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Review

Potential Interactions Between Invasive *Fusarium circinatum* and Other Pine Pathogens in Europe

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Received: 14 November 2019; Accepted: 10 December 2019; Published: 18 December 2019

Abstract: Pines are major components of native forests and plantations in Europe, where they have both economic significance and an important ecological role. Diseases of pines are mainly caused by fungal and oomycete pathogens, and can significantly reduce the survival, vigor, and yield of both individual trees and entire stands or plantations. Pine pitch canker (PPC), caused by *Fusarium circinatum* (Nirenberg and O'Donnell), is among the most devastating pine diseases in the world, and is an example of an emergent invasive disease in Europe. The effects of microbial interactions on plant health, as well as the possible roles plant microbiomes may have in disease expression, have been the focus of several recent studies. Here, we describe the possible effects of co-infection with pathogenic fungi and oomycetes with *F. circinatum* on the health of pine seedlings and mature plants, in an attempt to expand our understanding of the role that biotic interactions may play in the future of PPC disease in European nurseries and forests. The available information on pine pathogens that are able to co-occur with *F. circinatum* in Europe is here reviewed and interpreted to

theoretically predict the effects of such co-occurrences on pine survival, growth, and yield. Beside the awareness that *F. circinatum* may co-occurr on pines with other pathogens, an additional outcome from this review is an updating of the literature, including the so-called grey literature, to document the geographical distribution of the relevant pathogens and to facilitate differential diagnoses, particularly in nurseries, where some of them may cause symptoms similar to those induced by *F. circinatum*. An early and accurate diagnosis of *F. circinatum*, a pathogen that has been recently introduced and that is currently regulated in Europe, is essential to prevent its introduction and spread in plantings and forests.

Keywords: Pine pitch canker (PPC); forests; nurseries; microbiota; fungal interactions; pathogens

1. Introduction

Pines are native to Europe and are keystone components of several European terrestrial ecosytems, independent of climate and location within the continent. There are 12 native pine species and a large number of subspecies within Europe [1], with Scots pine (*Pinus sylvestris* L.) being the most widespread, covering an estimated area of 28 million hectares (mln ha) [2]. Other pine species have a relevant ecological role in Europe, particularly black pine (*P. nigra* Arnold), stone pine (*P. pinea* L.), and maritime pine (*P. pinaster* Aiton).

The economic significance of pines is due to their valuable wood, used for timber and pulp, to their resin, used for the manufacture of varnishes, adhesives, and food glazing agents, and to their nuts, used for consumption and mainly produced by stone pines in Southern Europe. Monterey pine (*P. radiata* D. Don), although native to the Central coast of California and Mexico, is, for commercial purposes, the most widely-planted pine in Europe and in the world, with large plantations cumulatively covering over 4 mln ha in New Zealand, Chile, Australia, Spain, and South Africa [3]. In Europe, Spain has the largest area planted with this species (ca. 287,000 ha) [3], and although plantations are relatively small in area when compared to the area covered by native pines, they provide 25% of Spanish conifer timber [4] due to the fast growth and short rotation time of Monterey pine.

Diseases of pines can significantly reduce the survival, vigor, and yield of individual trees, as well as of entire natural forests or plantations [5–7]. Most diseases of conifers are caused by fungal pathogens [8], some of which have major economic and ecological impacts [9]. For example, Dothistroma needle blight, caused by *Dothistroma septosporum* (Dorog.) Morelet and *Dothistroma pini* Hulbary, can cause extensive mortality in pine plantations [7–10], and recently led to the premature felling of 11,000 ha in the UK (Kath Tubby and Alan Gale, unpubl.) and 32,000 ha in the Basque region of Spain (Óscar Azkarate, unpubl.). Another example of the economic importance of fungal diseases of pines is provided by the root and butt rot fungus, *Heterobasidion annosum sensu lato*, known to cause losses in the European Union estimated at around 790 mln Euros in 1998 [11].

The risk of disease outbreaks caused by alien invasive forest pathogens is rapidly increasing with the intensification of international trade [9–12]. Pine pitch canker (PPC), caused by *Fusarium circinatum* (Nirenberg and O'Donnell), is among the most devastating known diseases for pine plantations, and is an example of an emergent disease in Europe. Outbreaks of the pathogen in Europe have occurred in plantations of *P. radiata* in Northern Spain [13,14]. The first official validated record of the disease in Europe was on *P. radiata* and *P. pinaster* in nurseries in Asturias (Northern Spain) and *P. radiata* in a plantation in Cantabria (Northern Spain) [15,16], although there were earlier unofficial reports in pine nurseries in northern Spain [17–21]. In Portugal, the first official record was in nurseries on *P. pinaster* and *P. radiata* seedlings [22]; later in 2016, the pathogen was detected in *P. radiata* plantations (H. Bragança, personal communication) and on two *P. pinaster* trees in 2018 [23]. In Italy and France, the pathogen has been officially eradicated; in Italy, there was a first report in urban parks on *P. halepensis* Mill. and *P. pinea* [24], and in France, the pathogen was officially reported from *Pseudotsuga menziesii* (Mirb.) Franco and *Pinus* spp. in a private garden [25,26], followed by a

report from *P. radiata* in nurseries [27]. *Pinus radiata* is regarded as the most susceptible species, while *P. canariensis* and *P. pinea* are often regarded as some of the most resistant pine species in Europe [28–31]. Differences in susceptibility among provenances of the same *Pinus* species have been reported for *P. sylvestris* [32,33] and *P. pinaster* [34,35]. The exploitation of genetic resistance is one of the most promising methods with which to manage PPC [29,36]. Among the species grown in plantations in the south east of U.S., inoculations of one year-old seedlings revealed *P. taeda* to be the most resistant, with shortleaf pine (*P. echinata* Mill.) and Virginia pine (*P. virginiana* Mill.) being the most susceptible, and *P. elliottii* ranking as intermediate. Even for susceptible species such as *P. elliottii* and *P. radiata*, intraspecific variation in susceptibility has been demonstrated [37].

Fusarium circinatum has a strong potential to become established in different parts of Europe [38]. According to the European Food Safety Authority (EFSA), the consequences of PPC in areas suitable to its spread will be potentially massive [39]. Such areas include central and northern Portugal, northern and eastern Spain, south and coastal parts of France, coastal areas of Italy, several coastal areas of Greece, and some other regions [40] (Figure 1). Although optimal conditions of temperature and humidity for fungal infection and conidial germination are known, the prediction of environmental suitability for PPC infection is complicated by the fact that the environment may affect not only *F. circinatum* itself, but also its hosts and vectors. Nevertheless, Garbelotto et al. [41] have identified the natural climatic conditions which are associated with high and low or nil sporulation levels in the field. High sporulation is associated with high levels of relative humidity in the form of either precipitation or fog and cool temperatures (15–25 °C); sporulation is depressed as temperatures increase, and nil when minimum temperatures approach zero. These patterns suggest that the disease may spread more easily in coastal, mild, wet climates, rather than in mountainous or continental climates characterized by extreme seasonal fluctuations in temperature. The spatial spread of the inoculum was noted to be successful to a distance more than 200 m [41] and up to a distance of 1000 m downwind [42], but not much more, which indicates a limited dispersal ability. Numerous insect species that commonly occur in pine nurseries and forests throughout Europe and elsewhere have the potential to spread PPC as either vectors, carriers, or wounding agents; however, to date, most of the evidence is circumstantial and ambiguous [43].

Möykkynen et al.[44] modelled the potential spread of *F. circinatum* in Europe as a function of the spatial distribution of pine and Douglas firs, the climatic suitability of different locations to *F. circinatum*, seedling transportation, insect-mediated transfer from tree to tree, and the spread of airborne spores. Some of these factors can be controlled by human decision making. Furthermore, the area with a suitable climate for the development of PPC in Europe was predicted to shift from the coastal areas of southern Europe northwards by the year 2100. This would be caused by decreasing summer precipitation and increasing summer and winter temperatures in southern Europe (south of latitude 50). In northern Europe (north of latitude 50), increasing summer and winter precipitation and rising summer and winter temperatures [45] make the climatic conditions more favorable for *F. circinatum*. However, the simulations indicated that PPC is not likely to spread to central and northern Europe unless new points of entry are created during those climatic periods when the region is suitable for the development of the disease.

The pathogen is an ascomycete with a complex biology; it can be airborne as well as seedborne, and may have an endophytic stage in its lifecycle (see below). When seedborne, it can survive both superficially and internally in the seeds [46,47], and it may cause pre- and post- emergence damping-off, as well as the mortality of established seedlings [46–48]. The main symptom of PPC in mature trees is the presence of pitch-soaked cankers in trunks and large branches that can girdle both trees and branches, although it can lead to tree death [29,49,50]. Occasionally, the canker may be in the primary roots, later expanding into the root collar and the lower part of the stem in planted pines [51]. It was also found to behave as an endophyte of corn [52], different grasses [53], asymptomatic *P. radiata* seedlings [47, and asymptomatic seedlings of the genera *Picea* and *Larix* [54].

In a risk assessment *of F. ciricnatum* for the EU territory [39], the following pathways for the entry from infested areas were identified: (i) plant material for propagation purposes (seeds, seedlings, and scions), (ii) wood, (iii) plant material for decorative purposes (Christmas trees, branches, cones, etc.),

(iv) soil and growing substrates, v) natural means (insects, wind, etc.), and (vi) human activities (travellers, machinery, silvicultural practices, vehicles, etc.). The risk management options were then identified and evaluated for their effectiveness, for entry, spread and for preventing or reducing infestation by *F. ciricnatum*.

A classical concept of plant pathology is the disease triangle, used to visualize the tripartite interaction among a virulent pathogen, a susceptible host, and an environment which is favorable to infection. The co-occurrence of these three factors results in a plant disease with a measurable effect on plant productivity. However, there is mounting awareness that additional interactions need to be considered in order to better explain the disease [55]. For instance, the possible effects of the microbiota on tree health have been underestimated until recently. In this regard, artificial inoculation trials testing the effect of a single pathogen on a host plant may be inadequate to assess diseases in the instance of co-occurring pathogens and in the presence of varying microbiota. The interest in endophytic microbiota of forest trees has increased over the years, and many recent studies have dealt with these organisms [56–60] and their importance in the management of plant diseases [61–63].

Microbiota can alter host fitness by affecting a plant's ability to survive, reproduce, compete, grow, or defend itself against parasites. The interactions between plant and microbiota, especially fungi, can range from parasitic to mutualistic. The net result of the interaction is determined by the characteristics of the organism and host, as well as ecological and environmental conditions [60]. There is also increasing evidence that the plant microbiota is influenced by the genetic variability of the host, both at intraspecific [64–66] and interspecific [67–70] levels. Both mechanisms, host plasticity and the genetic adaptation of the microbiota, may allow plant populations to cope with novel, emerging pathogens; thus, a current challenge for forest pathologists lies in the ability to assess their relative role in disease development [71]. Therefore, microorganisms other than *F. circinatum* may induce changes in the pine phenotype that can subsequently affect the suitability and behavior of the host to PPC infections, when acting either simultaneously or in succession.

In natural environments, trees are rarely attacked by a single pathogen; more typically, they face an array of pathogens. In this paper, we focus on pathogenic fungi and oomycetes potentially co-occurring with *F. circinatum* in pines. Interactions between pathogens and/or insects co-occcurring in the same tree are often of significant importance, and have been well documented [72,73]. The interaction between *F. circinatum* and *Tomicus piniperda* (L.) was studied by Lombardero et al. [74], who reported that terpene expression triggered by the insect reduced fungal growth in *P. radiata*. In contrast, interactions between pathogens occurring in trees have been less investigated [5,63,75]. Several scenarios can be depicted when pathogens co-occur on the same plant:

(1) Direct antagonistic interaction: a pathogen may colonize the same plant parts infected and colonized by *F. circinatum*, thus making those parts unavailable for PPC infection. This direct antagonism can be modulated by the environment; for instance, Kozanitas et al. [63] found that *Phytophthora nemorosa* E. M. Hansen et Reeser can persist at levels comparable to those of *P. ramorum* in ecologically-suitable plots when climate favors *P. ramorum* dormancy. However, *P. ramorum* prevalence increases to levels higher than those of the competing species when abundant rainfall triggers its sporulation. These results lead to the conclusion that understanding the determinants and outcomes of competition between these species has important implications for understanding their epidemiology and for devising possible control strategies for Sudden Oak Death.

(2) Indirect antagonistic interaction: a tree made sick because of prior infection by another pathogen may generally not be a good host for PPC, or a good sporulation substrate for *F circinatum*. It is also possible that the host may have been primed to resist *F. circinatum* infection by the prior infection of another pathogen, as in the case mentioned above of an insect attack curtailing infection by *F. circinatum* [74]. Priming is meant as a biochemical process, when infection by one ptahogen triggers a defense response that may hinder infection by another [76].

(3) Neutral interaction: when no direct or indirect effects or interactions among fungi occur.

(4) Synergistic interaction: a tree infected by a pathogen may be more easily infected due to reduced defences or the creation of infection courts caused by other pathogens. In some cases,

different pathogens are able to interact synergistically, causing together much more damage than would be expected from the addition of the impacts caused by each pasthogen individually [75].

Direct interactions between pathogens infecting the same plant part may thus result in greater or lesser disease severity, depending on the pathosystem in question. For instance, necrosis length was greater in *P. halepensis* seedlings inoculated with *Sydowia polyspora* (Bref. and Tavel) E. Müll and *Gremmeniella abietina* (Lagerberg) Morelet than in those inoculated with *G. abietina* alone [77]. Converseley, *Cenangium ferruginosum* Fr. was able to reduce the length of necrosis caused by *G. abietina* on *P. halepensis* [77]. Barrett [78] tested the ability of *Phaeolus schweinitzii* (Fr.) Pat. to infect wood already colonized by another fungus in a series of experiments using blocks of Sitka Spruce. Growth of *P. schweinitzii* was not inhibited by the presence of *Armillaria mellea* (Vahl) P. Kumm. or *Postia stiptica* (Pers.) Jülich, whereas its development was arrested by *Sparassis crispa* (Wulfen) Fr. There may be several instances where *F. circinatum* may reduce its vitality and ability to cause infection, e.g.: (a) host resistance responses may have been triggered by prior infection by another pathogen, (b) a viable substrate for infection may have been exclusively occupied by other pathogens, or (c) trees quickly decline because of a previous infection by other pathogens, and live tissues may not be available for growth or sporulation by *F. circinatum* or other pathogens. This last notion is supported by work showing that *F. circinatum* sporulation on dead or dying trees is reduced [68]. Interactions can also span across the belowground–aboveground divide [79]. Root pathogens, for instance, can affect foliar pathogens, and vice versa. Data from severely diseased *Fraxinus excelsior* L. stands in south-western Germany supported the hypothesis that *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz, and Hosoya is the major agent of collar necroses in ash, although *Armillaria* spp. play an important aggravating role [80]. Such cross-compartment interactions are indirect (i.e., plant-mediated), and involve systemic induction or priming of common plant defences or altered plant quality [73].

The goal of this paper is to expand our understanding of the biotic interactions that may play a role in the future trajectory and impact of PPC disease in European nurseries and forests. We estimate the potential spatial overlap, and the potential direct and indirect interactions between these pathogens and *F. circinatum*. The mechanisms influencing interactions between the pathogens and the climatic dependence of the disease incidence are discussed. In order to achieve such a goal, we updated the literature, including the so-called grey literature, regarding the geographical distribution and relevance of pathogens infecting pine species in Europe—whose host range overlaps with the host range of *F. circinatum*—with descriptions of the syndromes caused by these pathogens. These descriptions will make it easier to recognize them, particularly in nurseries, where they may cause symptoms similar to those induced by *F. circinatum*. Consequently, pathogens were grouped into those occurring in forest stands and those occurring in nurseries. For the first group, a differentiation between pathogens that cause root and butt rot, cankers, leaf damage, or vascular stain was made. This review is the product of a collaborative effort within the COST Action FP1406 PINESTRENGTH on *F. circinatum*. The pathogen compilation was done by the participating countries presented in Supplementary Tables S1–S4 for forest stands and Table S5 for nurseries.

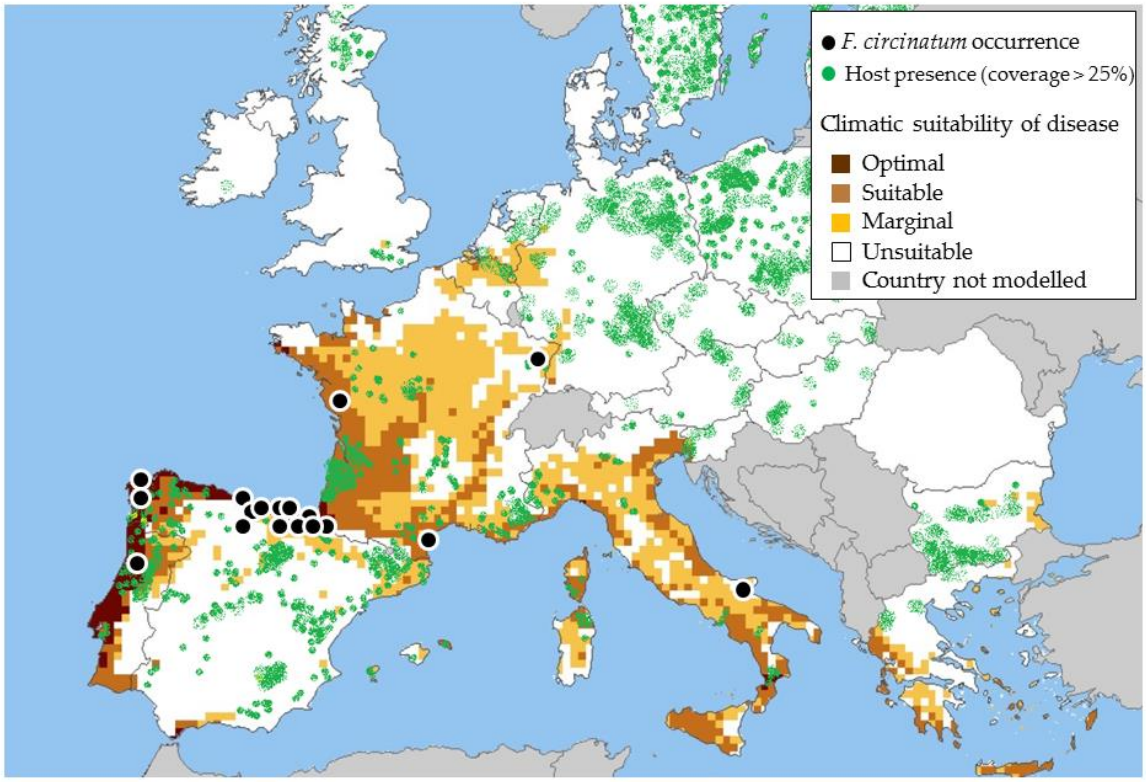

Figure 1. Geographical distribution of host species of *Fusarium circinatum* in Europe, including *Pinus brutia*, *P. canariensis*, *P. cembra*, *P. contorta*, *P. halepensis*, *P. heldreichii*, *P. mugo*, *P. nigra*, *P. pinaster*, *P. pinea*, *P. radiata*, *P. strobus*, *P. sylvestris*, and *P. uncinata* (in green, adapted from EFSA, [39]), and climatic suitability of pitch canker disease at a resolution of 25 km generated by CLIMEX model [39].

