymnopus fusipes* and links to chronic oak decline

Although described in the 1780s, *G. fusipes* was only documented as a pathogen in the 1980s, when it was reported to cause root rot on oak trees (Marçais et al., 2000b). Prior to this, *G. fusipes* was suggested to be a miscellaneous oak decline agent, responsible only for the initial weakening of the tree host and increasing susceptibility to attack by secondary pathogens (such as those in the genus *Armillaria*) or a typical member of the oak associated fungal community (Watling, 2014). However, since being described as a pathogen, *G. fusipes* has been documented as a primary root pathogen, capable of colonizing young and healthy root systems as well as mature hosts (Camy, Delatour, Caël, & Marçais, 2003; Marçais & Delatour, 1996). The species is now known to be involved in chronic oak decline, with a crucial role in disease development through deterioration of the root system and eventual disruption of water conduction (Marçais et al., 2000b).

Oak decline, including chronic oak decline in the UK, involves the combination of abiotic and biotic factors which lead to reduced vigour and eventual mortality of a tree host (Camy, Delatour, & Marçais, 2003; Manion, 1981; Marçais et al., 1999). Decline factors that are particularly important in *G. fusipes* infection include soil type and condition, weather events and moisture levels (Camy, Villebonne, Delatour, & Marçais, 2003), as these factors not only weaken the tree host but also are important in infection success. *Gymnopus fusipes* is negatively affected by waterlogging and high levels of ground water, leading to impaired growth, survival and infectivity success (Camy, Delatour, Caël, & Marçais, 2003; Piou et al., 2002).

Gymnopus fusipes infection develops at the root/soil interface under favourable soil conditions (Camy, Delatour, Caël, & Marçais, 2003) and progresses deeper into tissues of the tree, including the vascular cambium, where less susceptible hosts are able to defend against infection (Marçais & Caël, 2000). *Gymnopus fusipes* infection then progresses to the sapwood, causing large amounts of damage to the functional tissues of the host before spreading through the entire root system (Przybyl, 1994).

A characteristic symptom of oak decline is a deteriorating crown condition, although with *G. fusipes* infection, this symptom does not always correlate with a severe infection (Camy, Villebonne, Delatour, & Marçais, 2003; Marçais & Caël, 2001). In an extensive infection, a large percentage of the host root system can be damaged or killed (Marçais et al., 1999); however, trees can survive long after infection due to the surviving roots continuing to absorb water from deep beneath the ground, on occasion, adventitious roots develop to mitigate the effects of root loss (Marçais et al., 1999, 2000b; Marçais & Caël, 2001). This response could explain why a mature host it can take approximately 30 years from initial infection for *G. fusipes* to cause such a drastic infection (Camy, Delatour, Caël, & Marçais, 2003).

Although fruiting bodies could be considered the most distinctive sign of *G. fusipes* infection, these are not always present (Piou

et al., 2002; Thomas et al., 2002). In some cases, high numbers of trees in a forest ecosystem may present no fruiting bodies over a number of years, but still have lesions on the root system (Marçais et al., 2000b). The most definitive symptom of *G. fusipes* infection is the presence of yellow- or orange-coloured necrotic lesions on the main roots of the host beneath the soil line (Camy, Delatour, Caël, & Marçais, 2003). In more advanced stages of infection, this presents as dark orange wet rot, which extends deep into the sapwood of the tree (Marçais et al., 1999; Przybyl, 1994). Consequently, *G. fusipes* lesions are likely to be undetected due to the lack of obvious above-ground symptoms, potentially resulting in infected hosts remaining undiagnosed for long periods of time, leading to underestimations of the impacts of *G. fusipes*.

It is proposed that *G. fusipes* can work in tandem with numerous other species in the complex aetiology of oak decline, including *Armillaria* species, with which *G. fusipes* shares an ecological niche and *Phytophthora* species (Marçais et al., 2011). For example, mature oak trees co-infected with *G. fusipes* and *Armillaria* species, present severe decline symptoms, including twig shedding and poor crown density (Denman et al., 2017).

