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Review

Fungal Phytopathogens: Their Role in the Spread and Management of Invasive Alien Plants

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Abstract: Biological invasions pose a major environmental challenge, often facilitating the unregulated dissemination of pathogens and parasites associated with their hosts. These pathogens can severely impact native and cultivated species, with far-reaching ecological and economic consequences. Despite their importance, the mycobiota associated with invasive plant species remains relatively understudied, posing a complex challenge for researchers. The aim of this manuscript is to underscore the most significant threats posed by the uncontrolled transmission of fungal pathogens from invasive alien plants to native environments and agricultural systems, and to identify the factors influencing this phenomenon. We emphasize the role of pathogen spillback and spillover mechanisms in the domestication of invasive alien plants. The influence of environmental, host, and pathogen-related factors on the survival of fungal pathogens were also investigated. Finally, we explore the technical and legal feasibility of using plant pathogens as "green agents" to control invasive alien plants.

Keywords: biological invasion; phytopathogen; pathogens' transfer; invasive plant species monitoring; epidemics

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1. Introduction

The global spread of invasive alien species (abb. IAS) is recognized as one of the most significant ecological challenges of the 21st century, with profound implications for biodiversity, agriculture, and ecosystem stability [1]. Human activities, particularly increased global mobility, have accelerated the introduction of these species at an unprecedented rate, far outpacing natural processes. Due to their rapid growth and reproductive advantages, invasive alien plants often outcompete native flora, dominate ecosystems, and disrupt natural habitats [2]. This leads to widespread socio-economic, health, and ecological impacts on a global scale. For example, controlling black cherry (*Prunus serotina* Ehrh.) in Germany alone incurs an estimated annual cost of €25 million [3]. Invasive plants can destabilize national economies by adversely affecting agriculture, forestry, fisheries, and the ecosystems that provide critical livelihoods, particularly in developing regions [3]. Some invasive species, such as water hyacinth and knotweed, obstruct communication routes and infrastructure, while others, like *Ambrosia artemisiifolia* L. (common ragweed) and Sosnowsky's hogweed, pose direct health risks. Additionally, species such as black cherry and *Impatiens parviflora* DC. hinder forest regeneration, while *Solidago canadensis* L. (Canadian goldenrod) and common ragweed contaminate crops and disrupt traditional farming practices [4,5]. However, the challenges posed by invasive plants are not limited to the species themselves. The movement of IAS is often accompanied by the spread of pathogens and parasites associated with these plants. These pathogens play a complex role in biological invasions, acting both as facilitators and inhibitors of the invasive species' success. Once introduced, alien pathogens can pose a serious threat to native and cultivated species, amplifying ecological damage and destabilizing local economies. These intricate interactions between invasive plants and their associated pathogens highlight the need for a deeper understanding of their combined impacts on ecosystems and human livelihoods [6,7].

The dynamics between invasive plants and their associated pathogens can be explained through several ecological theories. The Enemy Release Hypothesis (ERH) [2] posits that invasive species often gain a competitive advantage in new habitats due to the absence or reduced presence of their natural pathogens and herbivores. This enemy absence allows invasive plants to allocate fewer resources toward defense mechanisms and more toward growth and reproduction, enabling their dominance over native species. However, this apparent advantage can be counterbalanced over time as pathogens present in the area of introduction adapt to the invasive host, a phenomenon referred to as the spillback mechanism [7]. In spillback, pathogens from the local environment colonize invasive plants, proliferate, and subsequently increase infection pressures on native co-occurring species, often with greater severity than on the invasive host. On the other hand, the spillover mechanism involves the introduction of alien pathogens alongside invasive plants, which then infect native flora unaccustomed to these new threats [7]. This process can lead to disease-mediated invasions, wherein pathogens become pivotal agents in the displacement of native species. For example, alien pathogens carried by IAS have driven severe epidemics, such as those caused by *Phytophthora infestans* (Mont.) de Bary and *Cronartium ribicola* J.C. Fisch., which have decimated staple crops and forest ecosystems, respectively. These dynamics underscore the potential of pathogens to act as "biological weapons" under the Novel Weapon Hypothesis (NWH), furthering the ecological advantage of invasive plants in their new environments [7]. The role of plant pathogens in invasive plant success is not limited to direct interactions. Indirect effects, such as the facilitation of hybridization between pathogens or the cryptic behavior of endophytic fungi transitioning to pathogenic lifestyles, further complicate this relationship. Additionally, anthropogenic activities such as global trade and urban horticulture have inadvertently facilitated the dissemination of invasive plants and their associated pathogens. It can be inferred that anthropogenic activities contribute to the pathogen spread and adaptation in new environments.