2. Pine Pathogens Potentially Co-occurring with *Fusarium circinatum* in Forests and Plantations

2.1. Root and Butt Rot Pathogens

Root infection by *F. circinatum* and associated plant losses have been well documented in nurseries, but rarely in adult trees. The impact of root infection in trees and its importance in PPC management has been underestimated, mainly because the characteristic symptoms of resin-soaked cankers are above ground. However, Garbelotto et al. [41] described, for the first time, resin-soaked sapwood lesions in the roots of 20-year-old Aleppo pines (*P. halepensis*) in California, resulting in varying stages of chlorosis in infected trees. *Fusarium circinatum* was successfully isolated from these root lesions all the way into the root collar and into the very base of the stem; however, the pathogen was never detected in the aerial parts (i.e., branches and trunk) of these infected trees. Similarly, in a survey carried out in *P. radiata* plantations in the Basque country (Spain), *F. circinatum* was isolated from the roots of non-symptomatic trees more often (16.6% isolation success) than from the roots of symptomatic trees with resinous cankers (3.3% isolation success) [81]. The underlying pathogenic interaction in root infection was recently studied in *P. radiata* seedlings by Martín-Rodrígues et al. [82], who found that the fungus employed features that are similar to those previously described for other root infecting pathogens, such as mycelial strands, single runner hyphae, and simple hyphopodia, as well as other features that are reminiscent of those that are known to be involved in biotrophic invasion, such as bulbous or filamentous invasive hyphae. The fungus can spread from the roots to the aerial parts of the plant; once there, colonization appears to be similar to the process that occurs when the pathogen is inoculated in the stem. Wilting symptoms and plant demise may

be the result of a reduction in water uptake by roots and of the blockage of the vascular system by fungal hyphae and resin.

Before the arrival of *F. circinatum* in Europe, the main causal agents associated with damping-off in European nurseries were *F. oxysporum* Schltdl., *F. proliferatum* (Matsush.) Nirenberg ex Gerlach and Nirenberg, *F. verticillioides* (Sacc. Nirenberg) [83,84], *Rhizoctonia* sp., *Botrytis cinerea* Pers., *Alternaria alternata* (Fr.) Keissl. [85], *Rhizina undulata* Fr. [86,87], and *Rhizoctonia solani* J.G. Kühn [88]. The genera *Heterobasidion*, *Armillaria*, and *Phytophthora* include root and butt rot pathogens with the highest impact in pine forests in Europe, and are expected to be the main pathogens to co-occur with *F. circinatum*. Infection by these root and butt rots appears to be facilitated by factors such as high humidity, which is known to favor *Fusarium* spp. [6]; therefore, interaction, including synergy, among these should not be ruled out in plantations.

Root and butt rot caused by *Heterobasidion annosum* (Fr.) Bref. sensu lato (Basidiomycota, Bondarzewiaceae) is the most destructive disease of conifer trees in the Northern Hemisphere [11,89–101]. The sensu lato species complex is composed of three European (*H. annosum*, *H. parviporum* Niemelä and Korhonen and *H. abietinum* Niemelä and Korhonen) and two American species (*H. irregulare* Garbel. and Otrosina and *H. occidentale* Otrosina and Garbel). Additionally, a third hybrid taxon has been recently described in North America [102]. These species were classified based on a diverse range of characteristics, including partial reproductive isolation, host preference, morphological, biochemical, phylogenetic, and genomic traits [6,103–107]. The worldwide distribution of *Heterobasidion* species reflects the distribution of their Pinaceae hosts, which are predominantly the *Pinus*, *Picea*, and *Abies* species, but also include Douglas-fir (*Ps. menziesii*) [6,11,96]. Pines are primarily attacked by *H. irregulare* in North America and *H. annosum* in Europe [90]. The former has also become invasive in the coastal pine stands of central Italy after its introduction from eastern USA in the middle of the nineteenth century [108]. *Heterobasidion irregulare* hybridizes with local *H. annosum* and represents a threat for European forest ecosystems [109–111]. In addition to the above, Douglas-fir and true firs have also been reported to be susceptible to *H. occidentale* and *H. abietinum* in North America and Europe, respectively [6].

Fusarium circinatum has been reported to be pathogenic to over 60 species of pines, Douglas fir [29,50], and seedlings of *Picea abies* (L.) and *Larix decidua* Mill., 1768 [32,112]; therefore, there is considerable host species overlap with *Heterobasidion* spp. For example, on the Iberian Peninsula Monterey pine and maritime pine have been reported to be susceptible to both pathogens, i.e., *H. annosum* [113] and *F. circinatum* [31]. Additionally, damage by *H. annosum* in forest plantations of maritime pine, Monterey pine, and Douglas fir are common [114], and in Spain, the pathogen has recently been associated with declining maritime pine plantations [100]. However, almost nothing is known about their interaction or co-infection in the natural forest environment, and indirect interactions mediated by the altered physiology of *Heterobasidion*-infected trees are possible, as demonstrated with pine bark beetles through surveys in the field [115,116] and with *Diplodia sapinea* (Fr.) Fuckel, through inoculation [117] and laboratory experiments [118]. Infection by *Heterobasidion* spp. may favor subsequent *F. circinatum* infection to a greater extent in pines than in Douglas firs, firs, or spruces, since in the former case, the cambium is attacked, often resulting in tree weakening and death, as opposed to Douglas fir, in which the heartwood or sapwood are colonized [6]. Nonetheless, extensive attacks by *Heterobasidion* spp. on species other than pines can also result in loss of tree vigor and higher susceptibility to climatic changes [119], thereby possibly influencing tree susceptibility to *F. circinatum*.

The main putative mechanism leading to increased susceptibility to *F. circinatum* of pines infected by *Heterobasidion* or other root pathogens may hinge on the documented higher susceptibility of these infected trees to insect attacks [116], which would result in significant wounding, thereby facilitating infection by *F. circinatum* [50]. On the other hand, there is no evidence that in the absence of insect wounds, trees weakened due to infection by root pathogens may be more prone to infection by *F. circinatum*. On the contrary, based on field and experimental results, it is possible that trees made less vigorous by previous fungal infections may support significantly less *F. circinatum* sporulation than healthy trees [41], or may be overall less susceptible to the pathogen [120]. If this

mechanism applies to trees previously infected by root pathogens, then such trees may either be less susceptible to *F. circinatum* or overall epidemiologically less relevant for the spread of PPC.

The genus *Armillaria* includes several economically-important phytopathogenic fungi causing root diseases on conifers [121]. Seven *Armillaria* species are present in Europe: *A. borealis* Marxm. and Korhonen, *A. cepistipes* Velen., *A. gallica* Marxm.and Romagn., *A. mellea* (Vahl) P. Kumm., *A. ostoyae* (Romagn.) Herink, and two *Desarmillaria* species, *Desarmillaria ectypa* (Fr.) R.A. Koch and Aime (Syn: *Armillaria ectypa* (Fr.) Lamoure) [122] and *Desarmillaria tabescens* (Scop.) R.A. Koch and Aime (Syn: *Armillaria tabescens* (Scop.) Emel). *Armillaria* species occur all across Europe [85,121,123–129]. The most common *Armillaria* species on pines in north-east Europe are *A. borealis* and *A. ostoyae* [130,131], while in Maritime and south-east Europe, *A. cepistipes*, *A. gallica*, *A. mellea*, and *A. ostoyae* are the most common [121,122,129,132,133]. *Armillaria* species can be aggressive primary pathogens as well as secondary pathogens of stressed trees and saprophytes [134]. They often attack hosts predisposed by various abiotic and biotic factors, such as drought, flooding, frost, and insect defoliation [122]. *Armillaria mellea* and *A. ostoyae* are the most aggressive species, while *A. cepistipes* and *A. gallica* are secondary pathogens [122]. As primary pathogens, *Armillaria* spp. cause lethal disease by invading and killing the living bark and vascular cambium of the roots and root collar. The extent of damage caused by *Armillaria* is determined by factors such as species, the vigor of the host, interaction with other diseases, soil properties, climate, plantation management, and previous land uses [135–139]. *Armillaria* species have a saprophytic stage in dead roots and stumps, which functions as a source of inoculum to infect living roots [139]. In the case of co-occurrence of the more pathogenic *Armillaria* species and *F. circinatum*, we envision a whole range of potential interactions. It is well known that *Armillaria* disease progression occurs at an extraordinarily fast rate when infected trees are also the subject of an additional stress factor, i.e., extended drought and, especially, anoxia caused by flooding are well known to cause rapid death of trees already infected by *Armillaria*. Thus, it is possible that advanced disease caused by *F. circinatum* may similarly hasten *Armillaria*-caused mortality. At the same time, this synergistic relationship may also result in an overall reduced sporulation by *F. circinatum*, given the fast decline of dying individuals. When *F. circinatum* coexists instead with less pathogenic *Armillaria* species, it is possible that co-infection may increase the pathogenicity of the *Armillaria* species involved, resulting in a complex disease syndrome that would otherwise not be observed.

The oomycete genus *Phytophthora* contains over 150 taxa [140,141], and is considered one of the most devastating plant pathogenic genera in the world [142–144]. *Phytophthora* spp. cause leaf blights, collar rots, stem cankers, and fruit rots [145], but root rots are among the most common symptoms [146], both in nurseries and forests [147,148]. Scots pine seedlings have been found to be susceptible to *P. cactorum* (Lebert and Cohn) J. Schröt), *P. cambivora* (Petri) Buisman, *P. plurivora* T. Jung and T.I. Burgess, and *P. cinnamomi* Rands [5,149–151]. Infected plants frequently show growth reduction, chlorosis, and dieback caused by extensive fine root losses and/or collar rot [144]. Littleleaf disease in eastern North America is caused by *P. cinnamomi* infection of pines in former agricultural lands, and leads to pervasive and widespread reduced vigor, reduced life span of infected trees, and predisposition to other diseases [5,152]. Based on the observations of trees affected by littleleaf disease, it is most likely that root infection by *Phytophthora* spp. may facilitate infection by *F. circinatum*, especially in planted stands that may, to some extent, resemble those plantations in disturbed agricultural lands where littleleaf disease is known to occur.

2.2. Canker Pathogens

The term "canker" describes a necrotic area, with swelling surrounding a sunken lesion or blister on the bark of trunks and branches affecting the underlying cambial layer. Cankers are commonly formed when pathogens, often fungi, invade wounded or injured bark tissues. Some of the most common ascomycete fungal pathogens causing canker in *Pinus* species include *F. circinatum*, *Diplodia sapinea* (Fr.) Fuckel, and *Caliciopsis pinea* Peck [153–156]. In native and exotic *Pinus* species, they cause copious pitching, cankers, and degradation of the wood quality of sawn timbers. *Diplodia sapinea* symptoms also include a blueish staining of the wood [156]. These canker diseases may cause

extensive damage to trees when they girdle a branch or the main stem, causing a dieback of all parts of the plant above the canker. Cankers may not kill trees outright, but can be sites for invasion by wood decay fungi, which can predispose the tree to breakage by strong winds, heavy hail, or snow [157,158].

Canker pathogens, sharing many of the same hosts with *F. circinatum*, are favored by similar environmental conditions, and may play similar ecological roles in forest ecosystems. For example, the co-occurrence of *D. sapinea* and *C. pinea* in *P. radiata* has been reported by Aglietti et al. [159]. *Pinus radiata* plantations infected by *F. circinatum* have been found to be simultaneously colonized by *D. sapinea* [81,160] or *C. pinea* [161]. *Diplodia sapinea* has also been reported to co-occur with *F. circinatum* in wounds made by bark beetles, suggesting competition for space and nutrients between these two pathogens, although a synergistic effect should not be dismissed [162,163]. Luchi et al. [164] suggested that the presence of *C. pinea* in Tuscany could be considered a bio-indicator of very favorable environmental conditions for *F. circinatum*, particularly considering their recently shown association. The infection severity of the three fungal pathogens has been related to drought stress, waterlogging, and high stand densities [160,165–170]. In addition, all cases of coexistence of *D. sapinea* or *C. pinea* with *F. circinatum* occur in the Mediterranean zone, i.e., in Spain and Italy, and exclusively on *P. radiata*. Whether co-infection always increases the severity of PPC is questionable; in some cases, in fact, some pathogenic fungi end up excluding other more pathogenic species known to occupy a similar niche. For example, *D. scrobiculata* J. de Wet, Slippers and M.J. Wingf. excludes the more pathogenic *D. sapinea* in native forests, whereas in plantation forests, *D. sapinea* dominates [171]. Likewise, *Phytophthora nemorosa* can exclude infection by the more aggressive *P. ramorum* [63].

In addition, other canker diseases caused by species such as *Gremmeniella abietina* (Lagerb.) M. Morelet and *Cenangium ferruginosum* Fr. have been detected in Italy and Spain, countries where *F. circinatum* has been already detected, although neither of these two fungal species in *Pinus* sp. has yet been reported to coexist with *F. circinatum*. The ability of *C. ferruginosum* to cause significant dieback is usually associated with climatic stressors such as high precipitation followed by long periods of drought and severe frost [172,173]. Otherwise, this fungus is normally regarded as a secondary pathogen or saprobic organism; accordingly, the presence of *C. ferruginosum* in Northern Spain does not appear to be associated with significant pathogenic activity [174]. *Gremmeniella abietina* is widespread in Europe and causes a common disease in *P. nigra*, *P. sylvestris*, *P. cembra*, *P. mugo*, and *Picea abies*. Its distribution ranges from the Boreal to the Mediterranean region [175].

Co-infection of *F. circinatum* and pine blister rusts has never been reported in the literature, although *Cronartium flaccidum* (Alb. and Schw.) Wint. (the causal agent of blister rust of two-needled pines) and *C. ribicola* JC. Fish (the causal agent of white pine blister rust), the two most relevant *Cronartium* species, are widespread in Europe. The distribution range of *C. flaccidum* includes countries such as Spain and Portugal, where PPC has been established. Both rusts cause a variety of symptoms on pine trees, including galls, yellowing and premature defoliation, cankers, resinosis, dieback of branches and stems, deformity, consistent growth reduction, and tree and cone death, that could, at least in part, overlap with symptoms caused by PPC. However, *C. flaccidum* is considered a minor pathogen of *P. radiata* in the EPPO region [176], while *C. ribicola* is only known to affect 5-needle white pines, and thus, should not have a significant host overlap with *F. circinatum*.

The coexistence of *F. circinatum* with other *Fusarium* species has been reported by Herron et al. [177], who explored the diversity of *Fusarium* species in Colombian pine plantations and nurseries with plants displaying symptoms typically associated with infection by *F. circinatum* (i.e., stem cankers and branch die-back on trees in plantations and root or collar rot of seedlings). More than ten *Fusarium* spp. were identified in the study, i.e., *F. circinatum*, *F. oxysporum*, species within the *F. solani* species complex, and seven novel species in the *F. fujikuroi* species complex (formerly the *Gibberella fujikuroi* species complex). *Fusarium marasasianum*, *F. parvisorum*, and *F. sororula* displayed levels of pathogenicity to *P. patula* that were comparable with those of *F. circinatum*. Although there are no reports on the effect that these species of *Fusarium* may have on the severity of *F. circinatum* infections, it is likely that interactions occur, since they share hosts and niches for infection, and produce similar symptoms.

2.3. Foliar Pathogens

Foliar pathogens primarily infect the leaves or needles of plants, but a few of them are also able to invade buds and young shoots. They can significantly reduce photosynthesis, affecting tree growth and influencing the capacity of the tree to defend itself against biotic or abiotic stress by directly or indirectly affecting the production of secondary metabolites which are essential in defense reactions [178–180]. Moisture and temperature are the two most important environmental factors for foliar pathogens, as they are critical for sporulation, dispersal, and infection.

There are numerous foliage diseases of pines caused by many different fungi, yet not all are of economic importance or global distribution [178,181]. Many foliage diseases are more likely to cause severe damage on conifers planted "off site" (i.e., the wrong type of site for a species or out of its native range e.g., Monterey pine plantations in Chile, Ecuador, New Zealand, or Spain). Monodominant plantations appear to be particularly susceptible, because disease contagion occurs more rapidly and effectively when trees are planted at a short distance from one another, and when stress may be high due to environmental and ecological conditions which are rather dissimilar from conditions found in native stands. Pines are susceptible to several fungi that cause needle blights and casts, leading to the premature loss of photosynthetic tissues. Worldwide, the most common and economically important foliar diseases of pines include *Dothistroma* needle blight (DNB, caused by *Dothistroma septosporum* (Dorog.) Morelet and *Dothistroma pini* Hulbary), *Lophodermium* needle cast (caused by *Lophodermium seditiosum* Minter, Staley and Millar), and *Cyclaneusma* needle cast (caused by *Cyclaneusma minus* (Butin) DiCosmo, Peredo and Minter). Brown spot needle blight (caused by *Lecanosticta acicola* (Thumen) H. Sydow (Syn: *Mycosphaerella dearnesii*) and Cercospora blight of pine (caused by *Mycosphaerella gibsonii* H.C. Evans) are also important emerging pine foliage diseases, both caused by pathogens listed as quarantine species for Europe [7,178,182–185]. New reports of *L. acicola* from Ireland, Portugal, Sweden, Russia, and Estonia, suggest that this pathogen is continuing to spread in Europe, and that it is well adapted to a wide range of climatic conditions [186].

Other foliar pathogens widely distributed in Europe include *Lophodermella sulcigena* (Link) Höhn, and *Sydowia polyspora* (Bref. and Tavel) E. Müll., as well as the rust pathogens *Coleosporium* spp. and *Melampsora* spp. In this review, we focus on the most common invasive and emerging fungal foliage pathogens of pines, the causal agents of DNB and brown spot needle blight, due to their potential to cause severe disease and predispose the trees to other biotic and abiotic stresses, potentially including *F. circinatum*. A significant intensification in the distribution and severity of these needle blight diseases has occurred in the past few decades both in North America [184] and Europe [7,183,187–195]. Furthermore, both needle blights have a range partially overlapping with the current range of PPC [160,196].

