Alien Invasive Pathogens and Pests Harming Trees, Forests, and Plantations: Pathways, Global Consequences and Management

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Abstract: Forest health worldwide is impacted by many invasive alien pathogens and pests (IAPPs) that cause significant harm, with severe economic losses and environmental alterations. Destructive tree pathogens and pests have in the past devastated our forests, natural landscapes and cityscapes and still continue to represent a serious threat. The main driver of pathogen and pest invasions is human activities, above all global trade, which allows these invasive species to overstep their natural distribution ranges. While natural transport occurs according to a regular, expected colonization pattern (based on the dispersive capacity of the organism), human-mediated transport takes place on a larger, unpredictable scale. In order for a pathogen or pest species to become invasive in a new territory it must overcome distinct stages (barriers) that strongly affect the outcome of the invasion. Early detection is crucial to enabling successful eradication and containment. Although sophisticated diagnostic techniques are now available for disease and pest surveillance and monitoring, few control and mitigation options are usable in forestry; of these, biological control is one of the most frequently adopted. Since invasion by pathogens and pests is an economic and ecological problem of supranational relevance, governments should endorse all necessary preventive and corrective actions. To this end, establishing and harmonizing measures among countries is essential, both for preventing new introductions and for diminishing the eventual range expansion of IAPPs present at a local scale. Research is fundamental for: (i) developing effective and rapid diagnostic tools; (ii) investigating the epidemiology and ecology of IAPPs in newly introduced areas; and (iii) supporting policymakers in the implementation of quarantine regulations.

Keywords: forest insects; forest diseases; diagnostics; mitigation options; citizen science

1. Introduction

Forests are of primary importance, being a source of both income and well-being for human populations worldwide; however, biological invasions pose a serious threat to their economic and ecological sustainability globally. The damage caused by biological invasions is estimated to be second only to that resulting from habitat destruction/fragmentation [1]. In fact, every year a substantial part of the world’s forests is destroyed or seriously damaged by invasive alien pathogens and pests (IAPPs) [2].

The exponential increase in introduction of IAPPs to new habitats is a complex phenomenon with multiple factors. Currently, the foremost cause is the increase in trade, especially that of plants, on a global scale [3]. The economic and social transformations that have taken place in recent decades have had, and continue to have, a direct effect on the introduction of harmful organisms. In particular, the evolution in transportation vehicles has favoured an ever greater and faster handling of plants, foodstuffs, and plant materials [4]. Another leading factor is the dramatic increase in human mobility, whether for work or tourism; it is not uncommon for alien organisms to be transported from one country to another this way, both inadvertently (for example, through contaminated seeds...
or dirt stuck to footwear or clothing) and intentionally (e.g., seeds, bulbs, fruits, souvenirs made with plant materials) [5,6].

Once the IAPPs have reached a new territory, other factors, such as anthropogenic disturbance, can favour their establishment. The alteration of habitats and changes to natural ecosystems—via the construction of roads, dams, power lines, buildings, or due to crop conversions, deforestation, changes in land use, etc.—create favourable conditions for their invasion [7,8]. Specifically, all these modifications: induce a release of resources; influence the interactions between species; alter the substrates; and modify the physical environment [9]. It is no coincidence that the habitats most disturbed by urbanization and tourism, such as those in coastal and island areas, lakes, rivers, and periurban forests, are where most alien species are found [10].

Another factor involved in IAPP invasions is climate change. The current climate trend towards global warming acts directly on IAPPs by creating favourable conditions for their establishment in formerly unsuitable areas [11]. In addition, higher temperatures enhance the fitness of the more thermophilic IAPPs, favouring their reproductive and dispersive biology; furthermore, milder climates increase the number of yearly reproductive cycles and of individuals surviving the winter season [12]. Changes in climate additionally bolster IAPPs indirectly by making plants more susceptible, since adverse climatic factors, such as extended drought and extreme weather events (e.g., rainstorms, windstorms, hail, and severe flooding), impact plant health, reducing plant growth and vigour, altering phenology, impairing physiological processes, and creating wounds that favour IAPP attacks [13,14].

Some of the major impacts of forest IAPPs are: reduction of primary production; alterations of evolutionary processes, both in host populations and in organisms taxonomically related to the invaders; changes in ecological relationships within tree communities (for example, alteration of symbiotic relationships, either mutualistic or antagonistic, between the tree species and their animal or microbial symbionts); decrease or loss of ecosystem services (water filtration and supply, climate mitigation, erosion prevention, nutrient cycling, carbon storage, and habitat provision); and demise of native species (extinction) [12,15].

The governments of various countries are paying great attention to the problem of the introduction of organisms harmful to agriculture and forestry; hence, phytosanitary protection has become an important component of their agricultural and forestry policies [16]. In an attempt to counter this growing phenomenon, many countries have started adopting increasingly stringent measures aimed at ensuring the early detection of banned pathogens and pests, as well as at eradicating harmful quarantine organisms present locally [17]. Furthermore, intergovernmental regional plant protection organizations try to tackle the problem on a regional scale, aiming to ensure adequate levels of plant protection through a coordinated series of phytosanitary actions [18].

