



Climatic Correlates of White Pine Blister Rust Infection in Whitebark Pine in the Greater Yellowstone Ecosystem

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Review

Pine Pitch Canker and Insects: Regional Risks, Environmental Regulation, and Practical Management Options

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Abstract: Pine pitch canker (PPC), caused by the pathogenic fungus *Fusarium circinatum* (Nirenberg and O’ Donnell), is a serious threat to pine forests globally. The recent introduction of the pathogen

to Southern Europe and its spread in Mediterranean region is alarming considering the immense ecological and economic importance of pines in the region. Pines in forests and nurseries can be infected, resulting in severe growth losses and mortality. The pathogen is known to spread in plants for planting and in seeds, and results from recent studies have indicated that *F. circinatum* may also spread through phoretic associations with certain insects. With this review, we aim to expand the current understanding of the risk of insect-mediated spread of PPC in different parts of Europe. Through the joint action of a multinational researcher team, we collate the existing information about the insect species spectrum in different biogeographic conditions and scrutinize the potential of these insects to transmit *F. circinatum* spores in forests and nurseries. We also discuss the impact of environmental factors and forest management in this context. We present evidence for the existence of a high diversity of insects with potential to weaken pines and disseminate PPC in Europe, including several common beetle species. In many parts of Europe, temperatures are projected to rise, which may promote the activity of several insect species, supporting multivoltinism and thus, further amplifying the risk of insect-mediated dissemination of PPC. Integrated pest management (IPM) solutions that comply with forest management practices need to be developed to reduce this risk. We recommend careful monitoring of insect populations as the basis for successful IPM. Improved understanding of environmental control of the interaction between insects, the pathogen, and host trees is needed in order to support development of bio-rational strategies to safeguard European pine trees and forests against *F. circinatum* in future.

Keywords: pine pitch canker; vectors; carriers; wounding agents; agro-climatic risk zones of the European and Mediterranean Plant Protection Organization; environmental factors; management; control; legislation compliance

1. Introduction

Pine pitch canker (PPC), caused by the ascomycete fungus *Fusarium circinatum* (Nirenberg and O'Donnell), is a severe disease of *Pinus* spp. and *Pseudotsuga menziesii* (Mirb.) Franco [1]. The disease, which can lead to severe damage and even mortality of seeds, seedlings, and large trees, was recently introduced into Europe, where its currently known distribution is limited to the Mediterranean and Southern Europe (Spain, Portugal, France, and Italy [2]).

Multiple factors determine the risk of further spread of *F. circinatum* in Europe, namely the presence of susceptible conifer hosts, climatic conditions, and diverse human-mediated activities (e.g., attempts to adapt to climate change by northward transfer of southern provenances or unintentional spreading from nurseries). In addition, phoretic associations between *F. circinatum* and some insect species have been demonstrated and other insects may create infection courts by wounding the trees [3–5], indicating that insects may significantly contribute to the spread of the pathogen. In this group of potential spore-transmitting insects are included the vectors that carry the pathogen (visiting susceptible plant hosts and capable of successfully transmitting the pathogen to plants not yet infected); the carriers (carrying inoculum from diseased plants which they visited before or on which they have developed); and the wounding insects (facilitating the pathogen to enter the host plant via damages caused by the feeding on shoots, twigs, and cones or due to their entrance holes in the bark and maternal galleries in the phloem). Möykkynen et al. [6] developed a model simulating the spread of *F. circinatum* in Europe, suggesting that the fungus is likely to disseminate to pine forests in Northern Spain and Southwest France, close to the existing affected areas. Although the authors considered the possible flight distance of the insects in the model, they did not discriminate between insect species or consider their European distribution ranges.

The presence or absence of possible vectors of *F. circinatum* and their local abundance has not been investigated in detail in earlier studies. Yet, because insects are likely to play a significant role in the spreading of PPC, these aspects should be included in assessments of the risks of PPC in Europe. Several potential insect vectors, such as pine shoot beetles (*Tomicus* spp.) and twig beetles (*Pityophthorus* spp.), are widespread and abundant in pine forests throughout Europe. There are, however, variations in the prevailing forest insect species between the different European biogeographic regions, which can shape the potential risk of *F. circinatum* establishment, dispersal, and impact. The activity of insects is strongly and directly affected by abiotic conditions, such as the temperature and humidity regimes, which may also influence the ability of the trees to resist insect attacks (e.g., drought stress may increase the vulnerability of trees to insect damage). An additional factor influencing not only the insects' environment (e.g., the age structure and species composition of the forests), but also the possibilities to control their populations through different interventions, is the forest management approach (FMA) that is practiced in the area [7]. The prevailing FMAs are largely dependent of, and differ across, the biogeographic regions, setting the practical and regulative frameworks for the different interventions to control the insects [8,9]. For instance, in areas dedicated to nature conservation, interventions are restricted; whereas in areas dominated by intensive management, a broader spectrum of control methods is applicable. Thus, the biogeographic regions and FMAs create a complex framework for the activity of the potential vector insects and for their management, shaping the risk of PPC spread in Europe. This framework should be considered when optimizing bio-rational control strategies against vector insects.

The goal of this review is to expand our understanding of the risk of PPC spread in different parts of Europe, considering the activity of potential vector insects (*sensu lato*) across the different biogeographic conditions and forest management approaches, and exploring the possibilities to control the vector insects through different pest management options. Specifically, we compiled information about the predominant forest insect pests (including those typical for plantations and nurseries), gathering information also from "grey literature" (e.g., publications in native languages, academic thesis, reports, working papers, and government documents). Data collection was made separately for European biogeographic regions, using the agro-climatic classification suggested by Bouma [10], which divides the European and Mediterranean Plant Protection Organization (EPPO) region into four prevailing agro-climatic zones (Mediterranean, Maritime, North-East, and Central), while comparing the dominant climate conditions which affect pest/host interrelationships. We then summarize the regulative effects of abiotic environment on the three partners of the interaction (insects, pathogen, and host trees), and discuss the practical possibilities for sustainable management of vector insects across different forest management regimes, using a classification of forest management approaches by Duncker et al. [8] and Hengeveld et al. [9] as a guideline.

2. Potential Spore-Transmitting Insects in the Biogeographic Regions

2.1. Mediterranean Agro-Climatic Zone

The Mediterranean zone comprises the countries (or parts of countries) around the Mediterranean Sea, together with The Republic of North Macedonia and Portugal. This region is characterized by its mild and relatively wet winters, and warm and dry summers [10]. This is one of the world's recognized "hotspots" of biodiversity and a major center of plant diversity, as approximately 10% of the world's higher plants can be found in this area, representing only 1.6% of the Earth's surface [11].

The Mediterranean basin is particularly vulnerable to the expansion of PPC, due to favorable climatic conditions, presence of various conifer hosts, and high diversity and abundance of possible insect vectors. Of the ca. 350 species of bark beetles (Coleoptera: Curculionidae) known to occur in Western Europe [12], 42 species live only or mainly on Mediterranean conifers, and are mostly associated with pines [13]. Although some species are endemic and have restricted distribution, others are found in several countries or in the entire Mediterranean basin, including primary forest pests such as pine shoot beetles (Coleoptera: Curculionidae) of the genus *Tomicus*, which are known plausible vectors of *F. circinatum* [14]. *Tomicus destruens* (Wollaston, 1865) is the most thermophilic species of its genus [15] and it thrives in coastal areas of circum-Mediterranean countries [16], causing pine mortality from Portugal in the west [17,18] to Lebanon in the east [19]. A sister species, *Tomicus piniperda* (Linnaeus, 1758), is abundant and widespread in Southern Europe, frequently infesting pine stands in several countries [20,21], and also considered a major pest. This species attacks shoots when callow adults emerge and flies to nearby tree crowns for maturation feeding. Through this feeding on current year shoots, *T. piniperda* can effectively transfer *F. circinatum* into living tissues of pines, which makes this insect particularly dangerous as a vector of *F. circinatum* and results in a high risk for the establishment of the disease wherever *Tomicus* beetles are present [14].

A high risk is also associated with twig beetles (*Pityophthorus* spp.) (Coleoptera: Curculionidae), a large group of similar species with analogous ecological characteristics. Considered secondary forest pests with negligible economic impacts [22,23], more than 20 species and sub-species of twig beetles occur in Europe, widely spread in the Mediterranean basin and mainly associated with conifers [24]. In Spain, *Pityophthorus pubescens* (Marshall, 1802) is known to be associated with *F. circinatum* [2,25,26], and therefore it can be assumed that other congeneric species may similarly act as vectors of the fungus elsewhere in Europe. Exotic twig beetles have successfully established in Europe, e.g., *Pityophthorus juglandis* Blackman, 1928 in Italy [27] and *Pityophthorus solus* (Blackman, 1928) collected at a *Pinus radiata* D. Don sawmill in Northern Spain [28], which constitutes an additional risk for novel alien's species associations with *F. circinatum* in Europe. Europe's Mediterranean zone is rich in alien bark beetles [29], which could potentially vector *F. circinatum*; one example being *Hypothenemus eruditus* Westwood, 1936 found in Northern Spain [30].