The causal agents of DNB, *D. septosporum* and *D. pini*, have a worldwide distribution and a host range of over 100 Pinaceae taxa, primarily *Pinus* spp. [7]. Currently, these fungi are no longer on the EPPO A2 list of quarantine pests due to their wide distribution throughout Europe. Characteristic symptoms of DNB include necrotic bands or spots on needles of all age classes and premature defoliation, leading to reduced growth and timber yields, and in some cases, high levels of tree mortality. The morphology and dimensions of the fruit bodies and conidia of both species are almost identical; therefore, the two pathogens can only be differentiated using molecular methods [197]. Recent population genetic studies indicate that *D. septosporum* could be native to Europe [195,198], while the origin of *D. pini* remains unknown.

Lecanosticta acicola, a heterothallic ascomycete currently on the European EPPO A2 list of quarantine pathogens, is the causal agent of brown spot needle blight of pines. Severe infection by this invasive needle pathogen can lead to premature defoliation, the reduction of growth, and tree mortality [199]. *Lecanosticta acicola* can infect more than 30 pine species. It usually reproduces asexually and spreads via rain-splash dispersed conidia [200]. As a result of a severe attack, whole needles become brown-colored and elongated grey-green to olive-black fruiting bodies (acervuli) develop under the epidermis of the necrotic portion of needles [185,195]. Infection and defoliation begin from the lower branches, as in the case of DNB. The sexual stage rarely appears on dead fallen needles, but little is known about the pathogen's sexual reproduction [201]. Symptoms of infection

by *L. acicola* are very similar to those caused by other fungal pathogens, such as *Dothistroma* spp., *Lophophacidium dooksii* Corlett and Shoemaker, *D. sapinea*, and various *Lophodermium* species.

Foliar pathogens are generally favored by warm temperatures and abundant moisture, the same conditions that favor *F. circinatum*; therefore, it is unsurprising that some foliar pathogens have been found to co-occur with *F. circinatum*, and we expect these co-occurrence rates to increase, although more detailed studies would be needed to fully understand the final outcome of such a co-occurrence. In the past several years, blight diseases, and especially brown spot needle blight, have become widespread in Europe [7,186,202–204], including in areas of Spain and Portugal where *F. circinatum* is already established [160]. *Lecanosticta acicola* is the most common needle blight pathogen affecting *P. radiata* in the Basque country (Spain), and its co-occurrence with *D. septosporum* has been reported at low levels [196]. In the same region of Spain, *F. circinatum* poses a serious risk to commercial plantations of non-native *P. radiata* and *Ps. menziesii*, as well as to native populations of *P. pinaster*, *P. nigra*, and *P. sylvestris* [13,15,30,160]. The presence of *L. acicola*, *D. septosporum*, and *F. circinatum* in the same *P. radiata* plantation is known (Iturritxa, E., personal communication); therefore, a synergistic effect between the needle blight pathogens and *F. circinatum* should not be dismissed.

Recent genetic studies have indicated that Mexico is probably the area of origin of *L. acicola* populations detected in the United States and Canada, and that at least two introductions of *L. acicola* have occurred from North America into Europe [179], where it was first reported from Spain [205]. It is also notable that the centre of origin of *F. circinatum* is likely to be Mexico or Central America [177,206], and population studies strongly suggest that USA could be the source of the *F. circinatum* introductions to Spain [207]. In Northern Spain, *L. acicola* was most commonly detected on planted *P. radiata* [194]. In the USA, *F. circinatum* commonly produces sporodochia containing macroconidia on dead needles attached to infected shoots in the upper crown of trees [208,209]. It is possible that in areas highly infected by these fungi, both pathogens may infect the same trees and form fruiting structures on the same tissues. This may also be the case for other blight and canker pathogens, such as *Dothistroma* spp., *D. sapinea*, and other recently-described pine pathogenic *Fusarium* species [177].

The presence of *S. polyspora*, a fungus previously believed to be mostly an endophyte or saprophyte [210,211], has been recently associated with current season needle necrosis (CSNN) on various conifer species [212,213]. Moreover, *S. polyspora* has been reported in Spain on *P. radiata* as a species frequently carried by insects in areas affected by *F. circinatum* [214]. Preliminary data suggest a negative interaction between the two fungi; however, further research needs to better address the actual outcome of this relationship.

Although *F. circinatum* is a primary and often lethal pathogen of pines, trees may survive infection for periods lasting several years. However, factors predisposing the host to PPC infection, or making it more vulnerable to biotic and abiotic diseases, will accentuate the effects of the infection and accelerate its decline. Severe foliage diseases are known to weaken their hosts and predispose them to biotic and abiotic stresses, so it is not unlikely they may also hasten infection by *F. circinatum*. Given that *F. circinatum* does not primarily infect foliage, a direct antagonistic interaction between *F. circinatum* and foliar pathogens is unlikely to dominate. Thus, a synergistic effect between foliar pathogens and *F. circinatum* is likely to occur. However, severe infection by foliar pathogens, leading to subsequent defoliation, or severe *F. circinatum* infection, leading to extensive branch dieback, is likely to make the host less suitable for infection by the other pathogen(s). By necessity, foliar pathogens sporulate on the foliage, and extensive branch dieback due to PPC would reduce the available sporulation material, particularly for those fungi requiring live foliage for sporulation, potentially leading to a slight reduction in inoculum load. More data is needed to untangle the variety of possible interactions and effects between foliar pathogens and *F. circinatum*.

2.4. Vascular Pathogens

Fungal vascular pathogens invade the xylem of roots and stems and interfere with water transport by cavitation and occlusion of vessels with mycelium and tyloses, thereby causing disfunction of the vascular tissue [215]. Some of the best-known tree pathogens are vascular inhabiting, and are known to cause discoloration of wood (caused by blue-stain and sapstain fungi)

and high rates of tree mortality [216,217]. The most common fungal vascular pathogens belong to the genera *Ceratocystis*, *Ophiostoma*, *Verticillium*, and *Fusarium*.

Although a number of *Fusarium* species are important vascular pathogens, *F. circinatum* is not considered a true vascular pathogen, even though it does affect the vascular system and behaves similarly to many of the true vascular pathogens. During the initial stages of pine stem colonization by *F. circinatum*, two predominant pathways can occur: a radial advance toward the pith via medullary rays, and a tangential invasion of the outermost layers of the stem through the phloem and the cortex [218]. The initial colonization of the cortex and pith by *F. circinatum* is through growth in intercellular spaces. Subsequent stages of the disease involve vertical colonization of the pine stem by three principal pathways: through the cortex and the phloem in the stem periphery (consistent with the external visual necrotic lesion), through the xylem via axial tracheids and resin ducts, and through the inner parenchymatous pith tissue [218].

Ophiostomatoid fungi are especially important as agents responsible for the discoloration and staining of the wood of several conifer tree species in the Northern Hemisphere, decreasing the economic value of timber without the structural damage caused by decay fungi [219,220]. They have a well-known association with bark beetles and include genera that are morphologically similar, even if not always closely related phylogenetically [220]. Genera in this group include *Ophiostoma*, *Ceratocystiopsis*, *Graphilbum*, *Raffaelea*, and *Leptographium* in the order Ophiostomatales, and *Ceratocystis* (sensu stricto), *Chalaropsis*, *Endoconidiophora*, and *Graphium* in the order Microascales [220]. Ophiostomatoid fungi vary greatly in pathogenicity, and include species that are weak secondary pathogens, as well as species known to be aggressive primary pathogens [216,217]. Staining by ophiostomatoid fungi is caused by fungal hyphae usually growing in ray parenchyma cells and, at a later phase of infection, in tracheid cells of the sapwood and phloem [220]. Thereby, ophiostomatoid fungi may play key roles in overcoming tree defences through the pathogenic colonization of the sapwood and the phloem, in weakening tree vigor by limiting the absorption of water and micronutrients, and in facilitating the establishment of other pathogens, including *F. circinatum*.

An ophiostomatoid species known to be virulent on pines is *Ophiostoma minus* (Hedgc.) Syd. and P. Syd. This fungus has the capacity to penetrate deep into the sapwood causing long necroses, a substantial blue-stain of the wood, and may ultimately kill infected plants [221,222]. In Spain, *O. minus* was recently found to be associated with *P. pinaster*, a species susceptible to PPC [223]. *Ophiostoma minus* is a very aggressive pathogen of Scots pine seedlings, and can also affect large trees [224–226]. The inoculation of Scots pine with *Ophiostoma ips* (Rumbold) Nannfeldt, *O. pallidulum* Linnak., Z.W. de Beer and M.J. Wingf., and *O. piceae* (Münch) Syd. and P. Syd. often results in relatively small lesions, indicating that these species are probably weak pathogens or are non-pathogenic fungi [227]. However, Jankowiak [221] obtained 30% mortality when artificially inoculating Scots pine seedlings with these ophiostomatoid fungi, suggesting they may play a significant role in the regeneration of this pine species [226].

A number of aggressive *Leptographium* species has been reported on pines. The species *Leptographium wingfieldii* M. Morelet, *L. procerum* (W.B. Kendr.) M.J. Wingf., and *L. wageneri* (W.B. Kendr.) M.J. Wingf. are responsible for blue stain of pine, pine root disease, and black stain root disease, respectively [228]. *Graphilbum* species, particularly *G. rectangulosporium* (Ohtaka, Masuya and Yamaoka) Z.W. de Beer and M.J. Wingf. and *G. brunneocrinitum* (E.F. Wright and Cain) Z.W. de Beer and M.J. Wingf., have not been studied in great detail, although they have been isolated from bark beetles in Spain, Israel, Poland, Ukraine, and China [229]. Jankowiak [222] also reported the association of *G. rectangulosporium* with a bark beetle, *Ips sexdentatus*, on *P. sylvestris* in Poland. The fungus had low virulence on *P. sylvestris*, with one isolate causing necrosis and mortality on seedlings, but *P. halepensis* and *P. brutia* were resistant to all isolates. *Ceratocystis comata* (V.V. Mill. and Tcherntz.) C. Moreau has also been reported as a weak pathogen capable of injuring and staining timber [230].

Several ophiostomatoid fungi were found to be associated with nine bark beetle species and one weevil infesting *P. sylvestris*, *P. nigra*, and *P. radiata*, in an area affected by PPC in Northern Spain. A

total of 11 fungal species (five species of *Leptographium* sensu lato including *L. absconditum* sp. nov., five species of *Ophiostoma* sensu lato including *O. cantabriense* Romón, Z.W. De Beer and M.J. Wingf., and one species of *Graphilbum*) were found. Only *L. wingfieldii*, *L. guttulatum*, and *O. ips* were capable of causing significant lesions in an aggresiveness experiment [231].

A single study involving Ophiostomatoid fungi and *Pinus* species showed varied effects on the host. They may negatively impact the vigor of infected trees, but to which extent seems to largely depend on the virulence of the fungal species, the relative susceptibility of the host species/genotype involved, and the fungal x host combination [232,233]. Studies demonstrating competition for niches or nutrients between co-occurring *F. circinatum* and Ophiostomatoid fungi are needed. Nevertheless, the presence of vascular pathogens in a host results in reduced transportation of water and nutrients, to a greater or lesser extent depending on the species, and causes the host to devote more energy to defense. The presence of multiple infections, by multiple pathogens, on the same host is likely to compound and accentuate these effects, leading to greater stress on, and more rapid decline of, the host. Furthermore, although infection by ophiostomatoid fungi may not directly affect infection by *F. circinatum*, it may increase attacks by insects, which, in turn, may favor infection by *F. circinatum*. Therefore, we conclude that it is likely that co-infection by *F. circinatum* and Ophiostomatoid fungi may increase overall disease severity and accelerate the decline of infected trees.

3. Pathogens Potentially Co-Occurring with *Fusarium circinatum* in Pine Nurseries

Nursery seedlings infected by *F. circinatum* as an exotic pathogen were first officially reported in South Africa and subsequently in Spain, Chile, Portugal, Uruguay, France, Brazil, and Colombia [18,22,29,48,234–237]. Nursery conditions are, in general, favorable to plant growth, but at the same time, those conditions may favor infection by pathogens. Some of the diseases occurring in nursery seedlings are unique to the nursery environment, and are not present in older trees in forests. The reason for this specificity may be related either to the environmental conditions of nurseries or to the type of disease, with diseases associated with juveniles or seedborne diseases being more frequent in nurseries.

Damage caused by PPC in nurseries includes reduced germination of seeds, pre-, post-emergence damping-off, needle and terminal shoot dieback, resinous cankers on lignified stems, wilting, and death of seedlings. Late damping-off results in stem lesions and a chlorotic or purplish foliage discoloration, followed by tip dieback, and occasionally, mycelium growth on the stem. However, the symptoms present in diseased seedlings are rather unspecific, and are easily attributed to other pathogens, thus highlighting the importance of correct laboratory analyses in disease diagnosis. Affected seedlings occur in patches which are often randomly distributed throughout the nursery. Latent infections are frequent on some pine species such as longleaf pine (*P. palustris* Mill.), Monterey pine [47], and maritime pine [34], and may emerge only after out planting.

The most common mode of entry of *F. circinatum* into the nursery is via infested seeds, soil, and contaminated trays [238]. The fungus can also enter the nursery as airborne inoculum from infected trees nearby, or can possibly be carried by insects. Fungus gnats (Diptera) have been suspected to be carriers of *F. circinatum* in pine nurseries in South Africa, as they are known to vector other fungal pathogens such as *Botrytis cinerea* and *F. proliferatum* [239]. There are many demonstrated associations between *F. circinatum* and insects (vectors, carriers, etc.) [43]. Since *F. circinatum* colonizes herbaceous hosts and sometimes even the pine seedlings with an endophytic behavior, it has been speculated that weeds might be an inoculum reservoir [240].

Fusarium circinatum is often found in nurseries before it is detected in natural or urban environments, and infected plant stock or seeds seem to be two plausible pathways for the introduction of the disease into many environments. In California, the pathogen has been repeatedly reported in Christmas tree plantations [49], even before it became established in natural or urban settings. In South Africa, where PPC is predominantly a problem in nurseries and in outplantings, the first outbreak in established forest stands was reported 15 years after its detection in nurseries [29], suggesting the introduction and spread of *F. circinatum* through infected nursery plants. Similarly, in Spain, PPC was first detected in nurseries in Galicia in 1995 [17], and Basque Country in

1998 [18–20]; it was not until 2003 that PPC was officially found in a plantation of P. *radiata* [15]. In Portugal, the first detection in nurseries was in 2007 [22], and its detection in a *P. radiata* plantation occurred some years later (H. Bragança, personal communication). In Italy, the only report of PPC was on adult trees in urban parks and gardens [23]. In France, *F. circinatum* was detected for the first time in 2005 on *Ps. menziesii* and *Pinus* spp. trees [25]. In 2009, the pathogen was again detected in seed lots imported from the USA, and an isolated outbreak was reported on *Ps. menziesii* trees in eastern France [241]. In the same year, *F. circinatum* was also reported on *P. radiata* in two nurseries (western France), and it was hypothesized that the inoculum had been introduced through a contaminated imported seed lot [27]. In 2011, the pathogen was officially declared as eradicated [26]. In South America, PPC has been found in nurseries from Uruguay [235], Chile [234], and Brazil [237], but the disease has not yet been reported in plantations. In Colombia, in contrast, the disease was simultaneously reported in nurseries and established plantations [236].

Wilting, collar rot, and root rot caused by *F. circinatum* in pine nurseries are not easily distinguishable from symptoms caused by common soilborne ascomycete and oomycete pathogens in the genera *Fusarium*, *Cylindrocarpon*, *Cylindrocladium*, *Macrophomina*, *Phytophthora*, *Phytopythium*, *Pythium*, *Rhizoctonia*, and *Trichotecium*. *Fusarium* species other than *F. circinatum* can be responsible for severe root rot and both pre- and post-emergence damping-off. Numerous species of *Fusarium* are commonly isolated from conifer seeds and seedlings in nurseries, including *F. acuminatum*, *F. avenaceum*, *F. lateritium*, *F. verticillioides*, *F. oxysporum*, *F. poae*, *F. proliferatum*, *F. roseum*, *F. sambucinum*, *F. solani*, *F. sporotrichoides*, and *F. tricinctum* [82,242–247]. *Cylindrocarpon* species cause severe root decay and have very wide host ranges. The most commonly-isolated *Cylindrocarpon* species from diseased conifer seedlings is *C. destructans* (Zinssm.) Scholten (now *Ilyonectria destructans* (Zinssm.) Rossman, L. Lombard and Crous). Other species, including *C. didymum* (Harting) Wollenw., *C. tenuis* (Bugnic.) Crous and M.J. Wingf., and *C. cylindroides* Wollenw. (now *Neonectria fuckeliana* (C. Booth) Castl. and Rossman) were only occasionally recorded [248]. *Calonectria* and their *Cylindrocladium* anamorphs have been reported on 17 species in the family Pinaceae [249]. *Cylindrocladium scoparium* Morgan (now *Calonectria morganii* Crous, Alfenas and M.J. Wingf.), *C. floridanum* (now *Calonectria kyotensis* Terash.), and *C. parasiticum* Crous, M.J. Wingf. and Alfenas (now *Calonectria ilicicola* Boedijnand Reitsma) are the most frequently-reported species in conifer nurseries.

Diplodia sapinea and *D. scrobiculata* cause shoot blight, canker, and collar rot in many conifers, leading to the deformity or death of seedlings [250]. *Diplodia sapinea* appears to be more common and aggressive than *D. scrobiculata* [251]. These pathogens also cause seed rot and the damping-off of seedlings of two- and three-needled pines, including Monterey pine, which is very susceptible to PPC [252]. *Diplodia sapinea* can be transported as a latent pathogen in asymptomatic seedlings and seeds [253] and, like *F. circinatum* and *Gremmeniella abietina*, increases seedling mortality after outplanting.

Pythiaceae, including species of *Phytophthora*, *Phytopythium*, and *Pythium*, can cause considerable losses in forest nurseries, particularly in water-saturated soils [148,254]. Some species of *Phytophthora*, such as *P. pinifolia* Alv. Durán, Gryzenh. and M.J. Wingf and *P. pluvialis* Reeser, W. Sutton and E.M. Hansen, may cause severe needle cast of Monterey pine [255,256]; however, they have not yet been detected in nurseries. Damage caused by *Pythium* root rot is usually limited to nurseries, while asymptomatically-infected nursery plants can transport potentially damaging, invasive *Phytophthora* spp. into forest stands [145–147]. Several species of *Phytophthora* may be present in a nursery, with most of them having a broad host range including pine species [257–261]. In a recent survey of more than 700 European nurseries producing forest transplants, more than 90% of nurseries producing Monterey pine seedlings were found to be infested by *Phytophthora* spp. [147].