3.6 | Morphology and lifecycle of *Gymnopus fusipes*

The genus *Gymnopus*, includes approximately 350 species, each with a small brown fruiting body, tough stipe and white spore print (Coimbra et al., 2015; Dutta et al., 2015). Species in this genus are also often compared with members of closely related genera, especially *Collybia* (Vinet & Zhedanov, 2011), due to the similar morphological characteristics of many genera in the family Marasmiaceae/Omphalotaceae (Putra, 2020).

A distinguishing feature of *G. fusipes* fruiting bodies is the tough tapering stipe, which decreases in diameter from the top (the cap) to the base and led to the common name of 'spindle-shank' (Pegler, 2001; Ványolós et al., 2016). The stipe, which appears rooted into the ground, is sometimes referred to as a pseudorhiza (Petersen & Hughes, 2017), or can be considered a pseudosclerotium, a dense group of hyphae that connect to colonized roots beneath the ground level (Campbell, 1939). The stipe of *G. fusipes* is tough in texture and able to withstand adverse weather conditions such as wind (Halbwachs et al., 2016). This tough texture and rigidity is potentially due to the presence of sarcodimitic tissues in the stipe (tissues which contain two types of interacting hyphae in a single tissue), especially at the cap end of the pseudorhiza, which results in the increased width at the top (Redhead, 1987). The pseudorhiza of *G. fusipes* is thought to be perennial which can result in fruiting bodies appearing in the same locality repeatedly (Norvell, 1998).

Gymnopus fusipes is thought to utilize two ecological strategies, parasitic and saprophytic, which may influence the morphology of the fruiting bodies. As a saprophyte on decaying tree stumps and roots, the basidiocarp is usually darker in colour, and smaller than when in the parasitic mode, fruiting as individual basidiocarps. When the species is acting as a parasite on the base of living

hosts, the basidiocarps are lighter in colour, larger in size and produced in groups. The parasitic phase fruits around the beginning of September, approximately 2 weeks later in the season than when in the saprotrophic life strategy which tends to fruit towards the end of August (Przybyl, 1994).

Gymnopus fusipes does not produce traditional cords (Boddy & Thompson, 1983); however, it can sometimes be found to produce cord-like structures on the bark surface, which have been suggested to aid in the spread of *G. fusipes* at the bark level (Marçais et al., 1999). *Gymnopus fusipes* spreads through the forest ecosystem via basidiospores, which has been proven by somatic incompatibility testing (Marçais et al., 2000a).

The lifecycle of *G. fusipes* has not been extensively investigated; therefore, it can only be assumed that the species follows a similar life cycle to other agaricomycetes (Figure 8). In this type of lifecycle, basidiospores are dispersed and germinate to form monokaryotic hyphae. Monokaryotic hyphae, with a single haploid nucleus in each cell compartment, separated by a septum (in the case of *G. fusipes*, as with most basidiomycetes, a septum with a dolipore system and perforated septal pore cap to prevent the movement of nuclei between the compartments) meet, and if compatible, fuse through anastomosis, the process by which single hyphae fuse to form a branching network, crucial for many fungal processes such as the exchange and migration of nuclei, nutrient flow and mycelial homeostasis, which