Other noteworthy bark beetles in the Mediterranean zone are *Ips* and *Orthotomicus* species, many of which have been associated with high pine mortality or reduced forest health following drought episodes or forest fires [13]. Species associated with pine mortality include *Ips sexdentatus* (Börner, 1776) [31–35], *Ips acuminatus* (Gyllenhal, 1827) [36], and *Orthotomicus erosus* (Wollaston, 1857) [37,38]. Areas prone to repeated forest fires are at particularly high risk for the dissemination of *F. circinatum*, with the scorched and burned trees attracting pyrophilous ("fire loving") bark and wood boring beetles, which can locally reach high population levels (e.g., [31,32,37,39]).

Cone-associated insects are ecologically and economically important in the Mediterranean region, with species such as *Pissodes validirostris* (C.R. Sahlberg, 1834) (Coleoptera: Curculionidae), *Dioryctria mendacella* (Staudinger, 1859) (Lepidoptera: Pyralidae), and *Leptoglossus occidentalis* Heidemann, 1910 (Hemiptera: Coreidae) considered primary pests of cones and edible seeds of *Pinus pinea* Linnaeus and other pines [40,41]. These three species are widespread and abundant in southern Europe. Originally North American, *L. occidentalis* is of particular interest, as it has demonstrated enormous ecological adaptability by establishing on available habitats across the entire European continent within a decade [42–44] after its original detection in Italy in 1999 [45,46]. In most countries, rapid spread and increasing population density were observed shortly after detection. Although this heteropteran demonstrates high reproductive and dispersal capabilities and is able of flying long distances, it also benefits from human-mediated translocation on conifer hosts with eggs, nymphs, and adults on them [47]. The feeding activity of adults and nymphs causes the abortion and infertility of seeds [48–50], leading to significant economic impacts for forestry, which are particularly important for *Pinus pinea* cone production in the Mediterranean area. Since the introduction of *L. occidentalis*, the production of the later pine nuts has decreased sharply in Italy and in other European countries [51].

The presence of insects has been suggested as one of the causes of the massive conelet abortion before ripening (known as the “dry cone syndrome”), observed with increasing frequency in southern Europe [52]. Furthermore, in Europe, *L. occidentalis* is associated with the native fungus *Diplodia pinea* (Desm.), a pathogen that also affects seed and cone production [53,54]. Overall, this widespread and damaging insect may contribute to the spreading of *F. circinatum* through its feeding activity (which may provide gates of infection for the pathogen). Its association with multiple conifers (mainly pines, but also species of genera *Abies*, *Calocedrus*, *Cedrus*, *Cupressus*, *Juniperus*, *Picea*, *Pseudotsuga*, and *Tsuga* [49]), and its enormous adaptability and ecological plasticity, result in an extremely well-succeeded exotic pest affecting Europe’s conifer forests.

Another about 20 insect species are associated with cones of pines in the Mediterranean basin, including members of the families Anobiidae (Coleoptera), Cecidomyiidae (Diptera), Pentatomidae (Hemiptera), Olethreutidae, Pyralidae, and Tortricidae (Lepidoptera) [40,55]. The role of these species in spreading of *F. circinatum* is unknown, but their feeding habits, polyphagy within pines and other conifers, abundance, and widespread distribution imply risks, which need to be evaluated.

Insects associated with nurseries and young pine plantations need to be considered for their risk. In the Mediterranean zone, special attention should be given to *Pissodes castaneus* (De Geer, 1775) (Coleoptera: Curculionidae), a thermophilous pine weevil which feeds on the inner bark and cambium of several pine species. Although, in general, European pine weevil species are generally considered secondary pests [56], this species is known to have a significant economic impact by causing mortality in regenerating stands and young (4–15-years-old) trees [57–59]. It can also be found on older trees and even in pine stumps [60,61]. The beetle usually attacks conifers which have been weakened by other abiotic or biotic agents [60,62]. In Italy, *P. castaneus* has been found damaging pine trees previously weakened by the scale, *Matsucoccus feytaudi* Ducassee, 1941 (Hemiptera: Margarodidae) [63], and in Spain it has been found after fires [64]. In contrast, in the south of France, this insect appears to be a primary pest of *Pinus pinaster* Aiton, without other agents associated [65]. The damage, polyphagy within pines, widespread distribution, and ability to attack trees of different ages, implies a higher risk for the dissemination of *F. circinatum* in areas where pine weevils (Coleoptera: Curculionidae) are abundant.

Several other insects can be regarded as potential indirect vectors of *F. circinatum*, including species which experience population outbreaks affecting the health condition of pine forests. This is the case for sawyer beetles of the genus *Monochamus*, with five European species colonizing pines and other conifers which are weakened or recently killed by other insects or by abiotic factors [66,67], including forest fires [39,68,69]. In such situations, sawyer beetle populations can rapidly increase and exhibit unusual aggressive behavior [70,71]. Maturation feeding of millions of insects causes branch dieback, defoliation, and tree weakening, which predisposes the trees to subsequent attacks by other pests and diseases [72]. A comparable situation was reported from Portugal, where the pine sawyer *Monochamus galloprovincialis* (Oliver, 1795) (Coleoptera: Cerambycidae) was the vector of the pine wood nematode *Bursaphelenchus xylophilus* (Steiner and Buhner, 1934) (Nematoda: Parasitaphelenchidae) and experienced an enormous increase of its population after the pest was introduced, hazarding the sustainability of *P. pinaster* forests ecosystems [73]. Moreover, the presence of a large number of dead and dying pines gave rise to outbreaks of bark beetles such as *O. erosus*, *I. sexdentatus* and *T. destruens* [18,74], which affected the sanitary condition of the pine forests.

Another risk species is the pine processionary moth, *Thaumetopoea pityocampa* (Denis and Schiffermüller, 1775) (Lepidoptera: Notodontidae), considered the most damaging defoliator of pines [75], and widespread in Mediterranean forests, southwestern Europe, and the Balkan Peninsula [76]. This moth can be extremely abundant and exhibits periodic outbreaks with a cycle of seven to nine years [77], causing severe and/or repeated defoliations, resulting in a severe growth reduction, tree decline, and even pine mortality [78–80]. These outbreaks favor the attack by other pests such as bark beetles [17,60], and can indirectly favor the dissemination of *F. circinatum* in affected areas.

In conclusion, there are several insect species with the potential to weaken pines and disseminate PPC in the Mediterranean basin. Some of them are known to cause severe, periodic or chronic damage to pines. Any activity of these insects should thus be considered a factor that directly or indirectly increases the vulnerability of pine forests to PPC in the Mediterranean region.

2.2. Maritime Agro-Climatic Zone

The Maritime zone comprises areas north of the line from the coastal zone of south-west France, the south border of Switzerland and Austria, west of the border between Austria and Hungary, west of the border between Czech Republic and Slovakia, and west of the river Oder between Poland and Germany. It also includes Ireland, southern parts of Sweden and Norway, and the United Kingdom. Climatically, this region is characterized by moderately cool or cold winter and fairly mild summer temperatures, with relatively wet winters and wet to occasionally dry summers [10]. The climate is strongly conditioned by the Gulf Stream, which keeps mild air (for the latitude) over northwestern Europe in the winter months, especially in Ireland and the United Kingdom.

Several potential conifer hosts of *F. circinatum* occur in Europe's Maritime zone, including important species in the natural and planted forests such as *Pinus cembra* Linnaeus, *Pinus mugo* Turra, *Pinus nigra* Arnold, *Pinus sylvestris* Linnaeus, and *Pinus contorta* Douglas, with the climatic conditions being suitable for the development of PPC [81,82]. While *F. circinatum* has already been reported within the Maritime zone in France, it is currently considered eradicated there [83]. In surveys of pine and *Pseudotsuga menziesii* (Mirb.) plantations and conifer nurseries in Germany, Sweden, Switzerland, and Austria, the pathogen has not been found. However, Möykkynen et al. [6] modeled the spread of the pathogen from specified points of entry such as harbors and infected nurseries with a 100-year simulation, assuming new arrivals and infestations of *F. circinatum* in France, Benelux countries, Germany, and Poland. They concluded that the highest risk of establishment was in central France and Northern Germany. The closeness of the zone to the Mediterranean zone where risk of PPC is high, the presence of susceptible hosts, and climatic conditions that allow disease establishment emphasize the importance of careful monitoring of the situation in this zone. Moreover, several possible insect vectors of *F. circinatum* occur in the region and need to be considered when assessing the risk of PPC spread in the Maritime zone.