2. IAPP Pathways

The movement of IAPPs to novel locations can occur naturally or through human-mediated processes. Natural movement, even over long distances, always occurs along a trajectory that follows a regular, expected colonization pattern [10]. The populations that colonize a new environment normally originate from nearby areas, such as neighbouring islands or the adjacent mainland, and, in any case, they follow a path that can be predicted according to existing knowledge about their biology, the biology of their vectors, the prevailing winds and water currents (in particular for oomycetes), as well as their dispersal capabilities (migratory capacity) [10]. Human-mediated transport, on the other hand, takes place on a much larger scale [19], since a given species can be taken from one point on the planet and released on the opposite side of the globe. Such transportation both breaks up natural biogeographic barriers and disrupts natural evolutionary processes, constituting a concrete threat to the planet’s biodiversity [20]. Such anthropogenic conveyance of agricultural and forest pests has increased immensely in terms of frequency, geographical breadth, and number of species involved.
Among the human-dependent causes of the introduction of forest IAPPs, postal traffic, tourist activities, and, of course, global trade play a leading role [6]. The movement of people in general, either internationally or domestically, influences the amount of interception. Liebhold et al. [21] has quantified this and showed how the number of insect pests intercepted in baggage was positively correlated to the number of travellers entering the U.S. As regards trade-related transport, the main pathways are germplasm (tree seeds, cuttings, and plants for planting) and wood (logs, firewood, processed wood, as well as packaging material, etc.). According to Meurisse et al. [6], live plants and wood packaging material are the main source for movement of forest IAPPs beyond their range limits into new, uncontaminated forest areas, based on the data collected in the ports of entry in the U.S. and New Zealand.

Live plants and wood packaging material have also been confirmed as the main pathways for IAPPs in Europe based on interceptions at ports of entry during the last 5 years (Figure 1). The European Union Notification System for Plant Health Interceptions (Europhyt) (https://ec.europa.eu/food/plants/plant-health-and-biosecurity/europhyt/interceptions_en, accessed on 1 June 2021) records interceptions of new pests and diseases made by EU Member States [22]. Among the main intercepted commodities in this database, there are the following categories: “plants”, which includes plants for planting, scions, cuttings, leaves, flowers, branches with foliage; “wood-packaging material”, such as wooden crates, wood pallets, wooden packaging material, dunnage; “wood and bark”, including roundwood, bark, and processed wood; “produce”, such as fruits, vegetables, seeds; “soil”, including soil and growing media. “Plants”, in particular those coming from Asia and Africa, constitute the most important pathway of forest IAPPs into Europe. The “plants” pathway is followed by the “wood-packaging material”, again mainly coming from Asia. Although wood has historically been one of the most common introduction pathways, Europhyt data relating to the 2016–2020 period show that interceptions of harmful organisms on this commodity have reduced significantly, while “wood-packaging material” has moved up to second place. In Europe, there is a third major pathway: “produce”, which is an important entry route mainly for agricultural IAPPs (Figure 1). One feature of imports which is overlooked is “soil”. The scarce or absent interception of alien organisms in the “soil” (Figure 1) is to be attributed to the very nature of this material, which hampers detection. This is because harmful IAPPs present in the soil remain hidden inside this matrix [5]. Asia was found to be the main source of alien plant insects, followed by Africa and, to a lesser extent, South America (Figure 1). On the other hand, fungal pathogens were intercepted on commodities coming mainly from South America, and secondly, from Asia. However, it should also be considered that EU phytosanitary rules impose a ban on different commodities imported to EU, a restriction that could impact the rate of interceptions on imports from different continents.

A fact that immediately stands out, according to McCullough et al. [23], is that insect interceptions largely prevail over fungal interceptions. This essentially depends on the fact that many fungal pathogens possess a latent phase during which they are not visible on plant surfaces [24,25]. Figure 1 shows how fungal infections become more frequent on fresh plant produce. This is because the herbaceous (fleshy) consistency of fresh plant produce makes this commodity more easily colonizable and, as a consequence, disease symptoms and/or signs become noticeable in a shorter time [23].

The higher frequency of insect interceptions at ports of entry compared to fungal pathogens, corresponds also to a higher number of insects established in new areas (Figure 2). This is because fungi, as microorganisms, are generally not visible (the fungal fruiting bodies are not always present), thus they remain less noticeable and less detected. However, even considering only the species with a high impact, whose effects have been tangible in terms of damage, insects continue to be reported in the highest numbers, as results from the European Alien Species Information Network indicate (EASIN; http://easin.jrc.ec.europa.eu, accessed on 10 June 2021).
Figure 1. The frequency of fungus and insect interceptions at ports of entry in Europe in the 2016–2020 period (data obtained from reports of Europhyt). Circle sizes indicate the relative amount of interceptions of IAPPs (fungi and insects) within each transport pathway according to their continents of origin. The black sector of the circle denotes the relative frequency of insect interceptions; the white indicates fungi interceptions. Legend: soil = soil and growing media; wood and bark = roundwood, bark, and processed wood; packaging material = wooden crates, wood pallets, wooden packaging material, dunnage; plants = plants for planting, scions, cuttings, leaves, flowers, branches with foliage; produce = fruits, vegetables, seeds.

Figure 2. EU geographical distribution of invasive alien species of fungi (a) and insects (b) introduced into terrestrial and fresh-water environments from 1999 to 2021 (source: EASIN—European Alien Species Information Network). Fresh-water environments were also surveyed to include water moulds (Oomycetes).
The European climate turns out not to be a key factor in determining the abundance of IAPPs introduced. In fact, high numbers of new reported infestations are found in countries from both southern and northern Europe (Figure 2). Instead, other factors, such as trade volume, the presence of roads, and human population density are all correlated with the introduction of alien species to Europe [26].