Black root rot is caused by a complex of microorganisms, and in particular, by *Macrophomina phaseolina* (Tassi) Goid and *F. oxysporum*. Charcoal root rot is instead caused by *M. phaseolina* alone [262,263]. Charcoal root rot and black root rot cause heavy mortality in nurseries and, like other soilborne nursery diseases, reduce survival and the growth of seedlings after outplanting. *Rhizoctonia* blight of pines caused by species of *Rhizoctonia* is of limited economic importance. It occurs sporadically in scattered disease foci that may coalesce over time. Root rot caused by a uninucleate *Rhizoctonia* sp., which was reported as a serious problem on container-grown pine in Finland in the

1990s, has become rare in modern nurseries due to improvements in hygiene and cultivation practices [264]. *Trichothecium roseum* (Pers.) Link has been found on the seeds of several conifer species, especially in the genus *Pinus*. Some researchers consider this fungus to be a saprophyte, while others believe it is an important pathogen of seeds causing decay and reduced viability similar to *F. circinatum* [252].

In general, measures aimed at preventing losses caused by *F. circinatum* in nurseries are effective against most of the aforementioned soil- and seed-borne diseases, since they are favored by the same factors, including high soil pH, high nitrogen levels, high humidity, water saturation of soil, and dense planting. To date, the interactions between *F. circinatum* and other soil- and seed-borne fungal pathogens of pines in nurseries have not been investigated. However, different assays, including some of those fungi involved in damping-off (that are sometimes considered to have an endophytic phase), were performed recently, with the aim of revealing their possible antagonistic effect on *F. circinatum* [265,266].

Foliage diseases can also cause significant damage to pine seedling in nurseries. Many of these are also problematic in the wider forest environment, and have therefore been discussed in detail in Section 2.3 (e.g., DNB or Red band needle blight, brown spot needle blight of pines, *Lophodermium* needle cast). However, certain foliar diseases are predominantly or uniquely problematic in nurseries, for example *Pestalotiopsis* foliage blight (*Pestalotiopsis funerea* (Desm.) Steyaert), *Phoma* blight (*Phoma eupyrena* Sacc.), and *Sirococcus* shoot blight (*Sirococcus conigenus* (Pers.) P.F. Cannon and Minter sensu stricto). *Pestalotiopsis funerea* has also been associated with damping-off, and root and collar rot of seedlings [267]. This fungus may be a primary pathogen or an opportunistic pathogen becoming established in wounds. With few exceptions (e.g., DNB; [268]), serious damage by foliar diseases in pines in nurseries have only occasionally been reported in Europe. Other minor nursery diseases of pine such as grey mold caused by *Botrytis cinerea* Pers. or snow molds seldom cause significant losses and are only locally important. Regardless of the particular pathogen causing foliar damage and defoliation, severe defoliation weakens seedlings [269], and may predispose them to infection by *F. circinatum*.

Fungal pathogens causing canker diseases in nurseries are also pathogens in plantations and forests, and have been described in the section above (Section 2.2). However, special mention is made here of particular pathogens and their interaction with *F. circinatum* in a nursery setting. *Gremmeniella abietina*, the causal agent of *Gremmeniella* canker, is an indigenous fungal pathogen to Europe that comprises a number of races and ecotypes. The European race of the fungus is more aggressive than the North American race and infects all pine species, but it is primarily found on Scots pine in Europe and on Scots and red pine (*P. ponderosa*) in the USA [270]. *Gremmeniella* canker can cause significant mortality of susceptible hosts in the nursery, mainly on *P. halepensis*, and latent infections reduce the survival of seedlings after outplanting [271]. This fungus has been found to be associated with *F. circinatum* in wounds made by bark beetles, suggesting a competition for space and nutrients between these two pathogens, but also a possible synergistic interaction in disease causation [162,163]. *Caliciopsis* canker (causal agent *Caliciopsis pinea*) has been shown to infect native and exotic pine nurseries in Europe and Eastern North America, and is usually associated with overstocked stands and poor soils [154]. In Tuscany (Italy), *C. pinea* is a serious disease of *P. radiata* and other pine species in nurseries, as well as in plantations [154], while in France, it has been described as only a weak pathogen.

In summary, the contamination of a nursery by *F. circinatum* can occur by contaminated material (seeds, soil, seedlings, and trays) or, more rarely, by environmental inoculum carried by wind and/or insect vectors from forest trees or weeds. The impact of *F. circinatum* in nurseries extends beyond the loss of nursery plants. Transplanting asymptomatic seedlings with latent infections increases failures in seedling establishment and the risk of the introduction of this pathogen in non-infested areas [29,47,238]. The symptomatology can be confused with that caused by other pathogens affecting roots, collar, or vascular tissues. Many other pathogens are able to infect seeds and seedlings in forest nurseries, attacking roots or collar (*Diplodia*, *Fusarium*, *Cylindrocarpon*, *Cylindrocladium, Macrophomina*, *Phytophthora*, *Phytopythium*, *Pythium*, *Rhizoctonia*, and *Trichotecium*), stems (*Gremmeniella*, *Caliciopsis*)

or foliage (*Dothistroma*, *Pestalotiopsis*, *Phoma*, *Sirococcus*, and *Botrytis*). The relationship with other pathogens is poorly understood at present. Probably, simultaneous infection of plants by *F. circinatum* and other pathogenic species may exacerbate losses, while possible competition between two or more pathogens deserves further research in order to develop biological control strategies [272].

4. Conclusions

Predictions of the future trajectory and impact of PPC in Europe should not be based solely on knowledge of the climate conditions that are favorable to the disease, but also on a better understanding of factors such as variation in host susceptibility as well as in the microbiota, and the possibility of disease introduction into new areas caused by the use of infected seeds and seedlings. In this review, we compiled a list of the most important pine pathogens in Europe and discussed the possible consequences of their co-occurrence with *F. circinatum*. The likelihood of potential co-occurrence of *F. circinatum* with other pine pathogens was also discussed in light of spatial and host overlaps, colonization niche, and favorable environmental conditions.

Simultaneous infections of the same host-plant by multiple pathogens and the implications of multiple interactions for the susceptibility of the host and disease dynamics have been the subject of an increasing number of studies in recent years. The outcomes of interactions among different pathogens may vary, and include antagonism, competition, synergism, coexistence, mutualism, and cooperation [63,273,274]. In most pathosystems, host–pathogen interactions and the detrimental effects to a plant caused by a single pathogen are well studied; however, pathogen–pathogen and host–multiple-pathogen interactions have been poorly investigated. Current knowledge on the interaction between *F. circinatum* and the host plant in the presence of other pathogens is affected by this general lack of knowledge on multipartite interactions. Thus, the majority of possible outcomes associated with the interaction between *F. circinatum* and other pine pathogens here reported still lack experimental evidence, and thus, have to be regarded mostly as plausible but hypothetical. In most cases, it has been assumed that: (1) simultaneous infection by *F. circinatum* and other fungal pathogens may exacerbate overall disease severity; (2) infections by *F. circinatum* may be detrimental to the defence systems, predisposing the plant to subsequent secondary infections of less virulent or opportunistic pathogens; (3) extant pathogens may directly outcompete *F. circinatum* or reduce the suitability of a host to infection by *F. circinatum*.

Biotrophic pathogens, in particular rusts, may increase disease incidence by *F. circinatum* in two ways. First, necrotic tissue generated when rust fungi infect a host may result in openings and wounds which are more easily infected by *F. circinatum*. Second, the death of plant portions, which occurs when rust fungi infect a host, may attract insects that will mechanically wound the host and favor infections by *F. circinatum*. Attacks by insects and secondary fungi associated with infection by rust fungi are well documented in the literature [275].

Foliar infections may have a similar effect to infection by rust fungi when infection of needles progresses into the twigs and branches, making them more susceptible to infection by *F. circinatum*. This would be the case for several anthracnose and blight fungi [276]. When foliar infections do not progress into the twigs and branches, as in the case of needle casts, the effect of such infections on *F. circinatum* may be similar to infection by root disease fungi. In brief, extensive foliar and root diseases may significantly weaken a host plant. This condition may favor infection by *F. circinatum* at first; however, at a later stage, plants displaying significant symptoms because of extensive foliar and root disease infection may not be ideal transmissive hosts for *F. circinatum*, meaning that infection may be favored, but pathogen sporulation may be rather limited in hosts with rapidly declining health [41].

The relationship of *F. circinatum* with the internal microbiota of seedlings has been poorly described, but some studies have shown that certain fungal endophytes isolated from pines are able to produce an antagonistic effect against *F. circinatum* [266], reducing the severity of *F. circinatum* when applied to seedlings as a preventive measure. Other studies have revealed how the exudates obtained from avirulent strains of a plant pathogen, living as an endophyte, induce systemic resistance against the virulent strain of the same pathogenic species [272]. Thus, the study of this relationship may reveal potential strategies for the biological control of PPC disease. However,

several aspects, such as the application timing in biological control agents, should be taken into account. Amaral et al. [272] demonstrated that *T. viride* preinoculation accelerated disease progression of PPC. They suggested that *T. viride* may subvert the plant defence mechanisms for successful root colonization, which would facilitate *F. circinatum* infestation.

However, independent of the outcome of the interactions between *F. circinatum* and other pine pathogens, the successful eradication, containment, and management of the quarantine pathogen *F. circinatum* necessitate effective methods to rapidly diagnose it, among the many pathogens causing similar symptoms. The development of sensitive, rapid, and robust molecular diagnostic methods is the most effective tool to meet this need [277]. The early and accurate diagnosis of *F. circinatum* would be particularly useful in nurseries, as it would offer the opportunity for the early detection of the pathogen, thus preventing the introduction of PPC and its spread in plantings and forests via asymptomatic infected transplantings. It is worth mentioning that the hygiene and prophylaxis measures applied in nurseries to manage seedling diseases caused by other soil- and seed- borne fungal pathogens are also effective in preventing and reducing the amount of *F. circinatum* inoculums and its spread[278]. Thus, the most efficient and effective measure against PPC is the prevention of its introduction into the nursery system in the first place. Careful screening of seeds ensures their disease-free status, and eliminates one of the most important pathways of disease spread. Eliminating the importation of infested soil and plant trays/containers is also of crucial importance in controlling the spread of PPC. A number of recent reviews have addressed the issues of best practice for sampling for PPC [279], the role of insects in the spread of PPC [43], and environmentally-friendly control methods for the disease [36].

Finally, recent advances in genomics and molecular techniques have led to new insights into the dynamics of complex pathosystems, and hold promise to better understand how pathogens and the microbiome may regulate plant infection [280–282]. So far, however, only a few metagenomic analyses have been performed in relation to PPC [283]. The recognition that plants are colonized by a large number of microorganisms, primarily commensals or mutualists, and the observation that certain diseases might be caused by co-infection of different pathogens have led to the definition of the term "pathobiome", which implies that the pathogen is a component of an integrated and complex biotic environment [284,285]. According to this concept, the microbiome plays a prominent role in host-plant fitness and resilience, and modulates plant–pathogen and pathogen–pathogen interactions. We need to understand all these interactions better to improve the prediction of disease incidence and severity, as well as to develop new sustainable approaches for plant disease management [286–289]. Endophytes and mycorrhizae associated with pine plants deserve more attention, given their potential for disease management as biocontrol agents [290], and to gain better insights into the ecology of *F. circinatum* and the epidemiology of PPC. Finally, a thorough understanding of the epidemiology of PPC will also necessitate more studies on the fungal–insect interface, e.g., the role that insect vectors may play in the spread of the disease [43], or in the induction of host resistance [32,36,291–293].

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, Table S1: Common pathogens causing root and butt rot on pines in European forest stands, Table S2: Common pathogens causing cankers on pines in European forest stands, Table S3: Common pathogens causing leaf damage on pines in European forest stands, Table S4: Common pathogens causing vascular stain on pines in European forest stands, Table S5: Common pathogens causing damages on pines in European nurseries

Author Contributions: Writing: M.E.-R., S.O.-C., A.S.-R., M.G. (Matteo Garbelotto), J.A., A.S., M.M., T.D., F.O., A.G.A.K., E.I., M.C., J.W., M.G. (Margarita Georgieva), I.P.-A., D.C., M.P., D.L.M., A.V.S., E.Y.V., K.A., S.M., N.M., K.D., P.C., B.S., P.G., P.T., J.M-G., C.M.-R., A.L., H.T.D., T.O., J.A.N., H.B., M.F-F., J.H., J.J.D. review: M.E.-R., S.O.-C., A.S-R., M.G. (Matteo Garbelotto), J.A., M.M. editing: M.E.-R, M.G. (Matteo Garbelotto), A.G.A.K, S.O.-C. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by COST Action FP1406 (PINESTRENGTH, Pine pitch canker – strategies for management of *Gibberella circinata* in greenhouses and forests). DLM's contribution was also supported by The Russian Foundation for Basic Research (Grant No. 17-04-01486). AVS's contribution was also supported by the Center for collective use of scientific equipment "Renewable resources, energy sources, new materials and

biotechnology (SPbFTU)" (Project 2019-0420). This study was also supported by the Spanish National project AGL2015-69370-R "Next Generation Sequencing NGS) technologies for the study of *Fusarium circinatum* mycoviruses" (MINECO/FEDER, UE). This work was partially funded by the Forestry Commission, UK and the *Phytophthora* Research Centre, a project funded by the Ministry of Education, Youth and Sports of the Czech Republic and the European Regional Development Fund, Grant No. CZ.02.1.01/0.0/0.0/15_003/0000453. This research was also supported by FEDER through COMPETE (Programa Operacional Fatores de Competitividade) and by National Funds through the Portuguese Foundation for Science and Technology (FCT) within the project URGENTpine (PTDC/AGR-FOR/2768/2014). Thanks are due to CESAM (UID/AMB/50017/2019) for financial support to FCT/MCTES through national funds. FCT also supported J. M.-G. (SFRH/BPD/122928/2016). D.C. and M.P. contribution was also supported by Romanian National projects PN18040105/2018 and PN19070206/2019.

Acknowledgments: Thanks are due to Pablo Martínez-Alvarez, Artur Alves, Alberto Santini, Nicholas McCarthy, Carolina Cornejo, Stanley Freeman, Radoslaw Lewon, Gerda Fourie, and Rodrigo Ahumada for their contribution in the collection of references related to the PPC disease.

Conflicts of Interest: The authors declare no conflict of interest.

Reference

1. Richardson, D.M. *Ecology and Biogeography of Pinus*; Cambridge University Press: Cambridge, UK, 2000; ISBN 9780521789103.
2. Houston Durrant, T.; de Rigo, D.; Caudullo, G. *Pinus Sylvestris in Europe: Distribution, Habitat, Usage and Threats*; European Atlas of Forest Tree Species; San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A., Eds.; Publ. Off. EU: Luxembourg, Luxembourg, 2016; p. e016b94.
3. Mead, D.J. *Sustainable Management of Pinus Radiata Plantations*; FAO Forestry Paper; Food and Agriculture Organization of the United Nations, Rome, Italy; 2013; p. 170.
4. Hermoso, E.; Carballo, J.; Fernandez-Golfin, J.I. Structural characterization of *Pinus radiata* D. Don timber from Pais Vasco (Spain) according to standard modifications. *Tecnologia* **2007**, *9*, 223–232, doi:10.4067/S0718-221 × 2007000300003.
5. Chavarriaga, D.; Bodles, W.J.A.; Leifert, C.; Belbahri, L.; Woodward, S. *Phytophthora cinnamomi* and other fine root pathogens in north temperate pine forests. *FEMS Microbiol. Lett.* **2007**, *276*, 67–74, doi:10.1111/j.1574-6968.2007.00914.x.
6. Garbelotto, M.; Gonthier, P. Biology, epidemiology and control of *Heterobasidio*n species worldwide. *Annu. Rev. Phytopathol*. **2013**, *51*, 39–59, doi:10.1146/annurev-phyto-082712-102225.
7. Drenkhan, R.; Tomešová-Haataja, V.; Fraser, S.; Vahalik, P.; Mullett, M.; Martín-García, J.; Bradshaw, R.E.; Bulman, L.; Wingfield, M.J.; Kirisits, T.; et al. Global geographic distribution and host range of *Dothistroma* species: A comprehensive review. *For. Pathol*. **2016**, *46*, 408–442, doi:10.1111/efp.12290.
8. Hansen, E.M.; Lewis, K.J.; Chastagner, G.A. *Compendium of Conifer Diseases*; American Phytopathological Society: Saint Paul, MN, USA, 2018.
9. Santini, A.; Ghelardini, L.; de Pace, C.; Desprez-Loustau, M.L.; Capretti, P.; Chandelier, A.; Cech, T.; Chira, D.; Diamandis, S.; Gaitniekis, T.; et al. Biogeographic patterns and determinants of invasion by alien forest pathogens in Europe. *New Phytol.* **2013**, *197*, 238–250, doi:10.1111/j.1469-8137.2012.04364.x.
10. Mullett, M.S.; Brown, A.V. Effect of Dothistroma needle blight on needle and shoot lengths. *For. Pathol.* **2018**, *48*, e12382, doi:10.1111/efp.12382.
11. Woodward, S.; Stenlid, J.; Karjalainen, R.; Hüttermann, A. Preface. In *Heterobasidion Annosum: Biology, Ecology, Impact and Control*; Woodward, S., Stenlid, J., Karjalainen, R., Hütterman, A., Eds.; CAB International: Wallingford, UK, 1998.
12. Brasier, C.M. The biosecurity threat to the UK and global environment from international trade in plants. *Plant Pathol*. **2008**, *57*, 792–808, doi:10.1111/j.1365-3059.2008.01886.x.
13. Pérez-Sierra, A.; Landeras, E.; León, M.; Berbegal, M.; García Jiménez, J.; Armengol, J. Characterization of *Fusarium circinatum* from *Pinu*s spp. in northern Spain. *Mycol. Res.* **2007**, *111*, 832–839, doi:10.1016/j.mycres.2007.05.009.
14. Iturritxa, E.; Ganley, R.J.; Wright, J.; Heppe, E.; Steenkamp, E.T.; Gordon, T.R.; Wingfield, M.J. A genetically homogenous population of *Fusarium circinatum* causes pitch canker of *Pinus radiata* in the basque country, Spain. *Fungal Biol.* **2011**, *115*, 288–295, doi:10.1016/j.funbio.2010.12.014.