Some of the most important vectors of PPC that are active in the Maritime zone are the pine shoot beetles. *Tomicus piniperda* is one the most destructive pine shoot pests in this zone, where it has been reported in several countries, e.g., Germany [84], Switzerland [85], Sweden [86,87], and Austria [88]. *Tomicus minor* (Hartig, 1834), also known to vector ophiostomatoid and ambrosia fungi, is also widespread across many countries in the Maritime region. In northern European forests, *T. piniperda* and *T. minor* depend almost exclusively on *P. sylvestris* as a host, with emerging adults feeding on vital shoots for maturation, causing considerable growth loss, and mature adults reproducing in the stems of weakened trees, slash or logs. As secondary colonizers of the stems of trees, their abundance can increase substantially following major disturbance events in the forest (e.g., windstorms) [89,90]. The common occurrence in the entire geographic range of *P. sylvestris*, large ecological plasticity, and a life cycle with two different periods of dispersal (the longer reproductive "spring flight" and the shorter maturation flights), combined with a destructive mode of action on pines, ability to fly several kilometres [90,91], and a demonstrated capacity to transmit blue-stain fungi, makes pine shoot beetles potential vectors of PPC throughout the Maritime region, similarly to the Mediterranean zone.

Engraver beetles (Coleoptera: Curculionidae) of the genus *Ips* are known as vectors of the pitch canker pathogen in California [3]. Several species of these bark beetles have been reported in Europe's Maritime zone, causing damages to conifer forests and plantations—in particular to the Swiss pines in Germany, Switzerland, and Austria [92]. Most damage reports come from *Ips typographus* (Linnaeus, 1758) and *I. sexdentatus* in Austria, Denmark, Norway, and Sweden [93–96]; *I. acuminatus* in Switzerland [97]; and *Ips amitinus* (Eichhoff, 1871) in Sweden [98]. As compared to their impact on pine forests, engraver beetles tend to cause more severe problems in *Picea abies* (Linnaeus) Karst. stands

in the Maritime region. For instance, attacks by *I. typographus* on *P. sylvestris* have been reported to be rare, mainly resulting of switching from nearby attacked *P. abies* trees [99]. This bark beetle has also been found to have a low preference for *P. contorta* [96]. On the other hand, another bark beetle, *Pityogenes chalcographus* (Linnaeus, 1761) that often occurs with *I. typographus*, commonly colonizes cut trees or parts of trees of the native *P. sylvestris* [100,101], and it has also been found to have a higher preference for *P. contorta* [96]. While these beetles might not be the primary concern as PPC vectors in the Maritime region, their involvement in dissemination cannot be excluded, especially in pine stands or nurseries near storm-felled spruce forests.

Frequently occurring beetles in mid-aged and mature *P. sylvestris* tree stands of the Maritime region are also the pine weevils (Coleoptera: Curculionidae), such as *Pissodes piniphilus* (Herbst, 1797) and *Pissodes pini* (Linnaeus, 1758). These weevils oviposit under thin bark and have been shown to carry spores of resin top disease fungus, *Endocronartium (Peridermium) pini* (Willd.) Y. Hirats [102], indicating their capacity to transmit fungal diseases.

In Germany, pine weevils have been reported after defoliations by the moth *Lymantria monacha* (Linnaeus, 1758) (Lepidoptera: Erebidae) [103]. The larvae of this species feed on pine needles. Some of the common moths causing damage on pine include *Rhyacionia buoliana* (Denis and Schiffmüller, 1775) (Lepidoptera: Tortricidae), which prefers two- and three-needled pines (*P. sylvestris*, *P. mugo*, and *P. nigra*). It destroys growing shoots and buds and it is problematic, especially in nurseries and young forests. Important defoliating pests with potential to transfer PPC or weaken pines in the Maritime region are also diprionid sawflies (Hymenoptera: Diprionidae), such as *Neodiprion sertifer* (Geoffroy, 1785), *Microdiprion pallipes* (Fallen, 1808), and *Gilpinia virens* (Klug, 1812) [104–106]. Their larvae cause damage on needles (young or older, depending on species). Although young and otherwise vital trees have good capacity to recover from defoliation, repeated infestations can weaken the trees, and wounds provide gates to pathogen spores, increasing the vulnerability of the trees to PPC infections.

The PPC disease has been reported to spread within nurseries very rapidly, causing devastating losses [107]. The simulation model of Möykkynen et al. [6] predicted that the spread of the pathogen would affect nurseries in most of the Maritime zone. Insect vectors are likely to contribute to, and magnify, this risk. One of the most common pests of pine in nursery-produced pine plants and in reforestation areas is the weevil *Hyllobius abietis* (Linnaeus, 1758) (Coleoptera: Curculionidae) [108]. For example, in Southern Sweden it causes significant economic losses every year, and problems may increase due to the tightened regulations regarding the use of insecticides in nurseries and in the forest production certified by the Forest Stewardship Council (FSC) [109]. The insect is attracted to clear-cuts, where the adult feeds on the stem bark of young seedlings, frequently killing newly planted seedlings. By wounding plants, it provides gates for the pathogen. Other insects associated with pine nurseries are the pine weevil *P. castaneus* and the bark beetle *Hylastes ater* (Paykull, 1800) (Coleoptera: Curculionidae), both of which have been reported in Germany, Austria, and Switzerland [28,110], and present local risk of disseminating the pathogen.

To conclude, the insect fauna of the Maritime zone includes several species that are highly potent vectors for PPC. While the risk of PPC in the countries in this zone may still be relatively small due to cooler climate, it is possible that the earlier simulations and prognoses [6] have underestimated the risk by not taking into consideration the activity and dynamics of the all these insects. In the changing climate, the Maritime zone may also experience environmental changes [111] that make the conditions more favorable for many potential vector insects (e.g., by allowing several generations to develop during one growth season, [112]), and for the pathogen.

2.3. Central Agro-Climatic Zone

The central zone comprises the countries of Bosnia-Herzegovina, Bulgaria, Croatia, Hungary, Moldova, Romania, Russian Federation south of 50° N latitude, Slovakia, Slovenia, Serbia and Montenegro, Turkey, and Ukraine, except the Mediterranean coastal zones. Moderately continental climate prevails in parts of the region, with local plant species adapted to grow in cold and relatively dry winters, and warm and dry to occasionally wet summers [10]. The territories close to the Black Sea coast extending from Sochi (Russia) to Sukhumi (Abkhazia), and further southwards in Georgia, are characterized by a humid and milder climate, with winter temperatures above freezing [113,114].

In the Central zone, a range of conifer hosts and climate conditions occur, which are suitable for the establishment and expansion of *F. circinatum*. The heterogeneous climatic conditions exist due to the contrasting influence of the continental and Mediterranean climate and the diverse landscapes, with extensive plains coexisting with mountain ranges. The mountains and valleys act as barriers or channels for air masses, often causing sharp contrasts in weather over relatively small temporal and spatial scales. Annual precipitation can be quite high in some regions, with mountain summits in southwestern Serbia receiving up to 1500 mm of annual precipitation. Snow cover can occur from late November to early March. The native and exotic pines commonly found in the region include *P. nigra*, *P. sylvestris*, *P. mugo*, *P. peuce* Griseb., and *P. heldreichii* (H. Christ), with *P. nigra* and *P. sylvestris* being the most abundant species due to planting activities.

In Bosnia and Herzegovina, lack of protective measures due to economic constraints influenced the health condition of the forests, leading to the appearance of diseases and pests, and with significant economic and ecological losses in pine forests [115]. In Serbia, adverse climatic conditions (snow, ice, and strong winds) have been reported to damage *P. nigra* and *P. sylvestris* plantations, creating favorable conditions for the development and reproduction of many pine-feeding insects, such as bark beetles [116]. Similar observations have been reported also from Bulgaria [117–119] and Bosnia [115,120], where bark beetles are a key concern for the health status of local coniferous forests.