Understanding the interplay between invasive alien plants and their pathogens is critical for addressing the ecological and economic consequences of biological invasions. This manuscript explores the mechanisms through which plant pathogens influence the invasion process, including enemy release, spillover, and spillback. It also highlights the challenges posed by the cryptic lifestyles of pathogens and the genetic shifts driven by environmental changes. By examining these relationships, we aim to inform strategies for monitoring and mitigating the spread of invasive plants and their pathogens, emphasizing the importance of integrated approaches to biodiversity conservation and ecosystem management. We also address the potential risks associated with the intentional introduction of pathogens, used as "green agents" to control IAS plants, and the concerns about this process.

2. The Role of Plant Pathogens in the Spread of Alien Plant Species from the Sight of Ecological Hypotheses

Environmental characteristics, including basal resources, species composition, and top-down control, may determine the success of IAS in novel habitats [8]. Following this establishment, there is often a lag phase during which the population may show little to no expansion. This lag phase can extend from several to numerous years. Notably, the majority of invasive plant species in New Zealand exhibit a lag phase, averaging around 20–30 years, with 4% of species having a lag phase lasting more than 40 years [9]. Historically, in Europe, lag periods for alien woody species average ~150 years, while this extends to around 180 years for terrestrial plants [10]. Often, these lag phases precede a rapid and exponential increase in the population of the alien species [8].

The Enemy Release Hypothesis (abb. ERH) [2,11–13] suggests that the success of invasive plants is influenced by both the characteristics of the alien species itself and the new habitat, where alien species are under low pressure from local enemies, such as pathogens, herbivores, or predators (Figure 1). Furthermore, the new plant often does not co-evolve with natural enemies, and local enemies may not recognize potential hosts or specialize on native hosts. While numerous studies have supported this hypothesis [11,14–16], it remains a subject of controversy, and the findings from tests do not consistently indicate its universal applicability [17–20]. In new areas, the absence of obligatory enemies that controlled the spread of the newly introduced host in its natural area allows invasive plants to reduce their investment into defense and re-allocate the saved resources to improve their competitive abilities. As a result, invasive alien species exploit the environment more efficiently than native plants do. This leads to an increase in the number and spread of alien species, leading to long-term negative impacts on the environment and economy.

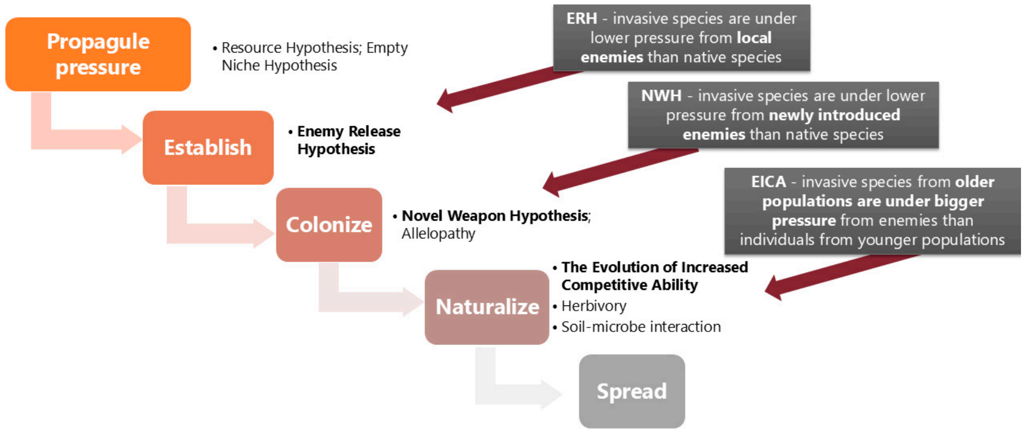

Figure 1. Salient hypothesis applicable at varying invasion stages (following Rai [21]). The graph highlights hypotheses in which plant pathogens play a crucial role.