15. Landeras, E.; García, P.; Fernández, Y.; Braña, M.; Fernández Alonso, O.; Méndez-Lodos, S.; Pérez-Sierra, A.; León, M.; Abad-Campos, P.; Berbegal, M.; et al. Outbreak of pitch canker caused by *Fusarium circinatum* on *Pinus* spp. in northern Spain. *Plant Dis.* **2005**, *89*, 1015, doi:10.1094/PD-89-1015A.
16. EPPO (European and Mediterranean Plant Protection Organisation). Efficacy evaluation of plant protection products. guidance on comparable climates. EPPO standard PP 1/241 (1). *EPPO Bull.* **2005**, *35*, 569–571.
17. Collar Urquijo, J. Informe de la reunion del grupo de trabajo de laboratorios de diagnostico Y prospecciones fitosanitarias. *Almeria* **1995**, *7*, 26-33
18. Laucirica, J.M.; Muguruza, J.R. Presencia de *Fusarium subglutinans* f. sp. *pini* En Viveros De *Pino radiata* En Bizkaia. In Proceedings of the Actas XIV Reunión anualdel Grupo de Trabajo Fitosanitario de Forestales, Parques y Jardines, Spain, 18–20 November 1997; pp. 301–303.
19. Dwinell, L.D.; Adams, D.; Guerra-Santos, J.J.; Aguirre, J.R.M. Pitch canker disease of *Pinus radiata*. In Proceedings of the VII International Congress of Plant Pathology, Edinburgh, Scotland, 9–16 August 1998; pp. 9–16. Available online: http://www.bspp.org.uk/icpp98/3.7/30.html (accessed on 04 Octomber, 2019).
20. Dwinell, D. Global distribution of the pitch canker fungus. Current and potential impacts of pitch canker in Radiata pine. In Proceedings of the IMPACT Monterey Workshop, Monterey, CA, USA, 1999; pp. 54–57.
21. Ridley, G.S.; Dick, M.A. Pine pitch canker disease: The name of the causal fungus and its distribution. *Australas. Plant Pathol.* **2000**, *29*, 263–266.
22. Bragança, H.; Diogo, E.; Moniz, F.; Amaro, P. First report of pitch canker on pines caused by *Fusarium circinatum* in Portugal. *Plant Dis.* **2009**, *93*, 1079.
23. EPPO. *Update of the Situation of Fusarium circinatum in Portugal*; EPPO Reporting Service: Paris, France, 2019; Num. article: 170.
24. Carlucci, A.; Colatruglio, L.; Frisullo, S. First report of pitch canker caused by *Fusarium circinatum* on *Pinus halepensis* and *P. pinea* in Apulia (Southern Italy). *Plant Dis.* **2007**, *91*, 1683.
25. EPPO. First Report of Gibberella Circinata in France, EPPO Reporting Service; EPPO Global Database: Paris, France, 2006; Num. article: 104.
26. Chapin, E.; Chauvel, G. Phytosanitary overview for 2006 of tree plantations, shrubs and clumps in green spaces. *PHM Rev. Hortic.* **2007**, *490*, 40–44.
27. EPPO. *Gibberella Circinata Detected Again in France*, *EPPO Reporting Service*; EPPO Global Database: Paris, France, 2010; Num. article: 034.
28. Gordon, T.R.; Okamoto, D.; Storer, A.J.; Wood, D.L. Susceptibility of five landscape pines to pitch canker disease, caused by *Fusarium subglutinans* f. sp. *pini*. *Hortscience* **1998**, *33*, 868–871.
29. Wingfield, M.J.; Hammerbacher, A.; Ganley, R.J.; Steenkamp, E.T.; Gordon, T.R.; Wingfield, B.D.; Coutinho, T.A. Pitch canker caused by *Fusarium circinatum*—A growing threat to pine plantations and forests worldwide. *Australas. Plant Pathol*. **2008**, *37*, 319–334.
30. Iturritxa, E.; Mesanza, N.; Elvira-Recuenco, M.; Serrano, Y.; Quintana, E.; Raposo, R. Evaluation of genetic resistance in *Pinus* to pitch canker in Spain. *Australas. Plant Pathol.* **2012**, *41*, 601–607.
31. Iturritxa, E.; Ganley, R.J.; Raposo, R.; García-Serna, I.; Mesanza, N.; Kirkpatrick, S.C.; Gordon, T.R. Resistance levels of Spanish conifers against *Fusarium circinatum* and *Diplodia pinea*. *For. Pathol.* **2013**, *43*, 488–495.
32. Martín-García, J.; Paraschiv, M.; Flores-Pacheco, J.A.; Chira, D.; Diea, J.J.; Fernández, M. Susceptibility of several northeastern conifers to *Fusarium circinatum* and strategies for biocontrol. *Forests* **2017**, *8*, 318, doi:10.3390/f8090318.
33. Davydenko, K.; Nowakowska, J.; Kaluski, T.; Gawlak, M.; Sadowska, K.; García, J.; Diez, J.; Okorski, A.; Oszako, T. A comparative study of the pathogenicity of *Fusarium circinatum* and other *Fusarium* species in Polish provenances of *P. sylvestris* L. *Forests* **2018**, *9*, 560.
34. Vivas, M.; Zas, R.; Solla, A. Screening of maritime pine (*Pinus pinaste*r) for resistance to *Fusarium circinatum*, the causal agent of pitch ca nker disease. *Forestry* **2012**, *85*, 185–192.
35. Elvira-Recuenco, M.; Iturritxa, E.; Majada, J.; Alia, R.; Raposo, R. Adaptive potential of maritime pine (*Pinus pinaster*) populations to the emerging pitch canker pathogen, *Fusarium circinatum*. *PLoS ONE* **2014**, *9*, e114971.
36. Martín-García, J.; Zas, R.; Solla, A.; Woodward, S.; Hantula, J.; Vainio, E.J.; Mullett, M.; Morales-Rodríguez, C.; Vannini, A.; Martínez-Álvarez, P.; et al. Environmentally friendly methods for controlling pine pitch canker. *Plant Pathol.* **2019**, *68*, 843–860.

37. Gordon, T.R.; Swett, C.L.; Wingfield, M.J. Management of Fusarium diseases affecting conifers. *Crop Prot*. **2015**, *73*, 28–39.
38. Vettraino, A.M.; Potting, R.; Raposo, R. EU legislation on forest plant health: An overview with a focus on *Fusarium circinatum*. *Forests* **2018**, *9*, 568.
39. EFSA Panel on Plant Health (PLH). Risk assessment of *Gibberella circinata* for the EU territory and identification and evaluation of risk management options. *EFSA J.* **2010**, *8*, 1620.
40. Watt, M.S.; Ganley, R.J.; Kriticos, D.J.; Manning, L.K. Dothistroma needle blight and pitch canker: The current and future potential distribution of two important diseases of *Pinus* species. *Can. J. For. Res*. **2011**, *41*, 412–424, doi:10.1139/X10-204.
41. Garbelotto, M.; Smith, T.; Schweigkofler, W. Variation in rates of spore deposition of *Fusarium circinatum*, the causal agent of pine pitch canker, over a 12-month-period at two locations in Northern California. *Phytopathology* **2008**, *98*,137–143.
42. Dvořák, M.; Janoš, P.; Botella, L.; Rotková, G.; Zas, R. Spore dispersal patterns of *Fusarium circinatum* on an infested Monterey pine forest in North-Western Spain. *Forests* **2017**, *8*, 432.
43. Fernández-Fernández, M.; Naves, P.; Witzell, J.; Musolin, D.L.; Selikhovkin, A.V.; Paraschiv, M.; Chira, D.; Martínez-Álvarez, P.; Martín-García, J.; Muñoz-Adalia, E.J.; et al. Pine pitch canker and insects: Relationships and implications for disease spread in Europe. *Forests* **2019**, *10*, 627, doi:10.3390/f10080627.
44. Möykkynen, T.; Capretti, P.; Pukkala, T. Modelling the potential spread of *Fusarium circinatum*, the causal agent of pitch canker in Europe. *Ann. For. Sci.* **2015**, *72*, 169–181.
45. Christensen, O.B.; Goodess, C.M.; Harris, I.; Watkiss, P. European and global climate change projections: Discussion of climate change model outputs, scenarios and uncertainty in the EC RTD Climate Cost project. In *The Climate Cost Project, Final Report*; Watkiss P., Ed.; Stockholm Environment Institute: Stockholm , Sweden, 2011; Volume 1, ISBN 978-91-86125-35-6.
46. Storer, A.J.; Gordon, T.R.; Clark, S.L. Association of the pitch canker fungus, *Fusarium subglutinans* f. sp. *pini*, with Monterey pine seeds and seedlings in California. *Plant Pathol.* **1998**, *47*, 649–656.
47. Elvira-Recuenco, M.; Iturritxa, E.; Raposo, R. Impact of seed transmission on the infection and development of pitch canker disease in *Pinus radiata*. *Forests* **2015**, *6*, 3353–3368.
48. Viljoen, A.; Wingfield, M.J.; Marasas, W.F.O. First report of *Fusarium subglutinans* f. sp. *pini* on pine seedlings in South Africa. *Plant Dis.* **1994**, *78*, 309–312.
49. Gordon, T.R.; Storer, A.J.; Wood, D.L. The pitch canker epidemic in California. *Plant Dis*. **2001**, *85*, 1128–1139.
50. Bezos, D.; Martìnez-Alvarez, P.; Fernadez, M.; Diez, J.J. Epidemiology and management of Pine pitch canker disease in Europe—A Review. *Balt. For.* **2017**, *23*, 279–293.
51. Garbelotto, M.; Schweigkofler, W.; Shaw, D. First report of *Fusarium circinatum*, causal agent of Pitch canker disease, from the roots of mature Aleppo pines in California. *Plant Health Prog*. **2007**, doi:10.1094/PHP-2007-0219-01-BR.
52. Swett, C.L.; Gordon, T.R. Endophytic association of the pine pathogen *Fusarium circinatum* with corn (Zea mays). *Fungal Ecol*. **2015**, *13*,120–129, doi:10.1016/j.funeco.2014.09.003.
53. Swett, C.L.; Gordon, T.R. First report of grass species (Poaceae) as naturally occurring hosts of the pine pathogen *Gibberella circinata*. *Plant Dis*. **2012**, *96*, 908–908.
54. Martin-Garcia, J.; Lukaćevićovŏ, A.; Pacheco, J.A.; Diez, J.J.; Dvořák, M. Evaluation of the susceptibility of several Czech conifer provenances to *Fusarium circinatum*. *Forests* **2018**, *9*, 72, doi:10.3390/f9020072.
55. Garbelotto, M.; Gonthier, P. Variability and disturbances as key factors in forest pathology and plant health studies. *Forest*s **2017**, *8*, 441, doi:10.3390/f8110441.
56. Arnold, A.E.; Mejia, L.C.; Kyllo, D.; Rojas, E.I.; Maynard, Z.; Robbins, N.; Herre, E.A. Fungal endophytes limit pathogen damage in a tropical tree. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, e15649–e15654.
57. Botella, L.; Santamaría, O.; Diez, J.J. Fungi associated with the decline of *Pinus halepensis* in Spain. *Fungal Divers.* **2010**, *40*, 1–11.
58. Botella, L.; Diez, J.J. Phylogenic diversity of fungal endophytes in Spanish stands of *Pinus halepensis*. *Fungal Divers*. **2011**, *47*, 9–18.
59. Agostinelli, M.; Cleary, M.; Martín, J.A.; Albrectsen, B.; Witzell, J. Pedunculate oaks (*Quercus robur* L.) differing in vitality as reservoirs for fungal biodiversity. *Front. Microbiol.* **2018**, *9*, 758, doi:10.3389/fmicb.2018.01758.

60. Garbelotto, M.; Lowell, N.; Chen, I.; Osmundson, T. Evidence for inhibition of a fungal biocontrol agent by a plant microbiome. *J. Plant Pathol.* **2019**, doi:10.1007/s42161-019-00247-0.
61. Terhonen, E.; Blumenstein, K.; Kovalchuk, A.; Asiegbu, F.O. Forest tree microbiomes and associated fungal endophytes: Functional roles and impact on forest health. *Forests* **2019**, *10*, 42, doi:10.3390/f10010042.
62. Doty, S.L. *Functional Importance of the Plant Endophytic Microbiome*; Springer International Publishing: Cham, Switzerland, 2017; Volume 1, p. 111, ISBN 978-3-319-65897-1.
63. Kozanitas, M.; Osmundson, T.W.; Linzer, R.; Garbelotto, M. Interspecific interactions between the Sudden Oak Death pathogen *Phytophthora ramorum* and two sympatric *Phytophthora* species in varying ecological conditions. *Fungal Ecol.* **2017**, *28*, 86–96.
64. Schweitzer, J.A.; Bailey, B.J.; Fischer, D.G.; LeRoy, J.C.; Lonsdorf, E.V.; Whitham, T.G.; Hart, S.C. Plant–soil–microorganism interactions: Heritable relationship between plant genotype and associated soil microorganisms. *Ecology* **2008**, *89*, 773–781.
65. Cordier, T.; Robin, C.; Capdevielle, X.; Fabreguettes, O.; Desprez-Loustau, M.L.; Vacher, C. The composition of phyllosphere fungal assemblages of European beech (*Fagus sylvatica*) varies significantly along an elevation gradient. *New Phytol.* **2012**, *196*, 510–519.
66. Bálint, M.; Tiffin, P.; Hallström, B.; O'Hara, R.B.; Olson, M.S.; Fankhauser, J.D.; Piepenbring, M.; Schmitt, I. Host genotype shapes the foliar fungal microbiome of Balsam poplar (*Populus balsamifera*). *PLoS ONE* **2013**, *8*, e53987. doi:10.1371/journal.pone.0053987.
67. Knief, C.; Ramette, A.; Frances, L.; Alonso-Blanco, C.; Vorholt, J.A. Site and plant species are improtant determinants of the Methylobacterium community composition in the plant phyllosphere. *ISME J.* **2010**, *4*, 719–728, doi:10.1038/ismej.2010.9.
68. Redford, A.J.; Bowers, R.M.; Knight, R.; Linhart, Y.; Fierer, N. The ecology of the phyllosphere: Geographic and phylogenetic variability in the distribution of bacteria on tree leaves. *Environ. Microbiol.* **2010**, *12*, 2885–2893, doi:10.1111/j.1462-2920.2010.02258.x.
69. Kembel, S.W.; Mueller, R.C. Plant traits and taxonomy drive host associations in tropical phyllosphere fungal communities. *Botany* **2014**, *92*, 303–311, doi:10.1139/cjb-2013-0194.
70. Kembel, S.W.; O'Connor, T.K.; Arnold, H.K.; Hubbell, S.P.; Wright, S.J.; Green, J.L. Relationships between phyllosphere bacterial communities and plant functional traits in a neotropical forest. *PNAS* **2014**, *111*, 13715–13720, doi:10.1073/pnas.1216057111.
71. Desprez-Loustau, M.L.; Aguayo, J.; Dutech, C.; Hayden, K.J.; Husson, C.; Jakushkin, B.; Marçais, B.; Dominique, P.; Robin, C.; Vacher, C. An evolutionary ecology perspective to address forest pathology challenges of today and tomorrow. *Ann. For. Sci.* **2016**, *73*, 45–67.
72. Milanović, S.; Lazarević, J.; Karadžić, D.; Milenković, I.; Jankovský, L.; Vuleta, A.; Solla, A. Belowground infections of the invasive *Phytophthora plurivora* pathogen enhance the suitability of red oak leaves to the generalist herbivore *Lymantria dispar*. *Ecol. Entomol*. **2015**, *40*, 479–482.
73. Moreira, X.; Abdala-Roberts, L.; Castagneyrol, B. Interactions between plant defence signalling pathways: Evidence from bioassays with insect herbivores and plant pathogens. *J. Ecol.* **2018**, *106*, 2353–2364.
74. Lombardero, M.J.; Solla, A.; Ayres, M.P. Pine defences against the pitch canker disease are modulated by a native insect newly associated with the invasive fungus. *For. Ecol. Manag*. **2019**, *437*, 253–262.
75. Corcobado, T.; Miranda-Torres, J.J.; Martín-García, J.; Jung, T.; Solla, A. Early survival of *Quercus ilex* subspecies from different populations after infections and coinfections by multiple *Phytophthora* species. *Plant Pathol*. **2017**, *66*, 792–804.
76. Conrath, U.; Beckers, G.J.; Flors, V.; García-Agustín, P.; Jakab, G.; Mauch, F.; Newman, M.A.; Pieterse, C.M.; Poinssot, B.; Pozo, M.J.; et al. Priming: Getting ready for battle. *Mol. Plant Microbe Interact.* **2006**, *19*, 1062–1071.
77. Santamaria, O.; Botella, L.; Diez, J.J. *Gremmeniella abietina* in North-western Spain: Distribution and associated mycoflora. *Acta Silv. Lignaria Hung. (Spec. Edition)* **2007**, *137*, 145.
78. Barrett, D.K. *Armillaria mellea* as a possible factor predisposing roots to infection by *Polyporus schweinitzii*. *Trans. Br. Mycol. Soc.* **1970**, *55*, 459–462.
79. Biere, A.; Goverse, A. Plant-mediated systemic interactions between pathogens, parasitic nematodes, and herbivores above- and belowground. *Annu. Rev. Phytopathol*. **2016**, *54*, 499–527.
80. Enderle, R.; Sander, F.; Metzler, B. Temporal development of collar necroses and butt rot in association with ash dieback. *iForest* **2017**, *10*, 529–536.