The most important bark beetles associated with pines in the central zone are *I. acuminatus*, *I. sexdentatus*, *T. piniperda*, *T. minor*, and *Orthotomicus laricis* (Fabricius, 1792) [116,121–126]. The engraver beetle *I. acuminatus* appears to be the most aggressive species in the region, being locally widespread and found mainly in *P. sylvestris* plantations, where it causes significant economic damage due to its ability to attack healthy trees [116,119]. The related *I. sexdentatus* is also widely distributed in *P. nigra* and *P. sylvestris* plantations, colonizing the lower part of the host's main trunk, while *Ips mannsfeldi* (Wachtl, 1879) is a more localized species which attacks mainly *P. nigra* stands in Bulgaria [119].

The pine shoot beetles of the genus *Tomicus* are also economically important pests and potential vectors of *F. circinatum* in the region [127–129], attacking healthy trees. They are widely distributed in *P. sylvestris* and *P. nigra* forests, and outbreaks of these insects are frequently observed in different regions of Bulgaria [118] and in neighboring countries.

Other important bark beetles in the region include *O. laricis*, which is relatively abundant in *P. sylvestris*, *P. nigra*, and *P. peuce* stands, while *O. erosus* is found on several different pine species in Bulgaria [119] and in Bosnia and Herzegovina [129]. The bark beetles *Pityogenes bidentatus* (Herbst, 1784) and *Pityogenes bistridentatus* (Eichhoff, 1878) attack branches of multiple pine species and other conifers [116], being common in the region. On the roots, *H. ater* and *Hylastes attenuatus* (Erichson, 1836) are also common [125,126,129]. Moreover, other bark beetle species, such as *Carphoborus pini* Eichhoff, 1881 and *Crypturgus numidicus* (Ferrari, 1867) were also found in some areas [129].

Longhorn beetles (Coleoptera: Cerambycidae) may also have local importance as vectors of *F. circinatum* in the Central zone. This family includes *M. galloprovincialis*, which develops on several pine tree species, mainly on *P. sylvestris*, *P. nigra*, and *P. strobus* Linnaeus. It is relatively local in mountainous areas of Bulgaria [130–132]. Other common species of pine sawyers, *Monochamus sutor* (Linnaeus, 1758) and *Monochamus sartor* (Fabricius, 1787), develop mainly on *P. abies*, and occasionally on firs and pines [131]. Other cerambycids that occur in the region include *Acanthocinus griseus* (Fabricius, 1792) and *Acanthocinus aedilis* (Linnaeus, 1758), which are relatively abundant in Bulgaria [131] in association with *P. sylvestris*, *P. nigra*, *P. peuce*, and *P. strobus* [132].

Phaenops cyanea (Fabricius, 1775) (Coleoptera: Buprestidae) is associated with pines. The larvae of this species develop between the bark and sapwood, damaging the phloem and leading to rapid weakening of the host. The attacks may cause rapid death of the trees, and severe outbreaks may profoundly change the state of the pine stands. This beetle is widespread and abundant in Bulgaria [133], being considered a destructive xylophagous pest both in pine plantations and in urban green areas [134,135].

Adding to the risk of PPC spread in the Central zone, *L. occidentalis* has recently colonized suitable habitats also in this region of Europe (e.g., [120,136,137]). In Bosnia and Herzegovina, the species has been found on *Pinus heldreichii* Christ, a rare mountainous pine species with a restricted natural distribution.

In recent decades, pine weevils have been frequently found in young pine plantations due to neglected sanitary conditions in the region, namely on *P. nigra*, *P. sylvestris*, and *P. strobus* plantations. In Serbia, *H. abietis*, *P. castaneus*, and *H. ater* are reported as the most frequent and dangerous pests in plantations [121], while other species of the genus *Pissodes* such as *P. pini*, *P. piceae* (Illiger, 1807), *P. piniphilus*, and *P. castaneus*, as well as *H. ater*, damage pines in nurseries and young conifer plantations in Bulgaria [134]. *Hylobius abietis* has been reported causing damages on seedlings in several countries in the mid of 20th century, but more recent surveys are missing [138–143]. *Rhyacionia buoliana* is also reported to cause damage in pine plantations in Serbia and Bosnia, often leading to permanent crookedness of the main trunk and formation of multiple terminal shoots. On the Kozara Mountains, Preslica (Doboj) and Ildjak (Visegrad) in Bosnia, *R. buoliana* has been found in high population densities, causing considerable reduction in height growth and density of *P. sylvestris*, *P. nigra*, and *P. contorta* plantations and forests [144].

Similar to other European regions, defoliating insects affect the forest's health state in the Central zone. *Thaumetopoea pityocampa* is an important pine defoliator in the sub-Mediterranean climatic areas of Bosnia and Herzegovina, where the species is mainly associated with black pine [145], and in Bulgaria, where the negative economic and environmental impact of this pest has been increasing in recent decades [126]. Other defoliating insects with regional importance include *Dendrolimus pini* (Linnaeus, 1758) (Lepidoptera: Lasiocampidae) in the even-aged *P. sylvestris* stands in Bosnia [120], and sawflies *N. sertifer* and *Diprion pini* (Linnaeus, 1758) (Hymenoptera: Diprionidae); the first species abundantly widespread in Serbia and Bulgaria, while the second one is mainly reported from Bosnia and Bulgaria [120].

2.4. Northeast Agro-Climatic Zone

The Northeast zone includes Poland, the Baltic countries, Ukraine, Belarus, Finland, and Russia north of 50° N latitude. The dominant climate is continental, with cold and relatively wet winters, and hot and dry summers [10]. In the area north of Odessa-Krasnodar-Sochi-Sukhumi line, extremely high summer temperatures of up to 50 °C and low winter temperatures down to −40 °C are found, resulting in conditions that are not appropriate for *F. circinatum*, which requires relatively mild temperatures for its development and for the germination of its spores [146].

Bark beetles are common in the Northeast zone [147–149]. Some of them are well known vectors of ophiostomatoid fungi [150–153], indicating the potential to act as possible vectors also for *F. circinatum*. *Tomicus piniperda* and *T. minor* are local pests of *P. sylvestris* [154–157]. In warmer regions of Ukraine, Crimea, Georgia, the Western Caucasus, Russia, and Abkhazia, *T. destruens* is also present, mainly associated with *Pinus brutia* var. *pityusa* (Steven) Silba [158–160]. In 2014, this bark beetle was recorded in Sochi (South-west Russia) on *P. pinea* plants imported from Western Europe [161].

Several bark beetle species occurring in this region are potential vectors of *F. circinatum*, including *Polygraphus poligraphus* (Linnaeus, 1758), *I. sexdentatus*, and *I. acuminatus*. In southern Finland, *I. acuminatus* has been associated with the killing of *P. sylvestris* after hot and dry summers, which has resulted in an increased susceptibility of pines to insect damage [162]. Yet, the most important forest pest in this zone is *I. typographus*, which is inherently associated with *P. abies* [163,164]. In recent years, there have been reports of numerous outbreaks by *I. typographus*, e.g., in Poland's Białowieża forest, the cyclic outbreaks of this pest have been occurring over the last decades, with an extremely severe mass outbreak enduring since 2012 [165]. Mass mortality of conifers caused by *I. typographus* benefits other bark and wood boring beetles, leading to a decline on the forest's health status and, thus, increasing the risk for the spread and establishment of *F. circinatum*.

A large number of species from the genus *Pityophthorus*, associated with pines, are also present in this zone, such as *Pityophthorus glabratus* (Eichhoff, 1878) and *Pityophthorus pini* (Kurentsov, 1941) [154, 156,157,166]. Another important and aggressive local forest pest is *Dendroctonus micans* (Kugelann, 1794) (Coleoptera: Curculionidae), affecting both young and old *P. sylvestris* trees [167,168]. Usually, *D. micans* colonizes healthy trees, but it will also attack trees that are stressed by logging damage, frost, snow, wind, lightning, poor soil nutrition or drought [169]. Similarly, *P. cyanea* (Fabricius, 1775) is considered an important pest of pines weakened by dry and hot summers [170], and can be a locally important pest in the Northeast agro-climatic zone [36].

Another species that benefits from availability of weakened trees is the longhorn beetle *M. galloprovincialis*, which is widely distributed in Russia and Ukraine [154,156,157,171]. By wounding the trees, this species can create points of entry for *F. circinatum*. In Poland, these beetles have been found to carry a blue-stain fungus *Ophiostoma minus* (Hedgc.) Syd. and P. Syd. [172], and introduction of pathogens through the cuts on the bark made by females of *Monochamus* spp. has been documented in coniferous stands in the Karelian Isthmus in Russia [173].