3. Factors Driving the Invasion Process

The chance of newly introduced harmful organisms becoming invasive in new geographic areas is always uncertain [10]. Indeed, few of these survive either the chronic or occasional forces they encounter in the new environment. Only a very small percentage of them ever become naturalized, and even a smaller fraction ends up becoming invasive [27]. In fact, all non-native species must survive three distinct phases, not always clearly distinguishable, before being able to inflict ecological and economic damage: (1) transport: individuals are taken from their area of origin, transported to a new area, and released into the recipient environment; (2) establishment: the newcomers settle in the non-native environment and implant a reproductive population—among the set of the transported individuals, only a few are capable of this; (3) spread: colonizers grow in abundance and expand their geographical range. These phases are mandatory steps in the invasion process, and the advancement from one to the next one involves overcoming hefty ecological barriers [28]. These hindrances, in fact, allow only a small percentage of the introduced species to advance to the next phase (generally between 5% and 20%, with an average of roughly 10%). Based on this assumption, Williamson [29] introduced the so-called “10 rule”, according to which only one out of 10 new introductions would be successful in overcoming any single barrier. This approach has made it possible to analyse the various opportunities IAPPs have to successfully establish into new areas. Invasions, for example, always start with a limited number of individuals being transported and released into a novel location; here, they must be able to survive and give rise to an initial population capable of persisting in this new area. Only when the newcomer species becomes numerically abundant and begins to spread rapidly may “an outbreak” be generated, causing damage to agriculture, the environment, and the local economy, and being perceived as “invasive”. If, on the contrary, the population is not able to grow and expand, it remains small in number and is only local (an “endemic occurrence”) [30,31]. However, there is an ongoing debate within the scientific community regarding the reliability of the “10 rule”, since it can lead to underestimating the impact the introduced organisms can have in new introduction areas [32].

An alien species may have different outcomes in distinct sites of a same region [33]. The first arrivals may survive, reproduce, and spread to become invasive at some locations, while they may succumb at others, even if all individuals of that species share the same traits: e.g., aggressiveness, competitiveness, frugality, polyphagy, tolerance to adverse environmental conditions [34]. In fact, the physical and biological external forces, collectively known as “environmental resistance”, which the alien species has to face, vary from site to site, ultimately determining their fate [35]. Among the most common physical forces the alien species has to withstand are: the availability of nutrients, water, oxygen, light, space, shelter, or protection (e.g., the inner tissues of a plant for a fungal endophyte). Biological forces that can effectively hinder the invasion, instead, are: competition, predation, parasitism, and diseases, as well as other interactions with the resident community, including anthropogenic perturbation [36].

Evidence exists that IAPPs perform better than native pathogens and pests in the invaded community, and this can be attributed to various factors. One key reason for their successful infiltration is a higher host susceptibility in the new non-native range, due to the absence of coevolution with the indigenous hosts, the newcomer IAPPs can grow very rapidly and inflict greater damage, in some instances generating overwhelming outbreaks [37]. Another cause is that in the new environment the IAPP may also jump onto new host(s), which may even be taxonomically unrelated to its native hosts [38].
is a fairly common phenomenon, whose frequency probably depends on the presence in the introduction area of native plants taxonomically close to the original host plant [39]. Another factor favouring IAPP outbreaks is the scarcity of natural enemies in the new range compared with their native range. According to this “enemy release hypothesis”, IAPPs leave behind all those natural enemies that would naturally keep their population under control in the area of origin. In the new environment, moreover, it encounters very few natural enemies able to use it as a trophic resource [40,41]. All these factors enable the IAPPs to exploit their enormous reproductive potential and to spread rapidly on a large scale, even displacing native species [42].

4. Invasive Alien Pathogens and Pests Harming Forests

The harm caused by the introduction of alien forest pathogens and pests is often difficult to fully quantify due to the multiple ecosystem services forests offer, and because each invasion event must be analysed within the specific context (forest, nursery, district, country, region) in which it occurs [43,44]. The damage may not only be significant at the economic, ecological and landscape level, but it might also generate negative repercussions in related sectors, such as in marketing and tourism [45].

4.1. A Retrospective Look

The forest and rural landscapes of various areas of the planet were transformed in the last century by the introduction of dangerous non-native forest pathogens [46]. Between the 1920s and 1940s, the agent behind Dutch elm disease (DED), Ophiostoma ulmi (Buisman) Nannf, spread pervasively throughout Europe and North America on native elm species [47]. The invasion by this vascular pathogen, native to Asia, soon turned into a true pandemic [48]. Moreover, the several variants the fungus spawned over time, including the more aggressive subspecies americana of Ophiostoma novo-ulmi Brasier, were introduced to Europe from North America via infected logs [49]. As clear evidence of the fungus’ high evolutionary potential and destructiveness, it eventually led to the almost total disappearance of the European field elm (Ulmus minor Mill.) from many countryside and urban districts of Europe [50].

Similarly, iconic tree species of the genus Castanea, such as the American chestnut Castanea dentata (Marsh.) Borkh. and the sweet chestnut Castanea sativa Mill., were, in the last two centuries, wiped out from forest ecosystems and orchards due to the combined, sometimes synchronous, attack of the two fearsome oomycete pathogens, Phytophthora cambivora (Petri) Buisman and Phytophthora cinnamomi Rands [51], as well as of the ascomycete chestnut blight agent Cryphonectria parasitica (Murrill) M.E. Barr [52]. In many European countries, the epidemic spread of chestnut blight led to a severe loss of chestnut cultivation. The disease devastated coppices and orchards, with tragic effects on the already poor economy of many farming communities, for which the edible chestnut fruit was a primary source of food, causing famine and emigration [12].