81. Hernandez-Escribano, L.; Iturritxa, E.; Aragonés, A.; Mesanza, N.; Berbegal, M.; Raposo, R.; Elvira-Recuenco, M. Root infection of canker pathogens, *Fusarium circinatum* and *Diplodia sapinea*, in asymptomatic trees in *Pinus radiata* and *Pinus pinaster* plantations. *Forests* **2018**, *9(3)*, 128; doi:10.3390/f9030128.
82. Martín Rodrigues, N.; Sanchez Zabala, J.; Salcedo, I.; Majada, J.; González Murua, C.; Duñabeitia, M.K. New insights into radiata pine seedling root infection by *Fusarium circinatum*. *Plant Pathol*. **2015**, *64*, 1336–1348.
83. Marin-Pinto, P.; Pajares, J.; Díez, J. Pathogenicity of *Fusarium verticillioides* and *Fusarium oxysporum* on *Pinus nigra* seedlings in northwest Spain. *For. Pathol*. **2008**, *38*, 78–82.
84. Romón, P.; Troya, M.; Fernández de Gamarra, M.E.; Eguzkitza, A.; Iturrondobeitia, J.C.; Goldarazena, A. Fungal communities associated with pitch canker disease of *Pinus radiata* caused by *Fusarium circinatum* in northern Spain: Association with insects and pathogen-saprophyte antagonistic interactions. *Can. J. Plant Pathol*. **2008**, *30*, 241–253.
85. Dobreva, M.; Georgieva, M.; Dermedzhiev, P.; Nachev, R.; Velinov, V.; Terziev, P.; Georgiev, G. Fungal pathogens associated with *Pinus* species in the region of forest protection station Plovdiv in the period 2013–2016. *For. Sci.* **2016**, *52*, 103–116. (In Bulgarian with English summary)
86. Hanso, S.; Hanso, M. Spread of *Heterobasidion annosum* in forests of Estonia. *For. Stud*. **1999**, *31*, 162–172. (In Estonian with English summary)
87. Kutorga, E.; Adamonytė, G.; Iršėnaitė, R.; Juzėnas, S.; Kasparavičius, J.; Markovskaja, S.; Motiejūnaitė, J.; Treigienė, A. Wildfire and post-fire management effects on early fungal succession in *Pinus mugo* plantations located in the Curonian Spit (Lithuania). *Geoderma* **2012**, *191*, 70–79.
88. Taut, I.; Simonca, V. Pathogens identified in the forest culture in Transylvania in the 2010 year. *Bull. UASVM Hortic*. **2011**, *68*, 561.
89. Neves, N.; Moniz, F.; De Azevedo, N.; Ferreira, M.C.; Ferreira, G.W.S. Present phytosanitory situation in Portuguese forests. *EPPO Bull*. **1986**, *16*, 505–508.
90. Piri, T.; Korhonen, K.; Sairanen, A. Occurrence of *Heterobasidion annosum* in pure and mixed spruce stands in Finland. *Scand. J. For. Res*. **1990**, *5*, 113–125.
91. Tsopelas, P.; Korhonen, K. Hosts and distribution of the intersterility groups of *Heterobasidion annosum* in the highlands of Greece. *Eur. J. For. Pathol*. **1996**, *26*, 4–11.
92. Chira, D.; Chira, F. Dynamics of wood fungi in wind-fallen stands from Oriental Carpathians. *Ann. For. Res.* **2001**, *44*, 54–59.
93. Gonthier, P.; Garbelotto, M.; Nicolotti, G. Swiss stone pine trees and spruce stumps represent an important habitat for *Heterobasidio*n spp. in subalpine forests. *For. Pathol.* **2003**, *33*, 191–203.
94. Kuz´michev, E.P.; Sokolova, E.S.; Mozolevskaya, E.G. *Diseases and Insect Pests in Forests of Russia. Vol. 1. Diseases of Woody Plants*; VNIILM: Moscow, Russia, 2004. (In Russian)
95. Lygis, V.; Vasiliauskas, R.; Stenlid, J.; Vasiliauskas, A. Silvicultural and pathological evaluation of Scots pine afforestations mixed with deciduous trees to reduce the infections by *Heterobasidion annosum* s. s. *For. Ecol. Manag*. **2004**, *201*, 275–285.
96. Asiegbu, F.O.; Adomas, A.; Stenlid, J. Conifer root and butt rot caused by *Heterobasidion annosum* (Fr.) Bref. s.l. *Mol. Plant Pathol*. **2005**, *6*, 395–409. doi:10.1111/j.1364-3703.2005.00295.x.
97. Bendel, M.; Kienast, F.; Bugmann, H.; Rigling, D. Incidence and distribution of *Heterobasidion* and *Armillaria* and their influence on canopy gap formation in unmanaged mountain pine forests in the Swiss Alps. *Eur. J. For. Pathol*. **2006**, *116*, 85–93.
98. Heydeck, P.; Knoche, D.; Dahms, C.; Rakel, T.; Bieler, T.; Sauermann, J.; Duhr, M. Prophylaktische maßnahmen zur bbwehr des Kiefern-Wurzelschwammes (*H. annosum*) in erstaufforstungen auf kippenstandorten im südlichen Brandenburg. *Eberswalder Forstl. Schr. Band* **2010**, *61*, 74.
99. Szewczyk, W. Damage of selected young Scots Pine plantations by certain biotic factors in Drawsko forest district. *Zarzdzanie Ochron Przyrody w Lasach* **2012**, *6*, 170–176. (In Polish with English summary)
100. Prieto-Recio, C.; Romeralo, C.; Bezos, D.; Martín-García, J.; Martínez-Álvarez, P.; Botella, L.; Diez, J.J. First report of *Heterobasidion annosum* on *Pinus pinaster* in Spain. *Plant Dis*. **2012**, *96*, 770.
101. Doğmuş-Lehtijärvi, H.T.; Erdoğan, R.C.; Lehtijärvi, A.; Woodward, S.; Aday Kaya, A.G. Pathogenicity of *Heterobasidion annosum* (Fr.) Bref. sensu stricto on coniferous tree species in Turkey. *For. Pathol*. **2016**, *46*, 22–28.

102. Sillo, F.; Gonthier, P.; Lockman, B.; Kasuga, T.; Garbelotto, M. Molecular analyses identify hybridization mediated nuclear evolution in newly discovered fungal hybrids. *Ecol. Evol.* **2019**, *9*, 6588–6605. doi:10.1002/ece3.5238.
103. Linzer, R.E.; Otrosina, W.J.; Gonthier, P.; Bruhn, J.; Laflamme, G.; Bussiĕres, G.; Garbelotto, M. Inferences on the phylogeography of the fungal pathogen *Heterobasidion annosum*, including evidence of interspecific horizontal genetic transfer and of human-mediated, long range dispersal. *Mol. Phylogenet. Evol.* **2008**, *46*, 844–862.
104. Dalman, K.; Olson, A.; Stenlid, J. Evolutionary history of the conifer root rot fungus *Heterobasidion annosum* sensu lato. *Mol. Ecol*. **2010**, *19*, 4979–4993.
105. Olson, Å.; Aerts, A.; Asiegbu, F.; Belbahri, L.; Bouzid, O.; Broberg, A.; Canbäck, B.; Coutinho, P.M.; Cullen, D.; Dalman, K.; et al. Trade-off between wood decay and parasitism: Insights from the genome of a fungal forest pathogen. *New Phytol*. **2012**, *194*, 1001–1013.
106. Sillo, F.; Garbelotto, M.; Friedman, M.; Gonthier, P. Comparative genomics of sibling fungal pathogenic taxa identifies adaptive evolution without divergence in pathogenicity genes or genomic structure. *Genome Biol. Evol*. **2015**, *7*, 3190–3206.
107. Zeng, Z.; Sun, H.; Vainio, H.; Raffaello, T.; Kovalchuk, A.; Morin, E.; Duplessis, S.; Asiegbu, F.O. Intraspecific comparative genomics of isolates of the Norway spruce pathogen (*Heterobasidion parviporum*) and identification of its potential virulence factors. *BMC Genom.* **2018**, *19*, 220.
108. Gonthier, P.; Nicolotti, G.; Linzer, R.; Guglielmo, F.; Garbelotto, M. Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. *Mol. Ecol*. **2007**, *16*, 1389–1400.
109. D'Amico, L.; Motta, E.; Annesi, T.; Scire, M.; Luchi, N.; Hantula, J.; Korhonen, K.; Capretti, P. The North American P group of *Heterobasidion annosum* s. l. is widely distributed in *Pinus pinea* forests of the western coast of central Italy. *For. Pathol.* **2007**, *37*, 303–320.
110. Gonthier, P.; Anselmi, N.; Capretti, P.; Bussotti, F.; Feducci, M.; Giordano, L.; Honorati, T.; Lione, G.; Luchi, N.; Michelozzi, M.; et al. An integrated approach to control the introduced forest pathogen *Heterobasidion irregulare* in Europe. *Forestry* **2014**, *87*, 471–481.
111. EPPO. Pest Risk Analysis for *Heterobasidion Irregulare*. EPPO, Paris. 2015. Available online: http://www.eppo.int/QUARANTINE/Pest_Risk_Analysis/PRA_intro.htm (accessed on 11 Octomber, 2019).
112. Martínez-Alvarez, P.; Pando, V.; Diez, J.J. Alternative species to replace Monterey pine plantations affected by pitch canker caused by *Fusarium circinatum* in northern Spain. *Plant Pathol*. **2014**, *63*, 1086–1094.
113. Prieto-Recio, C. Biotic, Abiotic and Management Factors Involved in *Pinus Pinaster* Decline in the Iberian Peninsula. Ph.D. Thesis, Universidad de Valladolid, Valladolid, Spain, 2016.
114. Mesanza, N.; Iturritxa, E. Root and butt rot caused by *Heterobasidion annosum* in Atlantic coniferous ecosystems of Spain. *For. Pathol*. **2012**, *42*, 514–520.
115. Stark, R.W.; Cobb, F.W. Smog injury, root diseases and bark beetle damage in Ponderosa pine. *Calif. Agric.* **1969**, *23*, 13–15.
116. Alexander, S.A.; Skelly, J.M.; Webb, R.S.; Bardinelli, R.R.; Bradford, B. Association of *Heterobasidion annosum* and the southern pine beetle on loblolly pine. *Phytopathology* **1980**, *70*, 510–513.
117. Bonello, P.; Capretti, P.; Luchi, N.; Martini, V.; Michelozzi, M. Systemic effects of *Heterobasidion annosum* s. s. infection on severity of *Diplodia pinea* tip blight and terpenoid metabolism in Italian stone pine (*Pinus pinea*). *Tree Physiol*. **2008**, *28*, 1653–1660.
118. Drenkhan, T.; Voolma, K.; Adamson, K.; Sibul, I.; Drenkhan, R. The large pine weevil *Hylobius abietis* (L.) as a potential vector of the pathogenic fungus *Diplodia sapinea* (Fr.) Fuckel. *Agric. For. Entomol*. **2017**, *19*, 4–9.
119. Linares, J.C.; Camarero, J.J.; Bowker, M.A.; Ochoa, V.; Carreira, J.A. Stand-structural effects on *Heterobasidion abietinum*-related mortality following drought events in *Abies pinsapo*. *Oecologia* **2010**, *164*, 1107–1119.
120. Schmale, III D.G.; Gordon, T.R. Variation in susceptibility to pitch canker disease, caused by *Fusarium circinatum*, in native stands of *Pinus muricata*. *Plant Pathol.* **2003**, *52*, 720–725.
121. Tsopelas, P. Distribution and ecology of *Armillaria* species in Greece. *Eur. J. For. Pathol*. **1999**, *29*, 103–116.

122. Guillaumin, J.J.; Mohammed, C.; Anselmi, N.; Courtecuisse, R.; Gregory, S.C.; Holdenrieder, O.; Intini, M.; Lung, B.; Marxmüller, H.; Morrison, D.; et al. Geographical distribution and ecology of the *Armillaria* species in western Europe. *Eur. J. For. Pathol.* **1993**, *23*, 321–341.
123. Greig, B.J.W.; Gregory, S.C.; Strouts, R.G. Honey fungus. *Forest. Comm. Bull.* **1991**, *100*, 11.
124. Wahlström, K.; Karlsson, J.O.; Holdenrieder, O.; Stenlid, J. Pectinolytic activity and isozymes in European *Armillaria* species. *Can. J. Bot.* **1991**, *69*, 2732–2739.
125. Szewczyk, W.; Macka, M. From the investigations on Armillaria root rot occurrence in young scots pine stands in Zielonka Forest District. *Acta Agrobot.* **2002**, *55*, 319–324. (In Polish with English summary)
126. Bragança, H.; Tenreiro, R.; Santos, N. Identification of portuguese *Armillaria* isolates by classic mating-tests and RFLP-PCR analysis of the ITS1 region of ribosomal DNA. *Silva Lusit.* **2004**, *12*, 67–75.
127. Bagdžiūnaitė, A. Phytopatological monitoring and protection against fungal diseases in young pine *Pinus sylvestris* L. stands in Lithuania. *J. Int. Sci. Publ. Agric. Food* **2013**, *1*, 49–56.
128. Mesanza, N.; Patten, C.L.; Iturritxa, E. Distribution and characterization of *Armillaria* complex in Atlantic forest ecosystems of Spain. *Forests* **2017**, *8*, 1–18.
129. Lehtijärvi, A.; Doğmuş Lehtijärvi, H.T.; Aday, A.G.; Unal, S.; Woodward, S. *Armillaria ostoyae* in managed coniferous forests in Kastamonu in Turkey. *For. Pathol*. **2017**, *47*, doi:10.1111/efp.12397.
130. Korhonen, K. *Intersterility Groups of Heterobasidion Annosum*; Commes Instituti Foralis Fenniae: Helsinki, Finland; 1978; Volume 94, p. 25.
131. Roll-Hansen, F.; Roll-Hansen, H. On Diseases and Pathogens on Forest Trees in Norway 1966–1975; *Communications* of the *Norwegian Forest Research Institute*: Aas, Norway. *1995; Volume 479, p.* 63.
132. Kile, G.A.; McDonald, G.I.; Byler, J.W. Ecology and disease in natural forests. In *Armillaria Root Disease*; Shaw, C.G., Kile, G.A., Eds.; Agricultural Handbook: Washington, DC, USA, 1991; pp. 102–121.
133. Lehtijärvi, A.; Doğmuş Lehtijärvi, H.T.; Aday, A.G. *Armillaria ostoyae* associated with dying 60-year-old Scots pines in northern Turkey. *For. Pathol*. **2012**, *42*, 267–269.
134. Wargo, P.M.; Shaw, C.G. Armillaria root rot: The puzzle is being solved. *Plant Dis*. **1985**, *69*, 826–832.
135. Mallett, K.; Maynard, D. Armillaria root disease, stand characteristics, and soil properties in young lodgepole pine. *For. Ecol. Manag*. **1998**, *105*, 37–44.
136. Solla, A.; Tomlinson, F.; Woodward, S. Penetration of *Picea sitchensis* root bark by *Armillaria mellea*, *Armillaria ostoyae* and *Heterobasidion annosum*. *For. Pathol*. **2002**, *32*, 55–70.
137. Hood, I.A.; Kimberley, M.O. Impact of Armillaria root disease and the effect of thinning in a late-rotation *Pinus radiata* plantation. *For. Pathol*. **2009**, *39*, 415–427.
138. Cleary, M.; van der Kamp, B.J.; Morrison, D.J. Effects of wounding and fungal infection with *Armillaria ostoyae* in three conifer species. II. Host response to the pathogen. *For. Pathol.* **2012**, *42*, 109–123.
139. Guillaumin, J.J.; Legrand, P. Armillaria root rots. In *Infectious Forest Diseases*; Gonthier, P., Nicolotti, G., Eds.; CABI: Wallingford, UK, 2013; pp. 159–177.
140. Abad, G.Z. The taxonomy of *Phytophthora*: What is done and what is needed for the correct identification and diagnostics of species in the genus. In Proceedings of the 7th International Union of Forest Research Organizations, IUFRO Working Party 7-02-09 Meeting, *Phytophthora* in Forests and Natural Ecosystems, Esquel, Argentina, 10–14 November 2014.
141. Ruano-Rosa, D.; Schena, L.; Agosteo, G.E.; Magnano di San Lio, G.; Cacciola, S.O. *Phytophthora oleae* sp. nov., causing fruit rot of olive in southern Italy. *Plant Pathol*. **2018**, *67*, 1362–1373.
142. Brasier, C.M. *Phytophthora Pathogens of Trees: Their Rising Profile in Europe*; Forestry Commission: Stockport, UK, 1999; p. 30.
143. Zhukov, A.M.; Gninenko, Y.I.; Zhukov, P.D. *Dangerous and Poorly Studied Diseases of Coniferous Trees in Forests of Russia*, 2nd ed.; Pushkino: Moscow, Russia, 2013; p. 128. (In Russian)
144. Jung, T.; Pérez-Sierra, A.; Duran, A.; Horta Jung, M.; Balci, Y.; Scanu, B. Canker and decline diseases caused by soil-and airborne *Phytophthora* species in forests and woodlands. *Persoonia* **2018**, *40*, 180–220.
145. Erwin, D.C.; Ribeiro, O.K. *Phytophthora Diseases Worldwide*; APS Press: Saint Paul, MN, USA, 1996; p. 562.
146. Migliorini, D.; Tondini, E.; Luchi, N.; Ghelardini, L.; Capretti, P.; Santini, A. Detection of *Phytophthora* species on different woody species in nurseries. In Proceedings of the 7th International Union of Forest Research Organizations, IUFRO Working Party 7-02-09 Meeting, *Phytophthora* in Forests and Natural Ecosystems, Esquel, Argentina, 10–14 November, 2014.
147. Marçais, B.; Caël, O.; Delatour, C. Interaction between root rot basidiomycetes and *Phytophthora* species on pedunculate oak. *Plant Pathol*. **2011**, *60*, 296–303.