Pine weevils of the genus *Pissodes* are important pests on young pines in the Northeast zone, being widely distributed in the Baltic countries, Poland, Ukraine, Russia, and Finland. The most common species are *P. castaneus*, *P. pini*, and *P. piniphilus* [94,166,174]. *Pissodes castaneus* is one of the most dangerous pests of *P. sylvestris* plantations and natural regenerations in the Baltic region. Pine bark beetles of the genus *Hylastes* are also important local pests of pine seedlings, with the insects mining short galleries inside the cambium of the young pines and causing their decline or even death. There are several species present in the region, including *H. ater*, *H. attenuatus*, *Hylastes brunneus* Erichson, 1836, *Hylastes cunicularius* Erichson, 1836, *Hylastes linearis* Erichson, 1836, and *Hylastes opacus* Erichson, 1836 (Coleoptera: Curculionidae) [154,157,166,168,175,176].

The most important local pests of seedlings and plantations in the Northeast zone are the pine weevils *Hylobius pinastri* (Gyllenhaal, 1813) (Coleoptera: Curculionidae) and *H. abietis* [154,157,166,171, 177,178]. These pine weevils are widespread, abundant, and economically harmful pests in young plantations in boreal coniferous forests across the northern Palearctic region [58,179]. While *H. pinastri* prefers *P. abies* [180], *H. abietis* is common on pines, being an important pest of young pine stands [181] and recently felled-trees [182] throughout its distribution range in Europe, northern Asia, and Japan. It has also been found to vector the pathogenic fungi *Heterobasidion parviporum* Bref. and *D. pinea* [183,184], as well as for the saprotrophic fungus *Phlebiopsis gigantea* (Fr.) Jülich [185]. In Poland, *H. abietis* has also been found transmitting the ophiostomatoid fungi *Leptographium procerum* W.B. (Kendr.) M.J. Wingf. and *Ophiostoma quercus* (Georgev.) Nannf. to *P. sylvestris* seedlings [174]. Its abundance, frequency

as a damaging agent on pines, and recurrent association with pathogenic fungi increase the risk of it becoming associated with *F. circinatum*.

Among the sucking insects, *Aradus cinnamomeus* (Panzer, 1806) (Hemiptera: Aradidae) has local importance in some regions of the Northeast zone, while the invasive *L. occidentalis* is widespread in suitable habitats across the region—including southern Poland [43], Ukraine, and Russia [186]—and has been locally expanding its range over the recent years [187]. This species actively flies from one pine to another to feed and breed, and during these activities, it can act as a vector for fungi.

Another insect associated with cones is the pine weevil *P. validirostris*, which has been found damaging pine cones in several countries of the Northeast zone [157,166,188,189].

Numerous defoliating insects are common in Europe's Northeast zone. The most important are the sawflies *D. pini* and *N. sertifer* (Hymenoptera: Diprionidae) and *Acantholyda posticalis pinivora* Enslin, 1918 (Hymenoptera: Pamphiliidae); and the moths *Panolis flammea* (Denis and Schiffermüller, 1775) (Lepidoptera: Noctuidae) and *Bupalus piniaria* (Linnaeus, 1758) (Lepidoptera: Geometridae) [154, 157,166,171]. The regular mass outbreaks of these insects cause significant damage in *P. sylvestris* forests. These species, along with *T. pityocampa* in the regions with warmer climate, can weaken pine stands during several years and increase the vulnerability of pines to attacks by bark and longhorn beetles. In Estonia, trees defoliated by *B. piniaria* are often subsequently attacked by *T. piniperda* and *T. minor*, followed by *Pissodes piniphilus*, and root-rot diseases caused by *Heterobasidion annosum* (Fr.) Bref and *Armillaria* spp. (Fr.) Staude [190]. The outbreaks of the defoliator pests frequently cease with the collapse of their populations. For instance, *B. piniaria* population peaks are often followed by high mortality caused by the entomopathogenic fungi *Beauveria bassiana* (Bals.) Vuillemin and *Metarhizium anisopliae* Metchnikoff (Sorokin) [191].

Overall, in the Northeast zone, there are several insect species with high potential to promote the spread of *F. circinatum* in forests, nurseries, and plantations. However, the harsh environmental conditions are likely to be suboptimal for *F. circinatum*, suppressing its establishment in this zone. Nevertheless, the annual mean temperatures are projected to rise in this century worldwide, with the largest warming occurring in Northern Europe during the winter months [111]. This can favor not only the PPC pathogen, but also the establishment and spread of several native and exotic insect pests by affecting their distribution, phenology, activity, and voltinism [192].

3. Environmental Attributes Influencing the PPC Disease Spreading

Each agro-climatic zone is characterized by a specific regime of environmental, abiotic conditions, which are likely to profound influence in the interaction between *F. circinatum*, the insects, and the host pines. For instance, abiotic variables influencing insect during development from larva to adult may determine the proportion of individual beetles to become vectors, carriers, or wounding agents of *F. circinatum* (Table 1).

Table 1. Effect of environmental factors and silvicultural measures on insects associated to the pine pitch canker (PPC) disease.

Insect Species	Factor	Effect	Location (Host)	References
<i>Tomicus piniperda</i>	Temperature	17 °C during the summer and 0 °C during the winter months benefit	Europe (<i>Pinus</i> spp.)	[193]
	Fire	Colonization of trees with less than 25% intact foliage	South and central Sweden (<i>Pinus sylvestris</i>)	[194]
	Snow-breaks	Increased colonization Stump colonization	Central Spain (<i>Pinus pinaster</i> and <i>Pinus nigra</i>) Central Sweden (<i>Pinus sylvestris</i>)	[31] [195]
	Artificial pruning	Pruned trees more heavily attacked than unpruned trees	Sweden (<i>Pinus sylvestris</i>)	[196]
<i>Tomicus minor</i>	Water stress	Increase outbreaks	Europe (<i>Pinus sylvestris</i>)	[197]
	Temperature	Main period of dispersal in spring, when temperatures exceed 12 °C in the shade	Worldwide	[198]
<i>Tomicus destruens</i>	Temperature	Warm and dry climates	Spain (<i>Pinus</i> spp.)	[15]
	Water stress	<i>T. destruens</i> has been found to preferentially attacking non-stressed pines during its shoot feeding phase and to have increased fitness as a result	Greenhouse (<i>Pinus pinaster</i>)	[199]
<i>Rhyacionia</i> spp.	Temperature	<i>Rhyacionia frustrana</i> is unable to sustain flight below 9.5 °C Temperature influences phenology and voltinism. Reduced male longevity during warmer portions of the year	Eastern US (<i>Pinus</i> spp.)	[200–202]
	Light	Attacks of <i>R. frustrana</i> increase if the shade is removed	Eastern US (<i>Pinus</i> spp.)	[203]
<i>Monochamus galloprovincialis</i>	Temperature	12.2 and 35 °C, lower and higher thresholds for larval development, respectively	Portugal (<i>Pinus pinaster</i>)	[204]
		During hot years, larval development is faster and results in earlier emergences	Portugal (<i>Pinus pinaster</i>)	[205]
	Elevation	−7 °C, threshold of mean minimum temperature in winter for beetle survival 1590 m threshold for beetle survival	Europe (<i>Pinus</i> spp.) Pyrenees (<i>Pinus uncinata</i>)	[206] [206]
<i>Ips sexdentatus</i>	Fire	Increased colonization	Central Spain (<i>Pinus pinaster</i> and <i>Pinus nigra</i>)	[31]
<i>Ips acuminatus</i>	Temperature	6 and 14 °C, for spring emergence and brood development, respectively	South-eastern Alps (<i>Pinus sylvestris</i>)	[207]
		At 18 °C flight starts	Central Spain (<i>Pinus sylvestris</i>)	[208]
<i>Hylastes ater</i>	Drought	Stressed seedlings less attacked but more girdled than non-stressed seedlings	New Zealand (<i>Pinus radiata</i>)	[209]
	Elevation and aspect	Catches decrease with increasing elevation. Beetles caught at north-facing than at south-facing sites towards the end of the flight season in autumn, leading to an extended flight period at northerly aspects	South Island, New Zealand (<i>Pinus radiata</i>)	[210]
<i>Hyllobius abietis</i>	Soil preparation, soil scarification and physical protection of plants	Reduces seedling attack and plant mortality	Southern Sweden (<i>Picea abies</i>)	[211,212]
	Water stress	Significantly greater girdling in water stressed plants	Central Finland (<i>Pinus sylvestris</i>)	[213]
	P fertilization	Increases the attack of seedlings	Northwest Spain (<i>Pinus pinaster</i>)	[214]
	Increments of temperature	Earlier emergence, shortened generation time, favor univoltine life cycles, and increase weevil populations and damages to transplants	Southern England (<i>Pinus sylvestris</i> and <i>Pinus nigra</i>)	[212,215]
	Temperature sum at the location and age of clear-cut at the time of planting	Directly and inversely related to weevil damage level, respectively	Central Sweden (<i>Picea abies</i> , <i>Pinus sylvestris</i> , and <i>Pinus contorta</i>)	[212]

Nevertheless, the detailed effects of different environmental variables on this interaction during the development of PPC disease are challenging to describe, because of the spatial and temporal dynamics that are typical for these factors and for the multiple biotic interactions involved. Because different interactions are likely to occur simultaneously in the affected trees and stands, it is difficult to identify which factors significantly affect the epidemiology.