Around the 1930s, another harmful pathogen, Ceratocystis platani (J.M. Walter) Engelbr. and T.C. Harr., the agent behind blue stain canker in plane trees or sycamores (Platanus occidentalis L.), spread epidemically first in the suburbs of Philadelphia, and then in many cities in the south-eastern U.S. [53]. Subsequently introduced into the Mediterranean basin either during World War II or soon after, in just a few decades this vascular pathogen gradually killed a multitude of monumental P. occidentalis and Platanus orientalis L., and their hybrid Platanus x acerifolia (Aiton) Willd., trees in city parks, squares, and boulevards [54]. The high genetic uniformity of host populations (most urban trees were clones) and the lack of knowledge about the high infectivity of fungus propagules, which can remain viable at length on pruning tools, favoured the outbreaks of blue stain canker [55].

Seiridium cardinale (W.W. Wagener) B. Sutton and I.A.S. Gibson, the agent behind cypress blight, is an anamorphic fungus native to the west coast of the U.S. (California), where it was first recorded on Monterey cypress (Cupressus macrocarpa Hartw. ex Gordon) in 1927 [56]. Despite lacking sexual reproduction, the pathogen was able to spread worldwide
epidemically in a short time [57]. Accidentally introduced into Mediterranean Europe during the mid-1900s [58,59], in a few decades it killed planted and ornamental cypress trees (Cupressus sempervirens L.) in stands, windbreaks, parks, villas, cemeteries, and treelines. The destructive cypress blight outbreaks deeply altered the Mediterranean landscape, causing a true ecological disaster [60]. Cypress is, in fact, an iconic part of the Mediterranean countryside, so its disappearance also impacted local economies and tourism [57].

Alien insects can pose a direct danger to plants, but they can also act as vectors for phytopathogenic microorganisms [61]. In addition, native insects sometimes also play an important role in the spread of exotic diseases. For example, the bark beetle, Phloeosinus aubei (Perris), native to the Caucasus, Asia Minor, and the Mediterranean area, contributed to the increase in damage caused by the exotic S. cardinale by carrying its fungal spores; thus the beetle facilitated the fungus’ colonization of host trees. In addition, over the last few decades, this bark beetle has continued to spread into Central Europe, where it is considered an alien pest [62]. Similarly, Scolytus multistriatus (Marsham) (Coleoptera: Curculionidae), with a Paleartic native range (from western Europe to Russia and northeast Africa) [63], is the main vector of D.E.D., not only in its native range but also in introduced areas, such as North America, where, before the 1930s, 50%–75% of the elm population in the north-eastern part of the continent were killed by this vascular pathogen [64].

Insects harmful to forest trees are also included among the world’s worst 100 IASs [65]; those of forest concern include the gypsy moth, Lymantria dispar L. (Lepidoptera, Lymantriidae), and the cypress aphid, Cinara cupressi (Buckton) (Hemiptera, Aphididae). The gypsy moth, native to Europe and Asia, was introduced near Boston, Maine, in the late 1860s, and currently is listed as one of the most destructive invasive pests, ranking third among the costliest IASs in the world [66]. Its larvae cause serious defoliation of many tree and shrub species, which may ultimately die or become susceptible to subsequent infestation by secondary pests. From 1924 to 2013, in the north-eastern and mid-western U.S., over 37 million hectares were defoliated [67], with a high impact on timber, costs and losses to urban and suburban forests, as well as damage to the recreational sector [68,69]. In addition, gypsy moth outbreaks have contributed to the decline of oak forests in eastern North America [70]. The cypress aphid is also a highly invasive insect; probably native to North America and Syria, since the 1960s it has become newly established in parts of Europe, Africa, South America, and the Middle East [71]. The cypress aphid, which sucks sap from twigs, causes yellowing to browning of the foliage. Depending on the severity and duration of the infestation, trees may suffer more or less severe damage, or even death in the worst cases [72]. In recent decades, sudden and explosive outbreaks of the cypress aphid have occurred in many countries (some African countries, Italy, Jordan, Yemen, Mauritius, and Colombia). As a consequence, populations of the host trees (Cupressus, Juniperus, Widdringtonia, and other Cupressaceae) have been decimated, both in commercial and ornamental plantings or native stands [73].

4.2. Emerging Invaders

Among the many currently emerging threats to forest ecosystems, oomycete Phytophthora species are at the pinnacle. For example, Phytophthora ramorum Werres, De Cock et Man in ‘t Veld, a polyphagous, invasive pathogen originally from the laurosilva forests of eastern Indochina and Japan [74], attacks a multitude of shrub ornamentals and tree species. After causing extensive tree mortality in oak (Quercus spp.) and tanoak Notholithocarpus densiflorus (Hook. & Arn.) Manos, Cannon and S. H. Oh) forests in California (for this it was called the agent of “sudden oak death”) [75], this destructive oomycete has been more recently killing off plantations of Japanese larch [Larix kaempferi (Lamb.) Carr.] in the UK, where it was renamed the agent behind “sudden larch death” [76]. Furthermore, the infamous P. cinnamomi, the causal agent of ink disease in chestnuts, already mentioned above, continues to destroy woody plants in natural environments, plantations and urban forests, as well as in parks, horticultural nurseries, and urban ornamental plantings
around the world, to the point of earning the nickname of “biological bulldozer” [77]. *P. lateralis* Tucker and Milbrath is considered to be of Asian origin, such as the several *Chamaecyparis* species that, due to the similar native range, exhibit some tolerance or resistance to infection. It is also a harmful pathogen, responsible for serious root and aerial infections [78]. This oomycete shows considerable host specificity, with Port-Orford cedar (*Chamaecyparis lawsoniana* (Murray) Parl.) its main host, but it has also caused epidemic damage to *Taxus brevifolia*, *Thuja*, and other *Chamaecyparis* species growing in proximity to infected *C. lawsoniana* in forests, plantations and in the landscape [79].