148. Jung, T.; Orlikowski, L.; Henricot, B.; Abad-Campos, P.; Aday Kaya, A.G.; Aguín Casal, O.; Bakonyi, J.; Cacciola, S.O.; Cech, T.; Chavarriaga, D.; et al. Widespread *Phytophthora* infestations in European nurseries put forest,semi-natural and horticultural ecosystems at high risk of Phytophthora diseases. *For. Pathol.* **2016**, doi:10.1111/efp.12239.
149. Jung, T.; Burgess, T.I. Re-evaluation of *Phytophthora citricola* isolates from multiple woody hosts in Europe and North America reveals a new species, *Phytophthora plurivora* sp. nov. *Persoonia* **2009**, *22*, 95–110.
150. Tkaczyk, M.; Sikora, K.; Nowakowska, J.; Aniśko, E.; Oszako, T.; Belbahri, L.; Milenković, I. Four different *Phytophthora* species that are able to infect Scots pine seedlings in laboratory conditions. *Folia For. Pol. Ser.* **2016**, *58*, 123–130.
151. Cleary, M.; Blomquist, M.; Vetukuri, R.R.; Böhlenius, H.; Witzell, J. Susceptibility of common tree species in Sweden to *Phytophthora cambivora*, *P. plurivo*ra and P. *cactorum*. *For. Pathol*. **2017**, *47*, e12329.
152. Schoeneweiss, D.F. Predisposition, stress, and plant disease. *Ann. Rev. Phytopathol*. **1975**, *13*, 193–211.
153. Fabre, B.; Piou, D.; Desprez-Loustau, M.L.; Marcais, B. Can the emergence of pine Diplodia shoot blight in France be explained by changes in pathogen pressure linked to climate change? *Glob. Chang. Biol.* **2011**, *17*, 3218–3227.
154. Capretti, P. Caliciopsis pinea Peck parassita di Pinus pinaster e Pinus insignis. *Phytopathol. Mediterr*. **1978**, *17*, 101–104.
155. Munck, I.A.; Livingston, W.; Lombard, K.; Luther, T.; Ostrofsky, W.D.; Weimer, J.; Wyka, S.; Broders, K. Extent and severity of Caliciopsis canker in New England, USA: An emerging disease of eastern white pine (*Pinus strobus* L.). *Forests* **2015**, *6*, 4360–4373.
156. Vanneste, J.; Hill, R.; Kay, S.; Farrell, R.; Holland, P. Biological control of sapstain fungi with natural products and biological control agents. A review of the work carried out in New Zealand. *Mycol. Res*. **2002**, *106*, 229–232.
157. Gardiner, B.; Berry, P.; Moulia, B. Wind impacts on plant growth, mechanics and damage. *Plant Sci*. **2016**, *245*, 94–118.
158. Varhola, A.; Coops, N.; Weiler, M.; Dan, M.R. Forest canopy effects on snow accumulation and ablation: An integrative review of empirical results. *J. Hydrol.* **2010**, *392*, 219–233.
159. Aglietti, C.; Luchi, N.; Capretti, P. Research about Dieback of *Pinus Radiata* in Tuscany Caused by *Caliciopsis Pinea*. Bachelor's Thesis, University of Florence, School of Agriculture, Florence, Italy, 2014.
160. Iturritxa, E.; Mesanza, N.; Brenning, A. Spatial analysis of the risk of major forest diseases in Monterey pine plantations. *Plant Pathol.* **2015**, *64*, 880–889.
161. Capretti, P.; Migliorini, D.; Diez Casero, J.; Martínez-Álvarez, P.; Luchi, N. Coexistence of *Caliciopsis pinea* and *Fusarium circinatum* on pine: Interactions among fungal pathogens. In Proceedings of the XXIV SIPaV Congress, Ancona, Italy, 5–7 September 2018.
162. Bezos, D.; Martínez-Álvarez, P.; Fernández-Fernández, M.M.; Diez, J.J. Fungi and insect diversity associated with *Pinus radiata* in pitch-canker-affected stands. *Int. For. Rev.* **2014**, *16*, 336.
163. Bezos, D.; Martínez-Álvarez, P.; Diez, J.J.; Fernández, M.M. Association levels between *Pityophthorus pubescens* and *Fusarium circinatum* in pitch canker disease affected plantations in northern Spain. *Entomol. Gen.* **2016**, *36*, 43–54.
164. Luchi, N.; Pepori, A.L.; Aglietti, C.; Migliorini, D.; Santini, A.; Capretti, P. Canker disease on *Pinus radiata* caused by *Caliciopsis pinea* in Italy. *J. Plant Pathol*. **2015**, *97*, 4.
165. Jankovsky, L.; Palovcikova, D. Dieback of Austrian pine—The epidemic occurrence of *Sphaeropsis sapinea* in southern Moravia. *J. For. Sci.* **2003**, *49*, 389–394.
166. Desprez-Loustau, M.L.; Marcais, B.; Nageleisen, L.M.; Piou, D.; Vannini, A. Interactive effect of drought and pathogens in forest trees. *Ann. For. Sci.* **2006**, *63*, 597–612.
167. La Porta, N.; Capretti, P.; Thomsen, I.M.; Kasanen, R.; Hietala, A.M.; VonWeissenberg, K. Forest pathogens with higher damage potential due to climate change in Europe. *Can. J. Plant Pathol.* **2008**, *30*, 177–195.
168. Baker, T.; Candresse, E.S.; Erzsebet Dormannsne, G.; Gilioli, J.; Gregoire, M.J. Risk assessment of *Gibberella circinate* for the EU territory and identification and evaluation of risk management options. *EFSA* **2010**, *8*, 1620.
169. Serra-Varela, M.J.; Alía, R.; Pórtoles, J.; Gonzalo, J.; Soliño, M.; Grivet, D.; Raposo, R. Incorporating exposure to pitch canker disease to support management decisions of *Pinus pin*aster Ait. in the face of climate change. *PLoS ONE* **2017**, *12*, e0171549.

170. Munck, I.A.; Luther, T.; Wyka, S.; Keirstead, D.; McCracken, K.; Ostrofsky, W.; Searles, W.; Lombard, K.; Weimer, J.; Allen, B. Soil and stocking effects on Caliciopsis canker of *Pinus strobus* L. *Forests* **2016**, *7*, 269.
171. Burgess, T.I.; Gordon, T.R.; Wingfield, M.J.; Wingfield, B.D. Geographic isolation of *Diplodia scrobiculata* and its association with native *Pinus radiate*. *Mycol. Res*. **2004**, *108*, 1399–1406.
172. Butin, H. *Tree Diseases and Disorders*; Oxford University Press: New York, NY, USA, 1995; p. 84.
173. Kunca, A.; Leontovy, R. Laboratory experiments with growth potential of *Cenangium ferruginosum* tested on natural nutrition soils. *For. J.* **2013**, *59*, 44–49.
174. Santamaría, O.; Tejerina, L.; Pajares, J.A.; Diez, J.J. Effects of associated fungi *Sclerophoma pythiophila* and *Cenangium ferruginosum* on *Gremmeniella abietina* dieback in Spain. *For. Pathol*. **2007**, *37*, 121–128.
175. OEPP/EPPO. Gremmeniella abietina. *Bull. OEPP/EPPO* **2009**, *39*, 310–317.
176. EPPO. EPPO Global Database Homepage. 2019. Available online: https://gd.eppo.int/taxon/PIURA/pests (accessed on 09 October, 2019).
177. Herron, D.A.; Wingfield, M.J.; Wingfield, B.D.; Rodas, C.A.; Marincowitz, S.; Steenkamp, E.T. Novel taxa in the *Fusarium fujikuroi* species complex from *Pinu*s spp. *Stud. Mycol.* **2015**, *80*, 131–150.
178. Bednářová, M.; Dvořák, M.; Janoušek, J.; Jankovský, L. Other foliar diseases of coniferous trees. In *Infectious Forest Diseases*; Gonthier, P., Nicolotti, G., Eds.; CABI: Wallingford, UK, 2013; pp. 458–487.
179. Kowalski, T. Foliar diseases of broadleaved trees. In *Infectious Forest Diseases*; Gonthier, P., Nicolotti, G., Eds.; CABI: Wallingford, UK, 2013; pp. 488–518, ISBN-978-1-780640402.
180. Hanso, M.; Drenkhan, R. Lophodermium needle cast, insect defoliation and growth responses of young Scots pines in Estonia. *For. Pathol*. **2012**, *42*, 124–135.
181. Tainter, F.H.; Baker, F.A. *Principles of Forest Pathology*; John Wiley and Sons: New York, NY, USA, 1996; ISBN 978-0471129523.
182. Bulman, L.S.; Tubby, K.; Bradshaw, R.E.; Fraser, S.; Martín-García, J.; Musolin, D.L.; Barnes, I.; La Porta, N.; Diez-Casero, J.J.; Koltay, A.; et al. A worldwide perspective on the management and control of Dothistroma needle blight. *For. Pathol*. **2016**, *46*, 472–488.
183. Janoušek, J.; Wingfield, M.J.; Monsivais, J.G.; Jankovský, L.; Stauffer, C.; Konecný, A.; Barnes, I. Genetic analyses suggest separate introductions of the pine pathogen *Lecanosticta acicola* into Europe. *Phytopathology* **2016**, *106*, 1413–1425.
184. Woods, A.J.; Martín-García, J.; Bulman, L.; Vasconcelos, M.W.; Boberg, J.; La Porta, N.; Peredo, H.; Vergara, G.; Ahumada, R.; Brown, A.; et al. Dothistroma needle blight, weather and possible climatic triggers for the disease's recent emergence. *For. Pathol*. **2016**, *46*, 443–452.
185. Cleary, M.; Laas, M.; Oskay, F.; Drenkhan, R. First report of *Lecanosticta acicola* on exotic *Pinus mugo* in southern Sweden. *For. Pathol.* **2019**, *49*, e12507.
186. Mullett, M.; Adamson, S.K.; Bragança, H.; Bulgakov, T.S.; Georgieva, M.; Henriques, J.; Jürisoo, L.; Laas, M.; Drenkhan, R. New country and regional records of the pine needle blight pathogens *Lecanosticta acicola*, *Dothistroma septosporum* and *D. pini*. *For. Pathol.* **2018,** *48*, e12440.
187. Broders, K.D.; Munck, I.; Wyka, S.; Iriarte, G.; Beaudoin, E. Characterization of fungal pathogens associated with white pine needle damage (WPND) in northeastern North America. *Forests* **2015**, *6*, 4088–4104.
188. Hintsteiner, M.; Cech, T.L.; Halmschlager, E.; Stauffer, C.; Kirisits, T. First report of *Mycosphaerella dearnessii* on *Pinus nigra* var. *nigra* in Austria. *For. Pathol.* **2012**, *42*, 437–440.
189. Piou, D.; Ioos, R. First report of *Dothistroma pini*, a recent agent of the Dothistroma needle blight (DNB), on *Pinus radiata* in France. *Plant Dis*. **2014**, *98*, 841.
190. Millberg, H.; Hopkins, A.J.M.; Boberg, J.; Davydenko, K.; Stenlid, J.; Woodward, S. Disease development of Dothistroma needle blight in seedlings of *Pinus sylvestris* and *Pinus contorta* under Nordic conditions. *For. Pathol*. **2016**, *46*, 515–521.
191. Perry, A.; Wachowiak, W.; Brown, A.V.; Ennos, R.A.; Cottrell, J.E.; Cavers, S. Substantial heritable variation for susceptibility to *Dothistroma septosporum* within populations of native British Scots pine (*Pinus sylvestris*). *Plant Pathol.* **2016**, *65*, 987–996.
192. Lazarević, J.; Davydenko, K.; Millberg, H. Dothistroma needle blight on high altitude pine forests in Montenegro. *Balt. For*. **2017**, *23*, 294–302.
193. Mullett, M.S.; Brown, A.V.; Fraser, S.; Baden, R.; Tubby, K.V. Insights into the pathways of spread and potential origins of *Dothistroma septosporum* in Britain. *Fungal Ecol.* **2017**, *26*, 86–98.

194. Piotrowska, M.J.; Riddell, C.; Hoebe, P.N.; Ennos, R.A. Planting exotic relatives has increased the threat posed by *Dothistroma septosporum* to the Caledonian pine populations of Scotland. *Evol. Appl.* **2017**, *11*, 350–363.
195. Adamson, K.; Mullett, M.S.; Solheim, H.; Barnes, I.; Müller, M.M.; Hantula, J.; Vuorinen, M.; Kacergius, A.; Markovskaja, S.; Musolin, D.L.; et al. Looking for relationship between the populations of *Dothistroma septosporum* in northern Europe and Asia. *Fungal Genet. Biol*. **2018**, *110*, 15–25.
196. Ortíz de Urbina, E.; Mesanza, N.; Aragonés, A.; Raposo, R.; Recuenco, M.E.; Boqué, R.; Patten, C.; Aitken, J.; Iturritxa, E. Emerging needle blight diseases in Atlantic *Pinus* ecosystems of Spain. *Forests* **2017**, *8*, 18.
197. Barnes, I.; Crous, P.W.; Wingfield, B.D.; Wingfield, M.J. Multigene phylogenies reveal that red band needle blight of *Pinus* is caused by two distinct species of *Dothistroma*, *D. septosporum* and *D. pini*. *Stud. Mycol.* **2004**, *50*, 551–566.
198. Barnes, I.; Wingfield, M.J.; Carbone, I.; Kirisits, T.; Wingfield, B.D. Population structure and diversity of an invasive pine needle pathogen reflects anthropogenic activity. *Ecol. Evol.* **2014**, *4*, 3642–3661.
199. Kais, A.G. Environmentl factors affecting brown-spot infection on longleaf pines. *Phytopathology* **1975**, *65*, 1389–1392.
200. Evans, H.C. The genus *Mycosphaerella* and its anamorphs *Cercosetoria, Dothistroma* and *Leconosticta* on pinea. *Mycol. Pap.* **1984**, *153*, 102.
201. Kais, A.G. Dispersal of *Schirrhia acicula* spores in southern Mississippi. *Plant Dis. Pap.* **1971**, *55*, 309–311.
202. Jankovsky, L.; Palovcikova, D.; Dvorak, M.; Tomsovsky, M. Records of brown spot needle blight related to *Lecanosticta acicola* in the Czech Republic. *Plant Prot. Sci.* **2009**, *45*, 16–18.
203. Markovskaja, S.; Kaćergius, A.; Treigien, A. Occurrence of new alien pathogenic fungus *Mycosphaerella dearnessii* in Lithuania. *Bot. Lith.* **2011**, *17*, 29–37.
204. Adamson, K.; Drenkhan, R.; Hanso, M. Invasive brown spot needle blight caused by *Lecanosticta acicola* in Estonia. *Scand. J. For. Res.* **2015**, *30*, 587–593.
205. Martinez, J.B. Las micosis del *Pinus insignis* en Guipuzcoa. *Publ. Inst. Investig. Exp.* **1942**, *13*, 23.
206. Wikler, K.; Gordon, T.R. An initial assessment of genetic relationships among populations of *Fusarium circinatum* in different parts of the world. *Can. J. Bot.* **2000**, *78*, 709–717.
207. Berbegal, M.; Pérez-Sierra, A.; Armengol, J.; Grünwald, N.J. Evidence for multiple introductions and clonality in Spanish populations of *Fusarium circinatum*. *Phytopathology* **2013**, *103*, 851–861.
208. Blakeslee, G.M.; Oak, S.W.; Gregory, W.; Moses, C.S. Natural associations of *Fusarium moniliforme* var. *subglutinans* with *Pissodes nemorensis*. *Phytopathology* **1978**, *12*, 208.
209. Barrows-Broaddus, J.; Dwinell, L.D. Variation in susceptibility to the pitch canker fungus among half-sib families of Virginia pine. *Phytopathology* **1984**, *74*, 438–444.
210. Pirttilä, A.M.; Pospiech, H.; Laukkanen, H.; Myllylä, R.; Hohtola, A. Two endophytic fungi in different tissues of Scots pine buds (*Pinus sylvestris* L.). *Microb. Ecol.* **2003**, *45*, 53–62.
211. Terhonen, E.; Marco, T.; Sun, H.; Jalkanen, R.; Kasanen, R.; Vuorinen, M.; Asiegbu, F. The effect of latitude, season and needle-age on the mycota of Scots pine (*Pinus sylvestris*) in Finland. *Silva Fenn.* **2011**, *45*, 301–317.
212. Talgø, V.; Chastagner, G.; Thomsen, I.M.; Cech, T.; Riley, K.; Lange, K.; Klemsdal, S.S.; Stensvand, A. *Sydowia polyspora* associated with current season needle necrosis (CSNN) on true fir (*Abies* spp.). *Fungal Biol.* **2010**, *114*, 545–554.
213. Tinivella, F.; Dani, E.; Minuto, G.; Minuto, A. First Report of *Sydowia polyspora* on Aleppo Pine (*Pinus halepensis*) in Italy. *Plant Dis.* **2014**, *98*, 281.
214. Muñoz-Adalia, E.J.; Sanz-Ros, A.V.; Flores-Pacheco, J.A.; Hantula, J.; Diez, J.J.; Vainio, E.J.; Fernández, M. *Sydowia polyspora* dominates fungal communities carried by two *Tomicus* species in pine plantations threatened by *Fusarium circinatum*. *Forests* **2017**, *8*, 127.
215. Pouzoulet, J.; Pivovaroff, A.L.; Santiago, L.S.; Rolshausen, P.E. Can vessel dimension explain tolerance toward fungal vascular wilt diseases in woody plants? Lessons from Dutch elm disease and esca disease in grapevine. *Front. Plant Sci.* **2014**, *5*, 253.
216. Kirisits, T. Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. In *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis*; Lieutier, F., Day, K.R., Battisti, A., Grégoire, J.-C., Evans, H.F., Eds.; Springer: Dordrecht, The Netherlands, 2004; pp. 181–236.