At the landscape level, abiotic factors have a strong influence on the distribution and abundance of potential spore-transmitting insects, and thereby on the potential rate at which pitch canker is spreading. A survey performed in California reported the severity of PPC associated with landscape type and geographic factors [216]. Among other causes, differences in disease intensity between inland and coastal locations were attributed to differences in the abundance of insects that vectored the disease and/or served as wounding agents. For example, the spittlebug *Aphrophora canadensis* (Walley, 1928) (Hemiptera: Aphrophoridae) is more common in coastal areas than in inland [216], and since it causes wounds associated with *F. circinatum* infections [217], its occurrence may have contributed to greater disease severity near the coast.

Temperature regime has a profound effect on most biological interactions. Ambient temperature can directly influence the insect (activity, metabolism), the fungus (sporulation, germination), or the host (defensive metabolism). It is well documented that certain external temperature thresholds have to be reached before insects emerge and fly (10 °C for the early flier *T. piniperda*), but their feeding activity is also modified by temperature [218]. As the air temperature increases to 25 °C and above, bark beetles become more active and move energetically, and this likely increases the probability that the spores of *F. circinatum* on the exoskeleton of the insects are scraped onto the surface of feeding wounds. Temperature can also have an impact on a micro-scale within and around the feeding gallery, although the quantity of viable spores delivered by an insect to a feeding groove is probably the most critical factor in whether or not infection of the phloem, pith, and ultimately the entire branch, takes place.

High level of humidity around a feeding gallery may enhance the probability of infection [219] and it even reduces the number of spores needed for infection (see below). For bark beetles such as *Pityophthorus* spp. that create only shallow wounds, the frequency of infection will likely be strongly influenced by the availability of ambient moisture or high humidity [220]. In contrast, other bark beetles that tunnel deeper into healthy tissue, such as *Conophthorus radiatae* (Hopkins, 1915) (Coleoptera: Curculionidae), can deliver inoculum to sites where the germination of the spores is less influenced by ambient conditions. This distinction should be incorporated into risk models, which are generally based on climate and assume that ambient conditions will have a determinative effect on the infection process.

The presence of viable spores in the environment and their movement with insect vectors are crucial factors in PPC epidemiology, which is strongly affected by the environmental factors. The airborne inoculum of *F. circinatum* could be used as a proxy of the potential risk of transmittance. In northwest Spain, airborne spores have been found to have a permanent occurrence throughout the whole year, with a slight trend to be higher after low air temperatures and low leaf wetness [221]. Neither air humidity nor rainfall had a significant impact on spore abundance in the air [221]. However, passive deposition of inoculum may be supported by rainfall, as the rain drops trap the aerial spores and can deliver it to the wounds. In California (USA), more spores were detected in months colder than June and July [222] and sea fog alleviated the water deficit during dry periods in summer, enhancing the fungal sporulation [223]. The pathogen's demand of temperatures around 20 °C, and the limiting effect of extremely high temperatures for developing fruiting structures such as phialides and sporodochia, may determine the abundance of *F. circinatum* air spores. Inman et al. [146] revealed that at 20 °C, the germination of spores was more than 20%. However, the presence of water on the host surface does not favor the development of fructification structures [221]. Thus, optimal conditions for sporulation appear to be different from those needed for spore germination, creating difficulties when describing PPC disease spread by insects.

The number of spores that are required for infection probably depends, at least in part, on the species of pine, its genetic level of resistance, and also its seasonal susceptibility. It is estimated that some twig beetles (*Pityophthorus* spp.) carry less than ten *F. circinatum* spores per individual [224], whereas *Ips* spp. were found to carry as many as 300 spores [225]. An additional factor in the success of disease transmission is the amount of inoculum carried by insect vectors, which depends on the insect size and the extent to which *F. circinatum* colonizes and sporulates on the walls of each pupal chamber. This, in turn, is probably influenced by the length of time the beetle remains within the chamber and environmental conditions. From a total of 118 *T. piniperda* specimens collected in northern Spain between May and July from *P. radiata* trees with symptoms of pitch canker disease, *F. circinatum* was isolated with 15, 13, 15, and 33% success from larvae, pupae, F1 adults, and parental adults, respectively [14].

More individuals will carry the pathogen if environmental conditions are likely to favor the development of *F. circinatum* in pupal chambers and feeding galleries. Mycelial growth rates in vitro were highest at 25 °C and progressively decreased at 20 °C, 15 °C, and 10 °C, and spore germination was also reported to occur more rapidly at 20 °C than at 10 °C [146]. It is suggested that low temperatures during spring will inhibit sporulation in pupal chambers and very hot temperatures during the summer will inhibit sporulation in feeding galleries (e.g., those of *T. piniperda*), since *F. circinatum* does not survive above 50 °C [226]. The summer-emerging adults of *Pityophthorus* spp. may be less effective vectors than the spring-emerging adults, because the time spent in pupal chambers in summer may be brief, with little time for the developing adult to come into contact with spores. *Tomicus piniperda* adults are especially active in June, often residing within a shoot for less than two weeks. In contrast, by late summer (e.g., September), fewer beetles—and even fewer newly attacked but empty shoots—are found [227], indicating that *T. piniperda* adults are less likely to infect new trees in late summer.

Several abiotic factors, such as water deficit, fire, and fertilization, may influence the susceptibility of the trees to insect attacks [31,194,228,229]. In some circumstances, these factors may be related to increased damage caused by *F. circinatum*. For instance, an association between drought and rapid spread of the disease has been observed in Florida [230] and California (USA), with high mortality of stands situated on soils with poor water holding capacity [231]. Susceptibility to PPC increases during water stress, waterlogging or shallow soils, especially when trees are planted at high-stand densities [1]. Fire-damaged stands may attract large numbers of primary bark beetles such as *T. piniperda* and *I. sexdentatus* [31,194] (Table 1), which increases the chances of outbreaks and disease transmission. As these insects are dependent on host trees with reduced vigor for successful reproduction, a feedback between insect population and PPC disease is expected. Outbreaks of pitch canker have also been associated with use of poultry manure [232], applications of high levels of chemical fertilizers [233,234], and nitrogen emissions from air-conditioned chicken houses [235]. Heavy fertilization may make pine tissues more succulent, facilitating the entry of the fungus, suppressing defensive mechanisms such as phenolic metabolism [236] or increase the attraction of insect vectors or insects causing suitable infection courts for the pitch canker. The effect of beetle host selection of beetles under different drought stress and nutrient availability regimes is probably mediated by the environmentally induced changes in resin duct characteristics, as reported elsewhere [229,237], but this needs to be tested in the pitch canker disease epidemiology. More information is also needed about the impacts of heat stress and fires on tree susceptibility to insects and *F. circinatum* infection.

4. Management Options to Control the Potential Spore-Transmitting Insects

4.1. Management Options

The reported management options against potential insect vectors of PPC fall to four basic categories: Mechanical control (including silvicultural operations), chemical control (including both synthetic insecticides and natural and low risk chemicals), semiochemical control (including pheromones), and biological control (using parasites or predators or natural resistance of the tree).

While a comprehensive exploration of these categories is beyond the scope of this review, the following sections provide a brief presentation of each category, with selected examples from literature.

4.1.1. Mechanical Control

Management of potential insect populations through mechanical measures includes sanitary measures and utilization of silvicultural operations to manipulate stand structure and conditions in a way that may suppresses vector insect populations. The successful application of these methods requires a good knowledge of the targeted and non-targeted environmental effects of the measures. For instance, storage of fresh logging residues and freshly cut stumps can attract pine weevils to close-by regeneration areas, and should therefore be avoided [238]. Scarification and uprooting of stumps for increased biomass uptake has been suggested as a means to reduce substrate for *H. abietis*, although contrasting results have also been obtained [238,239]. In pine wilt-affected zones in southern Portugal, the felling and removal of dead and dying trees during the winter months is used to prevent emergence of *M. galloprovincialis* carrying the pine wood nematode, thus preventing new infections of healthy pines. This process, although expensive and time consuming, is the most successful way to control pine wilt disease [73].