Rust fungi also pose a constant threat to many forest ecosystems, mainly because of their high dispersal ability over long distances. It is therefore no coincidence that rust fungi are the largest group of pathogenic fungi in the EPPO (European and Mediterranean Plant Protection Organization) A1 List of Pests Recommended for Regulation as Quarantine Pests (EPPO, https://www.eppo.int/ACTIVITIES/plant_quarantine/A1_list, accessed on 30 June 2021). One invasive rust that has been spreading pervasively throughout Europe in recent years is the fungus *Melampsoridium hiratsukanum* S. Ito ex Hirats. f., of Asian origin [80]. This rust is currently causing heavy defoliation, stunted growth and death to riparian *Alnus incana* (L.) Moench trees in the eastern Alps, threatening the stability of some riverbanks. In this mountain range the fungus has also found *Larix europea* L. to be a suitable alternate host on which to complete its life cycle [81].

Moreover, a highly destructive fungal disease of ash trees (*Fraxinus* spp.) is at present causing significant damage to ash populations throughout the European continent. The causative agent, *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz and Hosoya (anamorph: *Chalara fraxinea* T. Kowalski), kills young and coppiced ash trees in a very short time, whereas older trees can resist its irritative action for some time, until they are exposed to high inoculation pressure [82]. The resultant ash dieback is seriously impacting woodland biodiversity and ecology, reducing landscape aesthetics and gravely damaging hardwood industries, with heavy economic losses [83].

Yet another tree staple, pine stands, are currently being impacted worldwide by the destructive “Pine Pitch canker”, caused by *Fusarium circinatum* Nirenberg and O’Donnell, (teleomorph: *Gibberella circinata*) [84,85], as well as by some highly damaging foliar pathogens, such as *Lecanosticta acicola* (Thümen) H. Sydow [86], agent of Lecanosticta needle blight (LNB) and the related fungi, agents of Dothistroma needle blight (DNB) or of “red band needle disease” (*Dothistroma septosporum* (Dorog.) Morelet (syn. *Scirrhia pini* Funk and Parker, teleomorph: *Mycosphaerella pini* Rostr.) and *Dothistroma pini* Hulbary (teleomorph: unknown) [87–89]. *F. circinatum*, considered native to Mexico, has spread in the last half century to many pine growing areas, causing severe damage to artificial plantations in the Americas, the Far East (Japan and the Republic of Korea), and in southern Africa [90]. DNB causes premature needle abscission, stunted growth, and, in some cases, tree mortality [91]. The disease represents a serious threat to both natural forest ecosystems and exotic pine plantations on all continents (it occurs everywhere except Antarctica) [92]. The disease has been primarily associated with exotic plantations of Monterey pine (*Pinus radiata* D. Don) but, starting from the 1990s, it has caused serious damage in stands of both planted and native pine species, e.g., in *Pinus contorta* subsp. *latifolia* stands in Canada and in *P. nigra* subsp. *laricio* stands in the Mediterranean region [8,93].

Some invasive pests involve symbiotic relationships between insects and fungi; in this case, the whole complex (the insect and its fungal symbiont) is introduced into the new environment. For example, the complex of *Geosmithia morbida* Kolařík (Ascomycota, Hypocreales, Bionectriaceae) and its vector, the bark beetle *Pityophthorus juglandis* Blackman (Coleoptera, Curculionidae, Scolytinae) is responsible for Thousand Cankers Disease (TCD) in walnut trees. First described in North America, TCD causes progressive crown decline, with the fungus colonizing the copious feeding and reproductive galleries made by its symbiont, the phloem-boring bark beetle. This results in numerous, coalescent cankers that girdle branches and trunks, ultimately leading to the tree’s death [94]. This insect–fungus complex has been recorded in Italy, where in northern and central regions several
plantations were found to be being attacked [95,96]. Another example is the polyphagous shot hole borer, *Eucalyptus fornicata* (Eichhoff) (Coleoptera: Curculionidae), an ambrosia beetle native to Asia that was accidentally introduced into Central and North America, Israel, and South Africa. This emerging tree pest carries the spores of three ambrosial fungi within specific body structures (mycangia), which are the only trophic source for insect adults and larvae. One of these fungi, *Neocosmospora (= Fusarium euwallaceae*) (S. Freeman, Z. Mendel, T. Aoki and O’Donnell) Sand.-Den., L. Lombard and Crous, a moderately virulent pathogen, is responsible for causing dieback in a range of susceptible host trees, or even mortality, depending on the level of infestation. This insect–fungus complex has caused significant damage to orchards and ecosystems around the world, even attacking important forest species [97].

Other insect species of great impact are the Asian long-horned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), and the citrus long-horned beetle, *A. chinensis* Forster (Coleoptera: Cerambycidae). These are xylophagous insects native to Asia, whose big larvae can kill healthy broadleaf trees. The first record of an established population of *A. glabripennis* outside its native range was in 1996 [98], while that of *A. chinensis* was in 1999; both occurred in North America [99]. In Europe, eradication was successful at the sites where *A. chinensis* was discovered shortly after its introduction, proving how early detection is key to prevent the lasting establishment of the pest and to implement effective control measures [100]. Furthermore, the importance of citizen involvement in early detection was highlighted in 2008, when every new outbreak was first reported by members of the public [101].