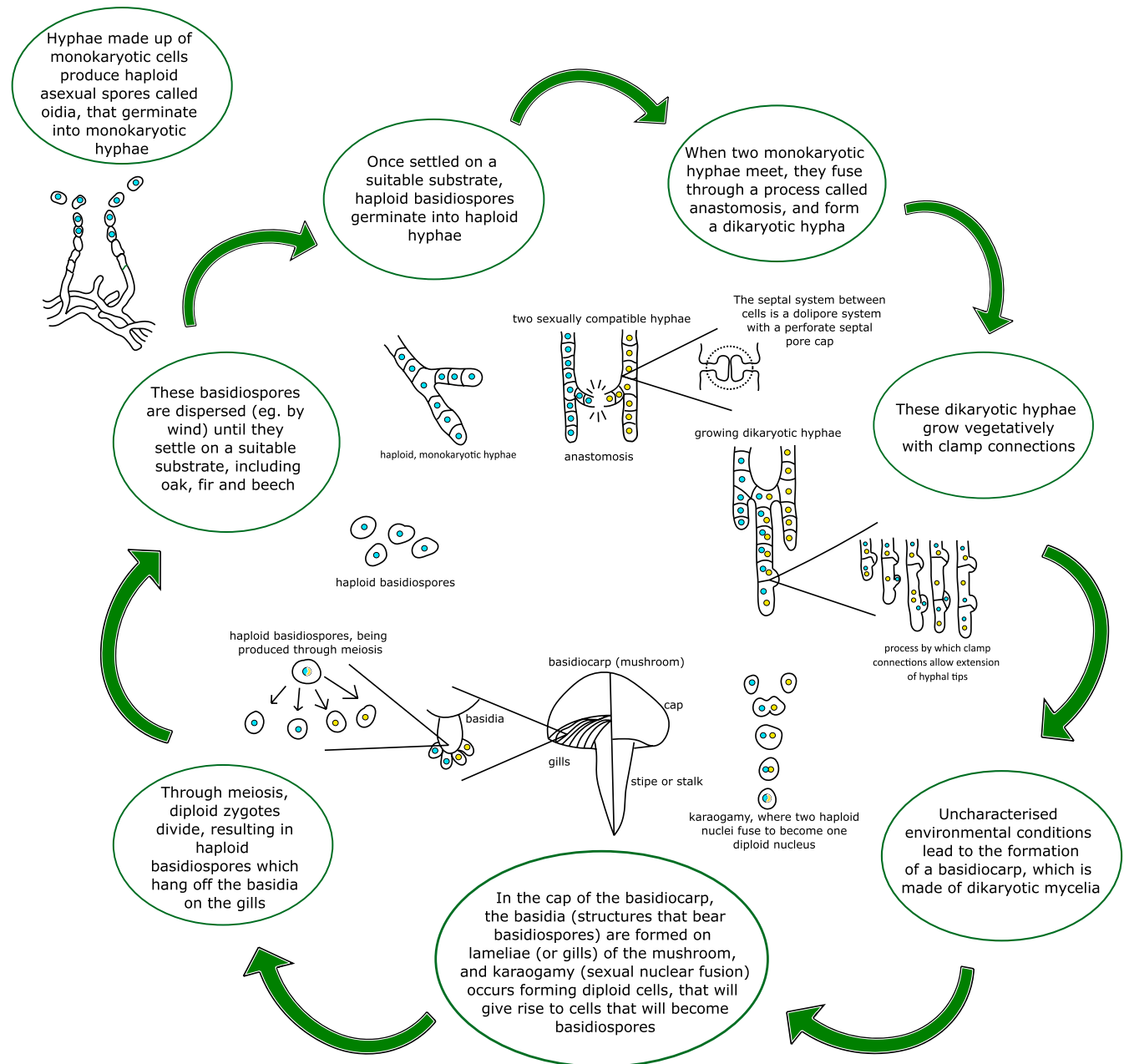


FIGURE 8 Diagrammatic representation of the typical agaricomycete lifecycle. This hypothetical framework was compiled to demonstrate the probable lifecycle of *Gymnopus fusipes*.

is imperative for survival (de Novais et al., 2017). This process leads to the development of dikaryotic hyphae, with two haploid nuclei in each cell compartment and the formation of clamp connections between cells, which is extremely stable during vegetative growth (Gao et al., 2019). Environmental conditions stimulate the production of a dikaryotic fruiting body (mushroom), on which form specialized structures called basidia: the process of karyogamy (fusion of two haploid cells to form one diploid cell) and subsequent meiosis (cell division to produce four haploid basidiospores) occurs. The resulting basidiospores are dispersed and the cycle continues (Casselton & Olesnicky, 1998).

3.7 | Somatic incompatibility and genomic analysis of *Gymnopus fusipes*

There is a noticeable lack of genomic analyses of *G. fusipes*, with only 6 publications presenting molecular data. This problem is reflected in databases such as NCBI GenBank and Unite which, at the time of writing, contained only 15 and 1 nucleotide sequences for *G. fusipes* respectively.