Silvicultural practices that improve tree vigour have been successfully applied to reduce stand susceptibility to damage from bark and wood-boring insects, which often exploit trees of low vigour [7]. For instance, Wermelinger [240] and Göthlin et al. [241] propose the preventive elimination of reproduction substrate for bark borers, such as the remains of wood existing in the forest or the felling of infested trees. These measures can be very effective and increase the mortality of the bark beetles up to 93% when the colonized trees are eliminated before the emergence of the beetles, and the infected logs are removed from the forest. Mechanical control of bark and root borers of the genus *Pissodes* involves removing infested branches and destroying them to reduce populations [242]. In some studies, however, the method resulted in high costs and unsatisfactory results [243]. Yet, in specific circumstances, it could be an efficient method [244].

In the EU, the interest in mechanical solutions is likely to further increase since the use of insecticides in forests is increasingly regulated, due to risk of non-targeted effects on environment (e.g., on pollinator populations) and on human health. For instance, in Sweden, insecticide containing a neonicotinoid imidacloprid was used in control of *H. abietis* until 2018, but after EU Commission prohibited use of this compound [245], the use of pesticides to control *H. abietis* is being phased out and replaced by combinations of stem coatings and silvicultural countermeasures [246]. In mechanical control of *H. abietis*, collars or coatings can be used to prevent the insects from reaching the bark. One of the newest methods against attacks by *H. abietis* was developed in Sweden and involves the automatic treatment of seedlings with wax and sand that prevents insects from consuming the bark of the seedlings [247]. The product utilizes knowledge from behavioral studies that showed how sand with a grain size less than 0.2 mm stops *H. abietis* feeding as the grains enter in between its mandibles. In addition, forest managers apply a variety of damage-reducing measures, such as site preparation followed by an optimal choice of planting spot, timing of planting, plant type, and plant size to protect the plants [212].

4.1.2. Chemical Control

The EU has strict regulations about use of pesticides in all plant production, including forest tree nurseries and forest settings. For instance, several of the chemicals that have earlier been reported in the USA as active components in control of *T. piniperda* (chlorpyrifos, lindane, cyfluthrin, bifenthrin, esfenvalerate, lambda-cyhalothrin, and carbaryl [248]) are not approved for use as pesticides in the EU or their approval is soon expiring. Recent changes in relevant EU regulations include, e.g., prohibition of neonicotinoids which were used in control of *H. abietis* (see above). This development directly implements EU Directive 2009/128/EC [249], which aims at sustainable use of pesticides in the EU and reduction of the risks and impacts of pesticide use on human health and the environment. The same

directive promotes the use of integrated pest management (IPM) and of alternative approaches or techniques, such as non-chemical alternatives to pesticides.

While the applicability of insecticides as solutions to suppress potential PPC vector insects may be restricted in the future, the topic has received considerable interest in earlier research. While chemical control can cause negative effects on the forest's biodiversity and human activities, in some cases, it may be the only effective option to control the pests. For instance, the flat bug *A. cinnamomeus* is a serious pest of pines in Northern Europe, causing remarkable growth delays [250]. The only option to control this species consists of chemical treatments with insecticides [251]. In other cases, chemical treatments are considered as just one of the several components of IPM. For example, it has been reported that control of shoot feeders (*Tomicus* spp., *Monochamus* spp.) includes forest sanitation measures in order to reduce the amount of material available for reproduction, the use of trap trees (logs) for attracting adults, and the use of insecticides to control feeding in shoots [252].

The effectiveness of chemical treatments may vary considerably. The chemical control of bark and root borers (*Pissodes* spp.) can be carried out in small trees (four years), and consists of spraying insects with insecticide [253]. According to these authors, significant reductions in attacks were achieved due to the mortality of the insects when synthetic pyrethroids were used. Iede et al. [254], meanwhile, mention that the chemical approach is not very effective, even in the case of treatments with fenitrothion (only authorized outside the EU) because insects often hide in the ground or in the cracks of the bark. On the contrary, Fraser and Heppner [255] reported good results when injecting the stem of *P. strobus*, the first year after application. It should, however, not be forgotten that just like for any chemicals, resistance against insecticides may appear in the insect population after long-term and repeated exposure [41].

Chemical control requires the use of different substrates treated with insecticides that insects will come into contact with. Especially in forests, the use of chemicals is challenged by the difficulty of applying the compounds to the right place and at the right time. Earlier, aerial spraying was an option to spread the insecticides to forests, but this method is banned in EU countries [256]. Preventive trunk injection of insecticides is an alternative method to control forest and urban pests, and although being labor-consuming and expensive, it can successfully protect healthy trees against insect pests for several years [257–259]. Trap trees have been used as devices to expose engraver beetles (e.g., *I. sexdentatus*; *O. erosus*; *Hylurgops palliatus* (Gyllenhal, 1813) (Coleoptera: Curculionidae); *H. eruditus*; and *Hylurgus ligniperda* (Fabricius, 1787) (Coleoptera: Curculionidae)) to insecticides. To increase attractiveness, they can be baited with commercial pheromones placed directly on the trees [260] or inside devices, such as tripods widely used in some countries [261].

Another chemical method for mass suppression of bark beetles consists of using insecticide-immersed nets to protect logs or wood stocks. These nets are made of synthetic textile fiber imbued with insecticide (usually pyrethroids) which is applied on the surface of the trees, creating a mechanical barrier for beetles that want to colonize the logs. Because of the contact with the insecticide from the net, the beetle is intoxicated and dies very quickly [262]. The insecticide nets are also used to cover wood infested with the pine wood nematode (*B. xylophilus*) for transport in trucks, in order to prevent the dissemination of the nematode and of its insect vector [74]. One way to apply chemicals is the use of toxic bark (fir or pine bark of 30 cm x 30 cm containing insecticides and adhesives), which has been tested against *H. abietis*. Pine weevils are attracted by the smell of the fresh bark and are poisoned. However, the method requires a lot of work and it is only widely used in Eastern Europe [59,260].

Insects may also be difficult to treat with chemicals because of their spatial location inside the tissue. For instance, the main challenge in chemical control against *Monochamus* spp. is how to apply the insecticide so that it is effective against xylophagous larvae. Similarly, cone insects (*P. validirostris*, *L. occidentalis*) are not readily exposed to chemicals due to their feeding inside the cones, where they are difficult to detect. Yet, the most well-known control methods of *P. validirostris* are chemical treatments [41]. So far, no specific chemical control methods are known for *L. occidentalis* but insecticides such as dimethoate, carbaryl, synthetic pyrethroid, and permethrin used to control other insects can

provide protection for pine cones [263–266]. In addition, the same authors suggest that visual traps (which emit light at visible wavelengths and inflected wavelengths) would be effective for mass capture of adults.

4.1.3. Semiochemical Control

Other types of chemicals with significance in pest control are semiochemicals, which are chemical compounds that many insects release and use in intra- and interspecific communication [267]. The olfactory system of insects is advanced, allowing them to detect volatile signals from congeneric individuals and trees, which then guides their behaviors, such as oviposition or host selection. Thus, semiochemicals can be used in pest monitoring or control, e.g., in pheromone traps. For example, for the genus *Ips*, in order to be efficient, the couple of one trap and one bait must capture on entire season thousands of adult insects [268]. A mixture of a volatile host compounds, alpha-pinene, ipsenol, and 2-methyl-3-buten-2-ol has been patented as an attractant for *M. galloprovincialis* adults [269], and later improved by Álvarez et al. [270] by adding a thin layer of Teflon in the traps and collection jars to prevent the escape of the individuals. The traps have to be installed in early summer near susceptible areas and must be periodically inspected. However, despite being effective for monitoring their use for mass-control of the insect populations, they still require substantial improving [271]. To capture engraver beetles, pheromone traps are also placed early in the spring, before the beginning of the flight of the insect, and are kept in the field until the end of their flight period [272]. For good results, long-term pheromone lures (four to five months) or the replacement of the lures with shorter release periods (a few weeks) is recommended. The pheromone method has been reported to be ineffective against *H. abietis*, even when a large number of traps were used (100 traps/ha) [273]. Encouraging results have also been obtained with the development of pheromone baits to catch twig beetles such as *P. pubescens*. For example, Lopez et al. [274] obtained good results in the Basque Country (Spain) using combinations of (E)-(+)-pityol and its racemic form, (E)-(±)-pityol. Moreover, the authors suggest using it as a potential mate-finding disruptor in the field due to its strong attractive effect. Some authors state that this method has some limitation, saying that pheromone traps capture only between 10–15% of bark beetles [275], which at some point could lead to a reduction in competition between beetles and the prolongation of the gradation period. A special case of this method is represented by the anti-pheromones (anti-aggregative) which act like repellents for some *Ips* and *Tomicus* species [276].