However, when an IAPP species is not considered a major pest in its native range, it is unlikely to be included on IAS watch lists. Consequently, specific early detection surveys for that pest are not in place. Furthermore, it is difficult to predict the invasiveness of a non-native species in a new environment. Such was the case not only for pathogenic fungi, such as the ash dieback agent *H. fraxineus*, but also for several insect species, such as, for example, the emerald ash borer, *Agrilus planipennis* (Fairmaire) (Coleoptera: Buprestidae), a phloem-feeding beetle native to Asia, where it was only marginally studied as a minor pest. Once accidentally introduced (in 2002) in the United States, however, it became the most destructive forest pest ever recorded in North America [102]. Millions of ash trees have already died because of *A. planipennis*; the infestations have spread over 35 US States and two Canadian Provinces, as of 2020 [103]. The emerald ash borer has also reached European Russia, being first recorded in Moscow in 2003; it is now already present in nine Russian regions [104]. In 2019, it was also confirmed for the first time in Ukraine, revealing how the beetle is continuing to expand its range towards Europe [105]. Because of what already happened in North America, the beetle is being addressed in Europe with more groundwork, trying to develop all the necessary measures to contain the problem [106]. However, it has yet to be determined whether the European ash (*Fraxinus excelsior* L.) is going to be susceptible to severe damage; in fact, most of the infested trees in Russia are in artificial urban settings of *F. pennsylvanica* Marshall [104].

5. Mitigating Threats to Forest Health: Possible Solutions and Action Strategies

In natural forests, the better approach is to actively maintain ecological integrity to ensure forest resilience, whereas in forest plantations the restoration of increasing levels of biodiversity should be favoured as the first line of defence against invasive pests and pathogens [107]. In this last case, the careful choice of appropriate plant material is always fundamental, specifically, avoiding the use of species unsuited to site conditions, as well as limiting the number of exotic plant species [108], since in the last century, non-native tree species, widely used as ornamentals or in afforestation programmes, acted as “Trojan horses” for many harmful diseases and pests [8]. Clear examples are the accidental introductions of *P. ramorum* into North America with nursery plant material [75], of *Teratosphaeria* (*Mycosphaerella*) *nubilosa* (Cooke) Crous and U. Braun, a causal agent of Mycosphaerella leaf disease of eucalypt, into South America (Uruguay) with propagation material of this exotic
Forests 2021, 12, 1364

10 of 20

tree species [109], of *Rhynchophorus ferrugineus* (Olivier), harmful to palm trees widely diffused in South Europe [110], and of *Ophelimus maskelli* (Ashmead) (Hymenoptera: Eu-olphidae), which damages eucalypt plants in the Mediterranean Basin [111]. Furthermore, in forestry it is always advisable to avoid genetic uniformity, such as clonal plantations, as in poplar cultivation. Mixed forests, instead, are generally less prone to diseases and pests than monotypic stands, with nonhost trees creating effective physical and chemical barriers to the spread of pathogens’ inoculum, as well as hindering host searches by pests. In addition, higher biodiversity favours natural enemies and competitors which, interacting with IAPPs, contribute to keeping the invaders’ population densities low [107].

Preventing the introduction of dangerous IAPPs into new areas is the first step in their management, so this has become an important priority in many countries. Preventing introductions is carried out through effective surveillance activities, namely phytosanitary inspections at ports of entry (ports, airports, and custom barriers), as well as at vulnerable sites, i.e., those places where the plant material is in transit or processed, such as nurseries, loading and sorting stations, and wood processing companies [112,113]. Considering the enormous volume of commerce at present, and the incessant mobility of humans for work, tourism, etc., many IAPPs elude preventative measures, it being practically impossible to intercept all the species that transit on all commodities [114,115].

Careful prediction of potential invasiveness of harmful pests and diseases can aid interceptions [116]. Important predictive tools are those provided by international organizations such as the CABI (Commonwealth Agricultural Bureaux International) and the EFSA (European Food Safety Authority), as well as various Regional Plant Protection Organizations such as the EPPO, the NAPPO (North American Plant Protection Organization) and the APPPC (Asia and Pacific Plant Protection Commission), which were created to develop international strategies to fight the introduction and spread of harmful pests and diseases and to promote safe and effective pest control methods. In fact, they provide constantly updated lists of organisms considered as threats to agriculture, forestry, and the environment and that are most likely to be introduced into Europe and North America. These agencies’ published assessments of invasion risks are important tools since they focus the efforts of inspection services, plant health scientists, and all the stakeholders affected by imported pests and pathogens [117]. Another important early warning system of new and emerging pest and pathogen risks is sentinel plants [118]. These can be: (a) plantings made with young, frequently exported native plants which are used to identify pests and diseases that may be introduced to import countries through the trade in live plants; and (b) plantings made of non-indigenous young or mature plants in import countries whose monitoring could give useful information about the potential damage of non-native pathogens and pests if they were to arrive and become established [119].

A primary obstacle to managing and mitigating alien forest pests is correctly identifying the agents of damage [117]. Traditional identification methods, essentially based on the analysis of macro- and/or micro-morphological characters, have inherent limitations. Considerable experience is necessary to induce the formation of fungal distinguishing structures in vitro and substantial expertise is needed for their microscopic observation and identification; moreover, special growth media (i.e., differential or selective substrates) may not be available for certain, fastidious microorganisms. In any case, these procedures are not applicable for unculturable microbes such as biotrophic fungi [120]. The above difficulties involve the fact that some taxa, for example, are not easily identified through morphological characters, so this entails inspectors with specific expertise [114]. In addition, some insects have juvenile stages that are indistinguishable by classical diagnostic methods. Furthermore, phytosanitary inspectors may face plant material that has been attacked, but which has already been abandoned by its phytophages; therefore, they have to track the pest only on the basis of the traces left behind, which becomes a more difficult task. It is also true, on the other hand, that the reproductive structures of many forest pathogens can be observed on infected plant material, and these are of a great diagnostic value [81]. Furthermore, when the reproductive structures (e.g., fruiting bodies) are not
present on the host surface, they can still be obtained in the laboratory by using a moist chamber; alternatively, the isolation from infected plant material into pure culture can permit the growth and identification of the causal agent.