217. Linnakoski, R. Bark Beetle-Associated Fungi in Fennoscandia with Special Emphasis on Species of *Ophiostoma* and *Grosmannia*. Dissertationes Forestales 119. Ph. D. Thesis, School of Forest Sciences, University of Eastern Finland, Kuopio, Finland, 2011.
218. Martín-Rodrigues, N.; Espinel, S.; Sanchez-Zabala, J.; Ortíz, A.; González-Murua, C.; Duñabeitia, M.K. Spatial and temporal dynamics of the colonization of *Pinus radiata* by *Fusarium circinatum*, of conidiophora development in pith and of traumatic resin duct formation. *New Phytol.* **2013**, *198*, 1215–1227.
219. De Beer, Z.W.; Wingfield, M.J. Emerging lineages in the Ophiostomatales. In *The Ophiostomatoid Fungi: Expanding Frontiers*; Seifert, K.A., de Beer, Z.W., Wingfi eld M.J., Eds.; CBS: Utrecht, The Netherlands, 2013; pp. 21–46.
220. Seifer, K.A. Sapstain of commercial lumber by species of *Ophiostoma* and *Ceratocystis*. In *Ceratocystis and* Ophiostoma. *Taxonomy, Ecology, and Pathogenicity*; Wingfield, M.J., Seifert, K.A., Webber, J.F., Eds.; The American Phytopathological Society: St. Paul, MN, USA, 1993; pp. 141–151.
221. Jankowiak, R. Fungi associated with *Tomicus piniperda* in Poland and assessment of their virulence using Scots pine seedlings. *Ann. For. Sci.* **2006**, *63*, 801–808.
222. Jankowiak, R. Ophiostomatoid fungi associated with *Ips sexdentatus* on *Pinus sylvestris* in Poland. *Dendrobiology* **2012**, *68*, 43–53.
223. Álvarez, G.; Fernández, M.; Diez, J.J. Ophiostomatoid fungi associated with declined *Pinus pinaster* stands in Spain. *For. Syst.* **2015**, *24*, 1–9.
224. Långström, B.; Solheim, H.; Hellqvist, C.; Gref, R. Effects of pruning young Scots pines on host vigour and susceptibility to *Leptographium wingfieldii* and *Ophiostoma minus*, two blue-stain fungi associated with *Tomicus piniperda*. *Eur. J. For. Pathol.* **1993**, *23*, 400–415.
225. Solheim, H.; Langstrom, B.; Hellqvist, C. Pathogenicity of the blue-stain fungi *Leptographium wingfieldii* and *Ophiostoma minus* to Scots pine—Effect of tree pruning and inoculum density. *Can. J. For. Res.* **1993**, *23*, 1438–1443.
226. Solheim, H.; Krokene, P.; Långström, B. Effects of growth and virulence of associated blue-stain fungi on host colonization behaviour of the pine shoot beetles *Tomicus minor* and *T. piniperda*. *Plant Pathol.* **2001**, *50*, 111–116.
227. Davydenko, K.; Vasaitis, R.; Menkis, A. Fungi associated with *Ips acuminatus* (Coleoptera: Curculionidae) in Ukraine with a special emphasis on pathogenicity of ophiostomatoid species. *Eur. J. Entomol.* **2017**, *114*, 77–85, doi:10.14411/eje.2017.011.
228. Jacobs, K.; Wingfield, M.J. *Leptographium Species: Tree Pathogens, Insect Associates, and Agents of Blue-Stain*; American Phytopathological Society: St. Paul, MN, USA,(APS Press): 2001.
229. Dori-Bachash, M.; Avrahami-Moyal, L.; Protasov, A.; Mendel, Z.; Freeman, S. The occurrence and pathogenicity of *Geosmithia* spp. and common blue-stain fungi associated with pine bark beetles in planted forests in Israel. *Eur. J. Plant Pathol*. **2015**, *143*, 627–639.
230. De Beer, Z.W.; Duang, T.A.; Barnes, I.; Wingfield, B.D.; Wingfield, M. Redefining *Ceratocystis* and allied genera. *Stud. Mycol.* **2014**, *79*, 187–219.
231. Romón, P.; De Beer, Z.W.; Fernández, M.; Diez, J.; Wingfield, B.D.; Wingfield, M.J. Ophiostomatoid fungi including two new fungal species associated with pine root-feeding beetles in northern Spain. *Antonie van Leeuwenhoek* **2014**, *106*, 1167–1184.
232. Owen, D.R.; Lindahl, K.Q., Jr.; Wood, D.L.; Parmeter, J.R., Jr. Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. *Phytopathology* **1987**, *77*, 631–636.
233. Solheim, H.; Safranyik, L. Pathogenicity to Sitka spruce of *Ceratocystis rufipenni* and *Leptographium abietinum* blue-stain fungi associated with the spruce beetle. *Can. J. For. Res.* **1997**, *27*, 1336–1341.
234. Wingfield, M.J.; Jacobs, A.; Coutinho, T.A.; Ahumada, R.; Wingfield, B.D. First report of the pitch canker fungus, *Fusarium circinatum*, on pines in Chile. *Plant Pathol.* **2002**, *51*, 397.
235. Alonso, R.; Bettucci, L. First report of the pitch canker fungus *Fusarium circinatum* affecting *Pinus taeda* seedlings in Uruguay. *Australas. Plant Dis. Notes*, **2009**, *4*, 91–92.
236. Steenkamp, E.T.; Rodas, C.A.; Kvas, M.; Wingfield, M.J. *Fusarium circinatum* and pitch canker of *Pinus* in Colombia. *Australas. Plant Pathol.* **2012**, *41*, 483–491.
237. Pfenning, L.H.; da Silva Costa, S.; Pereira de Melo, M.; Costa, H.; Ventura, J.A.; Auer, C.G.; Figueredo dos Santos, A. First report and characterization of *Fusarium circinatum*, the causal agent of pitch canker in Brazil. *Trop. Plant Pathol.* **2014**, *39*, 3.

238. Mitchell, R.G.; Steenkamp, E.T.; Coutinho, T.A.; Wingfield, M.J. The pitch canker fungus, *Fusarium circinatum*: Implications for South African forestry. *South. For.* **2011**, *73*, 1–13.
239. Hurley, B.; Govender, P.; Coutinho, T.A.; Wingfield, B.; Wingfield, M.J. Fungus gnats and other Diptera in South African forestry nurseries and their possible association with the pitch canker fungus. *S. Afr. J. Sci*. **2007**, *103*, 43–46.
240. Swett, C.L.; Porter, B.; Fourie, G.; Steenkamp, E.; Gordon, T.R.; Wingfield, M.J. Association of the pitch canker pathogen *Fusarium circinatum* with grass hosts in commercial pine production areas of South Africa. *South. For. J. For. Sci.* **2014**, *76*, 1–6.
241. EPPO. Gibberella circinata. *EPPO Bull*. **2009**, *93*, 298–309.
242. Landis, T.D.; Smith, R.S., Jr.; Toko, H.V.; *Tech. Coords. Forest Nursery Pests. Agriculture Handbook 680*; USDA Forest Service: Washington, DC, USA, 2012; pp.14–15.
243. Ocamb, C.M.; Juzwik, J.; Martin, F.B. *Fusarium* spp. and *Pinus strobus* seedlings: Root disease pathogens and taxa associated with seed. *New For.* **2002**, *24*, 67–79.
244. Salerno, M.I.; Lori, G.A. Association of seed-borne *Fusarium* species on *Pinus ponderosa* with germination and seedling viability in Argentina. *For. Pathol.* **2007**, *37*, 263–271.
245. James, R.L. Fusarium root and stem diseases, In *Forest Nursery Pests*; Cram, M.M., Frank, M.S., Mallams, K.M., Eds.; Technical Coordinators; United States Department of Agriculture Forest Service: Colville, WA, USA, 2012; Handbook No. 680, pp. 117–120. Available online: http://www.rngr.net (accessed on 1 Octomber, 2019).
246. González-Penalta, B.; Pintos-Varela, C.; Mansilla, J.P.; Aguín, O.; Pérez, R. Presencia de especies de *Fusarium* sobre semillas de *Pinu*s spp. en Galicia. *Sociedad Española de Ciencias Forestales* **2008**, *26*, 149–154.
247. Stewart, J.E.; Kim, M.S.; James, R.L.; Dumroese, R.K.; Klopfenstein, N.B. Molecular characterization of *Fusarium oxysporum* and *Fusarium commune* isolates from a conifer nursery. *Phytopathology* **2006**, *96*, 1124–1233.
248. James, R.L. Cylindrocarpon root disease. In *Forest Nursery Pests*; Cram, M.M., Frank, M.S., Mallams, K.M., Eds.; United States Department of Agriculture Forest Service: Colville, WA, USA, 2012; Handbook No. 680, pp. 31–32. Available online: http://www.rngr.net (accessed on 3 Octomber, 2019).
249. Lombard, L.; Crous, P.W.; Wingfield, B.D.; Wingfield, M.J. Phylogeny and systematics of the genus Calonectria. *Stud. Mycol*. **2010**, *66*, 31–69.
250. Phillips, A.J.L.; Alves, A.; Abdollahzadeh, J.; Slippers, B.; Wingfield, M.J.; Groenewald, J.Z.; Crous, P. The Botryosphaeriaceae: Genera and species known from culture. *Stud. Mycol.* **2013**, *76*, 51–167.
251. Santamaría, O.; Smith, D.R.; Stanosz, G.R. Interaction between *Diplodia pinea* and *D. scrobiculata* in Red and Jack pine seedlings. *Phytopathology* **2011**, *101*, 334–339.
252. Cram, M.M.; Fraedrich, S.W. Seed diseases and seedborne pathogens of north America. *Tree Plant. Notes* **2009**, *53*, 35–44.
253. Smith, D.R.; Stanosz, G.R. A species-specific PCR assay for detection of *Diplodia pinea* and *D. scrobiculata* in dead red and jack pines with collar rot symptoms. *Plant Dis.* **2006**, *90*, 307–313.
254. Sánchez, M.E.; Andicoberry, S.; Trapero, A. Phytophthora root rot of Aleppo pine seedlings in a forest nursery in Spain. *Plant Dis.* **2002**, *86*, 563.
255. Lehtijärvi, A.; Aday Kaya, A.G.; Woodward, S.; Jung, T.; Doğmuş Lehtijärvi, H.T.; Oomycota species associated with deciduous and coniferous seedlings in forest tree nurseries of Western Turkey. *For. Pathol.* **2017**, *47*, e12363.
256. Durán, A.; Gryzenhout, M.; Slippers, B.; Ahumada, R.; Rotella, A.; Flores, F.; Wingfield, B.D.; Wingfield, M.J. *Phytophthora pinifolia* sp. nov. associated with a serious needle disease of *Pinus radiata* in Chile. *Plant Pathol.* **2008**, *57*, 715–727.
257. Schwingle, B.W.; Smith, J.A.; Blanchette, R.A. *Phytophthora* species associated with diseased woody ornamentals in Minnesota nurseries. *Plant Dis.* **2007**, *91*, 97–102.
258. Moralejo, E.; Pérez-Sierra, A.M.; Álvarez, L.A.; Belbahri, L.; Lefort, F.; Descals, E. Multiple alien *Phytophthora* taxa discovered on diseased ornamental plants in Spain. *Plant Pathol.* **2009**, *58*, 100–110.
259. Bienapfl, J.C.; Balci, Y. Movement of *Phytophthora* spp. in Maryland's Nursery Trade. *Plant Dis.* **2014**, *98*, 134–144.
260. Prigigallo, M.I.; Mosca, S.; Cacciola, S.O.; Cooke, D.E.L.; Schena, L. Molecular analysis of *Phytophthora* diversity in nursery-grown ornamental and fruit plants. *Plant Pathol.* **2015**, *64*, 1308–1319.

261. Sims, L.; Tjosvold, S.; Chambers, D.; Garbelotto, M. Control of *Phytophthora* species in plant stock for habitat restoration through best management practices. *Plant Pathol.* **2018**, *68*, 196–204.
262. Reuveni, R.; Madar, Z. The role of *Macrophomina phaseolina* in mortality of pine seedlings in forest nurseries. *J. Phytopathol.* **1985**, *112*, 161–164.
263. Cordell, C.E.; Anderson, R.L.; Hoffard, W.H.; Landis, T.D.; Smith, R.S.; Toko, H.V., Jr. Charcoal root rot and black root rot. In *Forest Nursery Pests*; U. S. Department of Agriculture, Forest Service: Colville, WA, USA, 1989; Agriculture Handbook No. 680.
264. Lilja, A.; Poteri, M.; Petäistö, R.L.; Rikala, R.; Kurkela, T.; Kasanen, R. Fungal diseases in forest nurseries in Finland. *Silva Fenn.* **2010**, *44*, 525–545.
265. Martínez-Álvarez, P.; Alves-Santos, F.M.; Diez, J.J. In vitro and in vivo interactions between *Trichoderma viride* and *Fusarium circinatum*. *Silva Fenn.* **2012**, *46*, 303–316.
266. Martínez-Álvarez, P.; Fernández-González, R.A.; Sanz-Ros, A.V.; Pando, V.; Diez, J.J. Two fungal endophytes reduce the severity of pitch canker disease in *Pinus radiata* seedlings. *Biol. Control* **2016**, *94*, 1–10.
267. Enebak, S.A. Pestalotiopsis Foliage Blight, In *Forest Nursery Pe*sts; Cram, M.M., Frank, M.S., Mallams, K.M., Eds.; United States Department of Agriculture Forest Service: Colville, WA, USA, 2012; Handbook No. 680, pp. 52–53.
268. Brown, A.; Webber, J. *Red Band Needle Blight of Conifers in Britain*; Forestry Commission: Edinburgh, UK, 2008; pp. 1–8.
269. Cram, M.M.; Frank, M.S.; Mallams, K.M. *Forest Nursery Pests*; Cram, M.M., Frank, M.S., Mallams, K.M., Eds.; United States Department of Agriculture Forest Service: Colville, WA, USA, 2012; Handbook 680, pp. 5–12.
270. Ostry, M.E.; Juzwik, J. Selected Forest and Shade Tree Diseases of Significance in the 20th Century. *APSnet Features* **2008**, 1–12, doi:10.1094/APSnetFeatures-2008-0508.
271. Santamaria, O.; Pando, V.; Diez, J.J. Susceptibility of six pine species to *Gremmeniella abietina* isolates from Spain. *For. Pathol.* **2006**, *36*, 349–359.
272. Amaral, J.; Pinto, G.; Flores-Pacheco, J.A.; Díez-Casero, J.J.; Cerqueira, A.; Monteiro, P.; Gómez-Cadenas, A.; Alves, A.; Martín-García, J. Effect of *Trichoderma viride* pre-inoculation in pine species with different levels of susceptibility to *Fusarium circinatum*: Physiological and hormonal responses. *Plant Pathol*. **2019**, doi:10.1111/ppa.13080.
273. Susi, H.; Barres, B.; Vale, P.F.; Laine, A.L. Co-infection alters population dynamics of infectious disease. *Nat. Commun.* **2015**, *6*, 1–8.
274. Abdullah, A.S.; Moffat, C.S.; Lopez-Ruiz, F.J.; Gibberd, M.R.; Hamblin, J.; Zerihun, A. Host-multi-pathogen warfare: Pathogen interactions in co-infected plants. *Front. Plant Sci.* **2017**, *8*, 1806.
275. Hatcher, P.E. Three-way interactions between plant pathogenic fungi, herbivorous insects and their host plants. *Biol. Rev.* **1995**, *70*, 639–694.
276. Childs, T.W. *Elytroderma Disease of Ponderosa Pine*; Department of Agriculture, Forest Service: Colville, WA, USA, 1971; p. 42.
277. Ioos, R.; Aloi, F.; Piškur, B.; Guinet, C.; Mullett, M.; Berbegal, M.; Bragança, H.; Cacciola, S.O.; Oskay, F.; Cornejo, C.; et al. Transferability of PCR-based diagnostic protocols: An international collaborative case study assessing protocols targeting the quarantine pine pathogen *Fusarium circinatum*. *Sci. Rep.* **2019**, *9*, 8195, doi:10.1038/s41598-019-44672-8.
278. Cleary, M.; Oskay, F.; Doğmuş-Lehtijärvi, T.; Lehtijarvi, A.; Woodward, S.; Vettraino, A.M. Cryptic risks to forest biosecurity associated with the global movement of commercial seed. *Forests* **2019**, *10*, 459.
279. Vainio, E.J.; Bezos, D.; Bragança, H.; Cleary, M.; Fourie, G.; Georgieva, M.; Ghelardini, L.; Hannunen, S.; Ioos, R.; Martín-García, J.; et al. Sampling and Detection Strategies for the Pine Pitch Canker (PPC) Disease Pathogen Fusarium circinatum in Europe. *Forests* **2019**, *10*, 723.
280. Zeilinger; S.; Gupta, V.K.; Dahms, T.E.S.; Silva, R.N.; Singh, H.S.; Upadhyay, R.S.; Vieira Gomes, E.; Kin-Ming Tsui, C.; Nayak, C. Friends or foes? Emerging insights from fungal interactions with plants. *FEMS Microbiol. Rev.* **2015**, *40*, 182–207.
281. Abdelfattah, A.; Wisniewski, M.; Li Destri Nicosia, M.G.; Cacciola, S.O.; Schena, L. Metagenomic analysis of fungal diversity on strawberry plants and the effect of management practices on the fungal community structure of aerial organs. *PLoS ONE* **2016**, *11*, e0160470.

282. Feau, N.; Hamelin, R.C. Say hello to my little friends: How microbiota can modulate tree health. *New Phytol.* **2017**, *215*, 508–510.
283. Reis-Gonçalves, D.; Romeralo, C.; Martinez-Álvarez, G.; Martín-García, J.; Muñoz, J.; Diez, J.J. Next Generation Sequencing (NGS) and Quantitative PCR (qPCR) as Tools to Detect *Fusarium Circinatum* in Different Pine Species. Master's Thesis, University of Valladolid, Valladolid, Spain, 2018.
284. Brader, G.; Compant, S.; Vescio, K.; Mitter, B.; Trognitz, F.; Ma, L.J.; Sessitsch, A. Ecology and genomic insights into plant-pathogenic and plant-nonpathogenic endophytes. *Ann. Rev. Phytopathol.* **2017**, *55*, 61–83.
285. Bonfante, P.; Anca, I.A. Plants, mycorrhizal fungi, and bacteria: A network of interactions. *Annu. Rev. Microbiol*. **2009**, *63*, 863–883.
286. Berendsen, R.L.; Pieterse, C.M.J.; Bakker, P.A.H.M. The rhizosphere microbiome and plant health. *Trends Plant Sci.* **2012**, *17*, 478–486.
287. Abdelfattah, A.; Malacrinò, A.; Wisniewski, M.; Cacciola, S.O.; Schena, L. Metabarcoding: A powerful tool to investigate microbial communities and shape future plant protection strategies. *Biol. Control* **2018**, *120*, 1–10.
288. Mercado-Blanco, J.; Abrantes, I.; Barra Caracciolo, A.; Bevivino, A.; Ciancio, A.; Grenni, P.; Hrynkiewicz, K.; Kredics, L.; Proença, D.N. Belowground microbiota and the health of tree groops. *Front. Microbiol*. **2018**, *9*, 1006.
289. Aimé, S.; Alabouvette, C.; Steinberg, C.; Olivain, C. The endophytic strain *Fusarium oxysporum* Fo47: A good candidate for priming the defence responses in tomato roots. *Mol. Plant Microbe Interact* **2013**, *26*, 918–926.
290. Bonello, P.; Gordon, T.R.; Storer, A.J. Systemic induced resistance in Monterey pine. *For. Pathol.* **2001**, *31*, 99–106.
291. Gordon, T.R.; Kirkpatrick, S.C.; Aegerter, B.J.; Fisher, A.J.; Storer, A.J.; Wood, D.L. Evidence for the occurrence of induced resistance to pitch canker, caused by *Gibberella circinata* (anamorph *Fusarium circinatum*), in populations of *Pinus radiata*. *For. Pathol*. **2011**, *41*, 227–232.
292. Moret, A.; Munoz, Z. Control of *Diplodia pinea* and *D. scrobiculata* in *Pinus halepensis* by 5-chloro-salicylic acid. *Phytopathol. Mediterr*. **2007**, *46*, 150–156.
293. Aleandri, M.P.; Chilosi, G.; Bruni, N.; Tomassini, A.; Vettraino, A.M.; Vannini, A. Use of nursery potting mixes amended with local *Trichoderma* strains with multiple complementary mechanisms to control soil-borne disease. *Crop Prot.* **2015**, *67*, 269–278.