4.1.4. Biological Control

Use of natural enemies (parasites or predators) as biological control agents to control insect pests may provide sustainable solutions for control of several potential vector insects. Wegensteiner et al. [277] listed for *Ips*, *Tomicus*, and *Orthotomicus* species, more than 400 natural enemy species, which include birds (mostly, woodpeckers), Coleoptera (around 165 species), Diptera, Hemiptera, and parasitoids (mostly, Braconidae and Pteromalidae; Hymenoptera), as well as other pathogens such as viruses, bacteria, fungi, and algae. One of the best-known biological solutions in the control of forest insects includes the use of virus to suppress the population of the pine sawfly, *N. sertifer* [278]. In several other cases, promising results have been obtained, and detailed knowledge about biological systems is developing. For instance, the biological control of *Tomicus* spp. includes the use of the predator *Thanasimus formicarius* (Linnaeus, 1758) (Coleoptera: Cleridae), the threshold flight temperature of which closely matches that of *T. piniperda*. Moreover, *T. formicarius* is attracted by host volatiles such as alpha-pinene, and it is commonly associated with *T. piniperda* throughout Eurasia, causing high levels of mortality [279–281]. Another predator is *Rhizophagus grandis* Gyllenhal, 1827 (Coleoptera: Monotomidae) that has been used to control *D. micans* through inundation of stands with *R. grandis* at the leading edge of infested areas [169].

For the genus *Ips*, the most promising results were obtained using synthetic formulation of entomopathogenic fungi, such as *B. basiana*, which was demonstrated to cause a high level of mortality through release the insects captured in the pheromone traps after infecting them with the fungus [282].

In particular, for *I. sexdentatus*, the bacteria *Pseudomonas fluorescens* Migula was demonstrated by Sevim et al. [283] to express insecticidal toxins affecting the beetles.

In Spain, *Beauveria pseudobassiana* (Bals.) Vuill. was isolated from naturally infected *M. galloprovincialis* and the numbers of egg-laying wounds, eggs laid, live larvae after five days, and larvae entering the xylem after six months were significantly reduced in inoculated females, pointing to horizontally-induced reduction of progeny. These results validate the potential of the isolated *B. pseudobassiana* strain as an important natural population regulator [284].

In controlling *H. abietis*, several biological methods have been tested, such as the use of natural enemies (Braconidae, Hymenoptera) and nematodes (*Steinernema carpocapsae* (Weiser, 1955); Nematoda: Steinernematidae) that have worked well in the United Kingdom [285]. Other studies mention the effectiveness of the use of entomopathogenic fungi, such as *Metarhizium* spp. [286] or *Beauveria* spp. [287]. Integrated pest management of scarabeids (*Melolontha melolontha* (Linnaeus, 1758), *Polyphylla fullo* (Linnaeus, 1758), and *Amphimallon solstitiale* (Linnaeus, 1758); Coleoptera: Scarabaeidae) in nurseries through biological control (parasitoids, predators, and pathogens), pheromone and food lures are desired instead of using insecticides [288].

Leptoglossus occidentalis is another species for which there are biological pest control programs, such as the use of the parasitoid *Gryon pennsylvanicum* (Ashmead, 1893) (Hymenoptera: Scelionidae) [289]. Yet, laboratory tests have not yielded positive results on the eggs of *L. occidentalis* [290]. On the contrary, Barta [291] managed to inoculate artificially in the laboratory the fungi *M. anisopliae* and *Isaria fumosoreseae* (Wize) Brown y Smith, obtaining good results in adults. Successful results have also been obtained with predators of insect species of other insects such as *Ooencyrtus pityocampae* (Mercet, 1921) (Hymenoptera: Chalcidoidea), which generally parasitizes *T. pityocampa* [292].

4.2. Compliance of Management Options with Legislation and Forest Management Approach

Application of any methods to control or manage insect vectors in forests, plantations or nurseries should ensure compliance with the relevant EU and national regulation for plant protection. This is important, especially when considering the use of chemicals or living organisms to control the potential vector insects. For instance, the European Commission must approve any active substance that is used in a plant protection product in the EU.

In practice, any attempts to control or regulate insect populations through interventions will also have to be planned and executed within the frameworks of the prevailing FMAs. Duncker et al. [8], as well as Jactel et al. [293,294], determine FMAs that are dominating in the different regions of Europe and vary in terms of management goals and intensity. They differentiate five main approaches:

–FMAI: Nature reserves. In these areas, all interventions are basically prohibited, but control methods could be permitted in specific cases to avoid destruction of the valuable habitat that often is of limited size;

–FMAII: Close-to-nature forests. In these forests, interventions should mimic natural processes and chemical pest control can only be applied if major threats spread from the surrounding stands;

–FMAIII: Combined objectives forests. Chemical pest control can be used in major outbreaks that are introduced from the surrounding stands or place them at risk, but minor outbreaks should not be treated with pesticides. Natural pest control methods are preferred, and the goal is to increase resilience, e.g., by greater use of mixed species stands;

–FMAIV: Even-aged forests, where the interventions support biomass (timber) production goals. Chemical treatments are allowed, although they should be kept to a minimum, silvicultural measures such as whole tree extraction are allowed;

–FMAV: Short rotation forests include stands where intensive management aims for maximum biomass production, e.g., through fertilization, and chemicals are used in pest and weed control.

Hengeveld et al. [9] developed the classification further, presenting how the FMAs of Duncker et al. [8] could apply for *P. pinaster*, *P. sylvestris*, other pine species (*Pinus* spp.), and *Pseudotsuga* spp. across different biogeographic regions. In general, their analysis suggests that FMAIII and

FMAIV were most applicable approaches for pines and *Pseudotsuga* spp. across the different regions, i.e., possibilities to apply different interventions, including chemical treatments, to control insect pests of pines are generally high. In particular, a broad spectrum of possible interventions seems to be applicable for *P. pinaster* in Atlantic and Mediterranean regions, and for *Pseudotsuga* spp. in Atlantic, Mediterranean, and Continental regions where these species are considered highly amenable for the more intensive forest management approaches (FMAIII–FMAV). On the other hand, their analysis also indicates that FMAI and FMAII (with the highest restrictions in interventions) were applicable mainly for *P. sylvestris*, and especially in Atlantic and Continental regions (corresponding approximately to the Maritime and Central zones in the classification of Bouma [10]). This suggests that the practical possibilities to restrict the spread of PPC to *P. sylvestris* populations through vector insect control may be limited in these areas. Thus, new research on natural processes (e.g., insect behavior and inter-species interactions) is urgently needed to develop future-proofed, environmentally sound solutions to suppress the activity of vector insects without chemicals.

5. Conclusions

Overall, our analysis highlights the potential of a diversified community of native and exotic forest insects found in Europe, which can vector and/or favor *F. circinatum*, emphasizing the need to include the insects' distribution patterns and local population dynamics in greater detail in future simulations of PPC spread. Future research efforts should focus on testing the actual capacity of the most probable vector insects to actually carry PPC spores, and to transmit the disease in laboratory and field conditions. More knowledge is also needed to improve our understanding of the environmental control of the dynamic interaction between the insects, the pathogen, and host trees, so that the management methods can be effectively adapted to the changing climate. Currently, the combined threats due to climate change and new pests are often missing in the decision support systems in forestry. These systems should therefore be updated with comprehensive pest risk modules that also consider the interactions with changing climate (e.g., the changed patterns in geographic distribution and in voltinism). In future forestry, promising avenues may use forest management models based on species mixtures [295] that utilize landscape level patterns in biodiversity. On the other hand, for instance, the risks associated with new thinning regimes [296] need to be carefully evaluated to understand their consequences for insect pests and vectors. A thorough consideration of prevailing FMAs and EU and national level regulations is necessary for design of realistic and integrated intervention strategies against vector insects in different regions. Pathway-oriented strategies, rather than those based on quarantine lists should be considered when designing efficient and rapid intervention strategies against insects. Careful monitoring of the populations of potential vectors is also recommended regionally, in order to develop more rigorous risk assessments that include the dynamics of the local insect fauna. Considerable resources would, however, need to be allocated to this activity. The integrated management of PPC should include management of insect vectors in both forests and nurseries. It should focus on minimizing the need of chemical control, while intensifying the measures based on natural processes and biological control, in order to support bio-rational strategies that ensure effective suppression of further establishment and dissemination of *F. circinatum* in Europe.

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