Many of the difficulties inherent in traditional morphological identification can nowadays be overcome by employing molecular techniques. Furthermore, for an effective inspection system which can cover the ever-increasing volume of import–export material, simple, timely, and repeatable methods have to be developed. Modern molecular diagnostic tools, which detect DNA polymorphisms, ensure high accuracy and diagnostic sensitivity, allowing the detection of even minimal traces of nucleic acids, such as those remaining in the frass of xylophagous insects [113]. Some of these methods have the advantage of being able to process a large number of samples in a short time [121]. For example, loop-mediated isothermal amplification (LAMP) is a nucleic acid amplification method that offers rapid, accurate, and cost-effective diagnosis of diseases and pests [122–124]. The simplicity and the portability of the equipment also make it a tool of choice for carrying out tests in situ, making inspection greatly easier [8]. Molecular methods are therefore of great help when it is necessary to focus attention on clearly defined species, for example for delimiting surveys at vulnerable sites known or suspected to harbour a given pathogen or pest, while conventional (e.g., morphology-based) methods continue to retain their high validity for the control of the territory for the occurrence of unknown IAPPs. In other words, morphological and molecular methods should go hand-in-hand and complement each other, with DNA-based techniques representing versatile tools to support and extend more classical species identification and taxonomy [125].

Novel diagnostic methods are also useful in monitoring the dynamics and ecology of a given IAPP after its introduction. These techniques are in fact also highly effective in: detecting early disease and insect foci; tracing and quantifying pathogens’ inoculum (especially airborne inoculum) and insect populations; and locating infection and infestation reservoirs (e.g. storage facilities) that sustain invasion events [126]. National and local inspection services also make use of innovative strategies, including remote sensing technology (GIS and unmanned aerial vehicles like drones) [127,128] and detection dogs, whose keen smell can locate biological targets [129]. This last method was used for the first time for gypsy moths and later for other alien and invasive insect species [130].

The mobilisation of citizens as additional observers and reporters (citizen science) has become increasingly utilized for the early detection of unwanted IAPPs. Active monitoring by citizens, when extensively distributed throughout the territory, has in fact become an important part of biosecurity efforts to prevent IAPPs’ establishment and spread [131]. However, to obtain the consent and collaboration of citizens, they must be properly informed about the risks and dangers associated with non-native pathogens and pests for native plants, also because citizens have sometimes opposed management interventions aimed at containing and eradicating harmful alien organisms [132]. Well-informed citizens, besides supporting the accurate monitoring of the territory by inspecting sites and trees, are also a fundamental resource for collecting, categorizing, transcribing, and analysing data [133]. Citizen science is possible today due to a growing number of citizens with ecological awareness and knowledge eager to contribute as volunteers [134]. Some examples of citizen science projects include Observatree (https://www.observatree.org.uk, accessed on 31 July 2021) in the UK and LIFE ARTEMIS (https://www.fujerodne-vrste.info/en/, accessed on 31 July 2021) in Slovenia; in addition there are several citizen science networks, such as the EASIN (https://easin.jrc.ec.europa.eu/easin/CitizenScience/BecomeACitizen, accessed on 31 July 2021), which is an initiative of the European Commission that aims to connect citizens, scientists and policymakers in an effort to manage harmful alien invasive species.

Once an IAPP has been detected within an area of concern, the next move is to try to eradicate invasion foci [135,136]. Quick action while IAPP populations are still small is the most efficient way to prevent ecological or economic harm. With forest IAPPs the only control options are mechanical approaches (such as sanitation cutting) [137], biological
control, and the use of semiochemicals (e.g., mass trapping) [10]. While eradication of alien forest insects has been effective in some cases [138], the eradication of forest pathogens has always been incredibly challenging, with most of the successful interventions taking place in controlled environments (greenhouses and tree nurseries) or in urban green spaces (e.g., parks, trees, and gardens) [139].

After an IAPP population has newly established in a forest, biological control is one of the main measures to achieve self-sustaining long-term control [140]. In some cases, biological control has managed to restore more sustainable pest population dynamics, succeeding in keeping the population density of the invasive species below the damage thresholds [141–143]. For instance, the parasitoid Torymus sinensis Kamijo (Hymenoptera: Torymidae) proved to be a good control agent of the Asian chestnut gall wasp D. kuriphilus in several areas of the world, significantly reducing the pest populations with a self-sustaining effect [144]. Similarly, in North European conifer forests, the fungus Phlebiopsis gigantea (Fr.) Jul. has been successfully employed in the biological control of the root and butt rot pathogen Heterobasidion annosum (Fr.) Bref. [145,146]. Commercial formulations based on this biocontrol agent have even since been developed and are commercially available under the names of ‘PG suspension™’ in the UK, ‘Rotstop®’ in Finland, and PG IBL in Poland [146,147].