The success of alien species after their introduction into new areas is explained also by the hypothesis of the evolution of increased competitive ability (abb. EICA) [22] that derived from the ERH hypothesis. The EICA assumes that the pressure from enemies on the species increases over time because local pests and/or pathogens need time to adapt to newly introduced hosts (Figure 1). Consequently, individuals from older populations must invest more into defense against enemies than individuals from younger ones, which results in the decline of characteristics related to competitive abilities. In turn, individuals from the youngest populations at the forefront of the invasion are under the lowest pressure from enemies, which determines their highly competitive abilities [23–26]. The EICA hypothesis has been tested on numerous alien plant species [27–29], and even though not all the results prove the concept of EICA, scientists emphasize the value of this hypothesis in understanding the biology of invasion. Both the ERH and EICA hypotheses together provide a comprehensive understanding of the complexity of the invasion process and the gradual development of environmental resistance to alien species.

Another crucial hypothesis describing the invasion process is the Novel Weapon Hypothesis (NWH). The NWH posits that alien invasive organisms have an advantage over native taxa due to their “biological warfare advantage”; it includes allelopathins and toxins that directly affect the fitness of neighboring plants. Pathogens transmitted from alien to native plants may also serve as such “novel weapons” (Figure 1) [7]. Additionally, in 1999, Simberloff and Von Holle [30] introduced the term *invasional meltdown* to describe how non-native species facilitate one another’s invasions, enhancing their survival, spread, and impact. Based on that, invasive alien plants may serve as a wharf to new pathogens and facilitate their arrival.

3. Spillover and Spillback Mechanisms from the Sight of Novel Weapon Hypothesis

Over time, alien species become recognizable to organisms in the environment into which they have been introduced. This is evident, for example, in the gradual establishment of fungi, bacteria and pests. While this phenomenon can slow down the expansion of invasive alien species (IAS), it also may have some negative consequences. Spillback mechanism assumes that local native pathogens colonize alien species, leading to an unnatural increase in the number of colonies of these pathogens. This results in an increase in the infections rate in the environment. Although the IAS plant may still have sufficient resources to sustain itself despite being affected by the new pathogen, the pathogen often returns to its native host, causing stronger effects on native plants than on the alien ones (Figure 2). Examples of this mechanism include the following IAS species: *Avena fatua* L. and *Bromus* sp. affected by barley/cereal yellow dwarf viruses (B/CYDVs) in California; Siam Weed (*Chromolaena odorata* (L.) R.M.King & H.Rob) in India, affected by soil fungi like *Fusarium* spp. and *Fusarium semitectum* Berk. & Ravenel; and Ice plant (*Carpobrotus edulis* (L.) N.E. Br) in Europe, affected by chytrid fungi [7]. As emphasized by Strauss et al. [7], the spillback mechanism occurs more often in the insect–plant relationship than in the fungi–plant relationship.

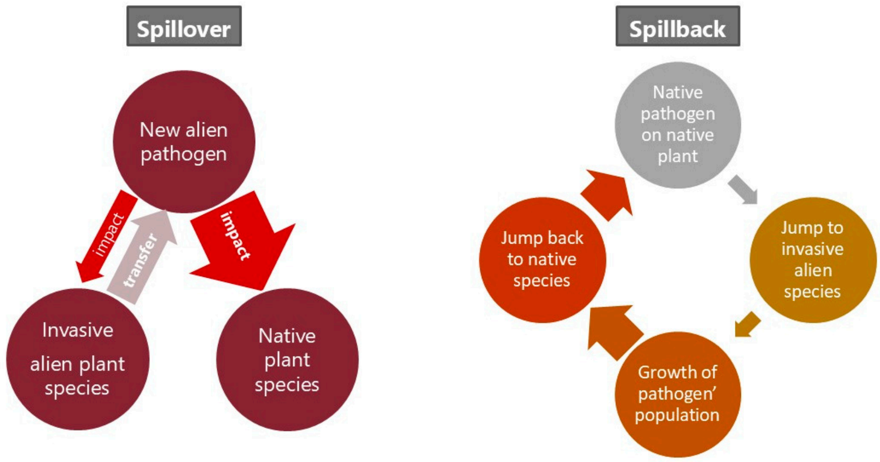

Figure 2. Spillback and spillover mechanisms.