The majority of genetics-based work on the species has focused on somatic incompatibility, the prevention of fusion between two genetically incompatible hyphae (Worrall, 1997). Somatic incompatibility in *G. fusipes* is suggested to be controlled by at least three multiallelic gene loci responsible for the response exhibited in vegetative incompatibility reactions (Marçais et al., 1998), and that a strong incompatibility response is controlled by just one locus out of a possible three or more loci involved in compatibility (Marçais et al., 2000a). Somatic incompatibility experiments illustrated that isolates from neighbouring tree root systems are mostly incompatible, indicating that they are genetically distinct, providing evidence to show that *G. fusipes* does not spread via root-to-root contact and supporting the hypothesis that *G. fusipes* spreads via basidiospores (Marçais et al., 2000a).

The lack of genomic analysis specifically relating to *G. fusipes* has resulted in an incomplete and changing phylogeny depending on the gene being analysed. Research using the nuclear ribosomal internal transcribed spacer (nrITS) and large subunit regions proved that the genus *Collybia* falls into a completely different clade to *Gymnopus* and *Rhodocollybia*, despite these genera previously all being classified as *Collybia* (Antonin et al., 1997; Mata et al., 2004). Single gene phylogenetic analysis can provide different results depending on the gene targeted; for example, *G. fusipes* grouped with different species in analyses using the large ribosomal subunit (LSU) compared with the internal transcribed spacer (ITS) region (Saar et al., 2009).

Traditionally the classification of fungal species (phylogeny, taxonomy and systematics) was determined by morphological analysis of macroscopic and microscopic characteristics as well as chemical characteristics (Pfyffer et al., 1986). However, it is suggested that there are too many variables in morphological analysis for this process to be totally accurate. For example, *G. fusipes* was documented to have morphological differences (size, colour, fruiting schedule and

number of fruiting bodies) depending on whether it is acting as a saprotroph or a parasite (Przybyl, 1994).

A more complete and state-of-the-art approach to classification is therefore needed, which includes both morphological data and molecular information to provide more accurate identification of fungal species. A comprehensive database storing all of the relevant details on fungal species, such as 'Faces of Fungi' would be an ideal scenario (Jayasiri et al., 2015) but would need to be widely used and regulated to be effective and accurate.

3.8 | Biochemical properties of *Gymnopus fusipes* and potential for commercial application

Although there is a lack of information on the biochemistry of *G. fusipes*, there have been some investigations of the biochemical properties of this species. For example, it is known that *G. fusipes* possesses genes encoding laccase production, which is a class of enzymes important in lignin degradation in white-rot fungi (Luis et al., 2004, 2005).

Wood decay fungi can be grouped by the different types of decay caused. Brown-rot and soft-rot fungi, degrade mainly cellulose, whereas white-rot fungi degrade both cellulose and lignin, leading to a more complete degradation of host tissues (Pandey & Pitman, 2003). White-rot fungi produce a number of classes of extracellular enzymes such as lignin peroxidases, manganese peroxidases and laccases (Hatakka, 1994).

Fungi produce secondary metabolites, compounds with bioactive properties which help the fungus adapt to the environment (Hautbergue et al., 2018). *Gymnopus fusipes* produces exudates when grown in culture on different types of media (Petre & Tanase, 2013). These exudates contain compounds with antimicrobial properties and are often produced in the environment when in competition with other microbes. *Gymnopus fusipes* produced antimicrobial compounds (Wilkins, 1952) active against the bacterial species *Pseudomonas aeruginosa*, a widely antimicrobial-resistant pathogen known to cause infection in plants and animals (including humans) with a high mortality rate (Poole, 2011), *Serratia marcescens*, a pathogen affecting immunocompromised humans in various capacities (Cristina et al., 2019), and *Bacillus subtilis*, a ubiquitous bacteria used as a model organism for studying numerous prokaryotic processes (Su et al., 2020; Suay et al., 2000).

In recent years, the biochemical properties of *G. fusipes* have been studied closely in relation to human health. Compounds extracted from *G. fusipes* have the potential to block G-protein-coupled inwardly rectifying potassium (GIRK) channels (Ványolós et al., 2019), the abnormal functioning of which has been linked to cardiac arrhythmia as well as other disorders such as neuropathic pain and drug addiction (Walsh, 2011). *Gymnopus fusipes* has also been studied in connection with the recently isolated and biosynthesised Gymnopeptides A and B, natural products originally extracted from the species and found to have potential anti-cancer activities (Ványolós et al., 2016). With further analysis, these gymnopeptides

were found to be members of the borosin RIPP family of peptides, with the potential to be up to 1000 times more potent in antiproliferative cancer activities than cisplatin, which is currently used as the positive control in anti-cancer studies (Quijano et al., 2019). These gymnopeptides were effective in antiproliferative activities against a number of human cancer cell lines including cervical, skin and breast (Ványolós et al., 2016).