Biological control is not, however, a universal remedy; it is not always effective and several negative effects may occur. This variability in the efficacy of biological control in forest ecosystems is a frequent drawback, mainly due to the complex and multi-partite interactions between the tree, the IAPP, the biocontrol agent, and the other biotic factors [148], all of which are, in turn, impacted by the physical environment and human interference. Biological control in heterogeneous forest ecosystems, therefore, in order to be successful, should take into consideration the multiple biological factors involved: including the environmental conditions (e.g., soil properties, microclimate, etc.), type of forest stand, and silvicultural management [149]. Controlling IAPPs by introducing their natural enemies, many of which are exotic themselves, is a controversial issue whose effects may be viewed as “deliberate ecological invasions”. Retrospective analyses of several biological control programs around the globe are now available, thus providing quantitative data on negative effects: parasitism/predation on non-targets; competition with native natural enemies; intraguild predation; vectoring of pathogens [150]; and risk of hybridization with related native species [151]. Due to the increasing awareness of the related environmental and economic risks, many countries have implemented regulations for the release of biological control agents [152].

For the management of IAPP invasions, more stringent rules and policies are needed to protect plant health and to ensure a safer trade [153]. The need for such measures has long been recognised: at a regional level Plant Protection Organizations are trying to enforce phytosanitary policies, regulations and technical recommendations [154]. For example, the defence of the European territory and its plants has been recently tackled with the adoption of new rules (Regulation (EU) 2016/2031), which improve the European phytosanitary regime through more effective measures. A global effort is also required, involving all the countries and policymakers that in various ways may contribute to counteracting the problem. Specifically, international politics should work towards: consolidating phytosanitary coordination among the countries; harmonizing phytosanitary measures; eliminating the gaps between international and national laws; filling legislative gaps by implementing preventive and/or corrective legal actions; promoting more incisive and restrictive actions at national, regional, and international levels; and establishing legal responsibility frameworks to sanction countries that do not respect international regulations [117].

6. Role of Research

The introduction of IAPPs into new territories is a current environmental issue and a dominant theme of scientific research. Phytosanitary protection has become one of the priorities of many nations, as proven by the numerous funded research projects on this
subject [155]. Information about the taxonomy, biology, and ecology of IAPPs during the onset of an invasion process is often lacking, especially as regards their reproduction and dispersal abilities into areas where they have been newly introduced; this knowledge gap may favour their establishment and uncontrolled spread [156]. Plant health scientists, besides being involved in the diagnosis of IAPPs, which, often being new, are sometimes little known, are also concerned with their taxonomic positioning, as well as with the characterization of those subspecific entities that are difficult to determine by traditional approaches [157]. The development of diagnostic methods is especially important for those IAPPs endowed with a latent phase, because latency increases the risk of their spreading undetected. However, research also needs to be performed in other, fundamental aspects of the IAPPs’ life history strategies: their demographic history (gene flow, migration); mode of reproduction (i.e., sexual vs. asexual); recombinational events outside the sexual cycle, such as parasexuality and horizontal gene transfer, affecting pathogen virulence [158]; occurrence of hybridization events between related taxa [159]; microbial/pest virulence/aggressiveness versus host resistance. A constant threat is posed to forests by the possible arrival and co-occurrence of new mating types and haplotypes. While the coexistence of different mating types increases the chances for sexual recombination between genetically divergent lineages, continual haplotype introgression can give rise to the emergence of new pathotypes with heightened virulence. These natural events, which have become more frequent as a result of international trade and climate change, are strongly feared in many pest–plant interactions. The evolutionary and pathogenetic potential of P. ramorum, H. fraxineus, as well as of the walnut twig beetle P. juglandis, vector of TCD, to cite but a few examples, strongly depend on these mechanisms [78,137,160]. Research can thus dramatically advance our understanding of the evolution of pathogenesis and aggressiveness of pathogens and pests and of the epidemic risks associated with these phenomena.

This knowledge is crucial for enabling stakeholders (landowners, foresters, phytosanitary inspection services, and policymakers) to implement adequate management strategies. In addition, accurate information from the research community would also permit valid, standardized phytosanitary certification, which could be adopted in participating countries and support inspections of feared IAPP introduction, including in the exporting country. On an open market, which allows the free movement of plant material, the certification of propagation material is of primary importance to avoid the spread of diseases and pests into new areas [161].

7. Conclusions

The problem of invasions by forest IAPPs is enormous and complex. It concerns countries, international organizations, and agencies; it affects economic interests, involving a multitude of activities from local to global scales [155,162]. At a local level, the problem must be tackled by concentrating efforts both on preventing new introductions and on eradicating early invasion foci [136]. Since trade-related transport is the main source of forest IAPPs, particularly that involving germplasm and wood-packaging material, this is where immediate action should be taken [6]. Implementing surveillance campaigns on these pathways would therefore help prevent, or at least minimize, the risks of introducing forest IAPPs.

In addition, forest health monitoring has now become of crucial importance. It is, however, challenging, due not only to the vast expanse of many forested areas, but also to the complexity of forest ecosystems, whose various compartments (soil, water, live plants, snags and logs) must be inspected by well-trained personnel [129]. Furthermore, due to the increasing rate of introduction of IAPPs, monitoring should be continual, and articulated across several activities: extensive monitoring of vast areas; intensive monitoring of vulnerable sites (loading stations, nurseries, import–export material checking points) [112]; the use of sentinel plants [118]; early warnings assisted by both conventional
and innovative molecular diagnostic tools [123]; and involving volunteers in early detection (citizen science) [131].

Research has always played a key role in pest management and it continues to do so even more nowadays when dealing with IAPPs. As we have pointed out in this paper, the scientific community is looking into a multitude of issues related to IAPPs, from correct taxonomic positioning [157] to diagnosis [126], from the analysis of recombinalional events between non-native and native species [159] to investigations into IAPPs’ adaptation to new environments [137]. This scientific support will also be crucial to government agencies’ setting up of effective control strategies [100], as well as to lawmakers tasked with enacting laws and regulations [117], who should be routinely notified of scientific advancements in this field.

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