4 | CONCLUSIONS AND RESEARCH PRIORITIES

In this literature review, existing knowledge on the distribution, ecology and infection biology of the root rot pathogen *Gymnopus fusipes* has been synthesized. A systematic literature search across five databases revealed that there are relatively few primary publications pertaining to *G. fusipes* compared to other tree-associated pathogens, such as *Dothistroma septosporum* and *Fusarium circinatum*, highlighting the need for more focussed work on the species.

Gymnopus fusipes is confirmed to be common throughout Europe; however, there are records linking it to much of the northern hemisphere including countries in Europe, North America, northern Africa and parts of Asia. The pathogen has been confirmed to associate with three genera of host tree, although it has been linked to tree species across 13 genera including both broadleaf and coniferous species. The most common association documented in the literature is with the oak species, *Quercus robur*. Many factors relating to the distribution and host range of *G. fusipes* affects its survival and infection success, such as temperature, soil type and weather. *Gymnopus fusipes* has the typical morphology of an agaricomycete with a stipe tapering in width towards the base, however this tapering is often below the ground level. The basidiocarps can appear individually (saprophytic life-style) or as small clusters (parasitic) and vary in size and colour, although the caps are always brown.

Gymnopus fusipes is a saproparasite, with the ability to function as either a saprophyte or parasite, although the factors determining the ecological strategy are currently unknown. As a slow growing primary pathogen, *G. fusipes* has a key role in the early stages of oak decline, following the decline spiral. Infection by *G. fusipes* often goes unnoticed due to the lack of correlation between the above-ground symptoms and the infection status of the host. Symptoms of infection by *G. fusipes* can include a deterioration of the crown and the presence of fruiting bodies (although neither are always present), but always includes orange necrotic lesions on the root tissues and small white mycelial fans beneath the bark. In a severe infection, whole root systems can be destroyed, leaving the tree host vulnerable to wind failure.

Gymnopus fusipes spreads from host to host via basidiospores, which has been confirmed through somatic incompatibility tests that illustrated that neighbouring trees are infected by genetically distinct isolates. Other genomic information regarding *G. fusipes* is lacking, and there is a severe deficit of molecular data present

in databases such as NCBI GenBank and Unite Fungal database. Although there have been some reports on gene expression in the existing literature, it is basic and requires further attention. The biochemical properties of *G. fusipes* are of interest, as certain fungal products have antiproliferative activities against a number of human cancer cell lines.

Future work should aim to use molecular techniques to confirm the distribution of *G. fusipes* and also to clarify host range. It is crucial that more focussed research is performed to increase understanding of the factors influencing the *G. fusipes* life strategy of saprophyte or parasite, and whether the former can change into the latter. This investigation could help to explain why there is protracted delay between infection and mortality of the tree host. The mechanisms by which *G. fusipes* degrades tree root tissues, and the genes expressed at each stage of infection also need to be examined in order to provide a timeline of infection and the processes occurring at each stage which would be highly beneficial to informing management. There would also be a benefit to increasing the number of nucleotide sequences available in databases such as NCBI GenBank and in preparing an up-to-date phylogeny based on multiple genes. This work would help to create a rapid diagnostic tool that could be deployed both in the field and the laboratory to quickly and accurately identify *G. fusipes* infection.

In conclusion, *G. fusipes* is an understudied root rot pathogen, capable of destroying almost the whole root systems of host trees, leading to a high risk of wind failure. *Gymnopus fusipes* not only impacts tree health but also with a reasonably large number of potentially susceptible host trees being present on lands open to the public (country parks and gardens), *G. fusipes* also has the potential to threaten human safety. More research is required to fill the knowledge gaps in the literature, in order to help inform management.

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DATA AVAILABILITY STATEMENT

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

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