In contrast, spillover is a process wherein a non-native alien pathogen or pest is carried by an invasive alien species to a new area than infect local organisms. The impact on the invasive alien plant, with which it has coexisted for years, is typically smaller than on the new host plant. Native species, with no resistance to the new pathogen, become vulnerable to its attack [7]. Examples of this mechanism include the spread of *C. ribicola*, which causes white pine blister rust in North American pines [31,32], *Cryphonectria parasitica* (Murrill) M.E. Barr, responsible for chestnut blight in North America and Europe [33], and *Austropuccinia psidii* (G. Winter) Beenken, causing myrtle rust that threaten *Myrtaceae* species native to New Zealand and Europe [34]. A recent study by Chen et al. [35] revealed that some plant pathogens, such as fungi from the family *Didymellaceae* associated with the invasive species *Ageratina adenophora* (Spreng.) King & H.Rob., are more virulent toward native plants than their invasive hosts. Notably, many of these pathogens remain unknown to science. This highlights a key challenge in studying spillover mechanisms in interactions between invasive alien species and plant pathogens. Limited plant monitoring in the past and a lack of molecular studies have led to many introductions of plant pathogens being overlooked. Over time, these pathogens spread to new areas, making it difficult to trace their origins [35]. This is why spillover involving insects has historically been better studied, while the lack of accessible and affordable identification methods has limited the number of documented cases for fungal pathogens.

As suggested by Strauss et al. [7], the impact of spillover and spillback on native plants can be so significant that the pathogen may drive the invasion process, promoting the predominance of IAS over closely related native species, leading to disease-mediated invasions (DMI).

3.1. Cryptic Lifestyle

It is crucial to consider that some pathogens, particularly fungi, lead a cryptic, endophytic lifestyle for most of their existence, remaining beyond the reach of researchers [36–39], which can create favorable conditions for the uncontrolled spread (Figure 3). The study of cryptogamous fungi, which requires specialized equipment for detection, also leads to underestimation of the prevalence of this phenomenon [39]. Moreover, research on animals is more prevalent [40–44], and the focus of phytopathology, which deals with plant diseases, is often directed towards crop plants, leaving wild-growing native or non-economically important plants understudied. Additionally, it is challenging to determine whether a particular pathogen colonizing the tissues of an invasive species is an alien, native, cryptogenic, or a cosmopolitan taxon [45]. These factors contribute to invasive plants accumulating undescribed species, including potential pathogens [41]. According to the authors, the main reasons are as follows: (1) limited research on fungi–invasive plant interactions; (2) the amplification of previously rare fungi by introduced invasive alien plants; and (3) the insufficient investigation of fungi co-introduced with IAS plants from their native range. This lack of information creates favorable conditions for the uncontrolled spread of IAS' plant pathogens (Figure 3).

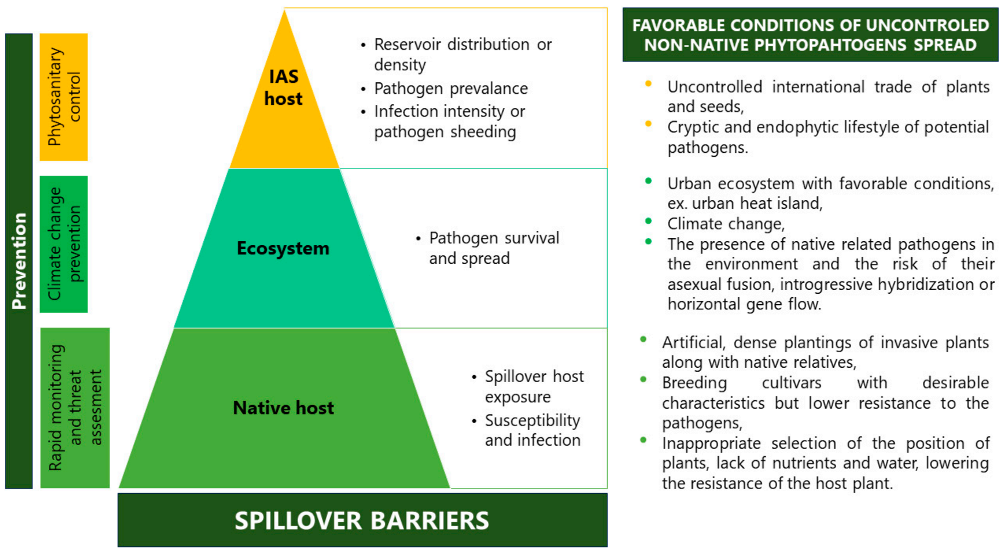

Figure 3. The barriers impacting the spillover mechanism at three following stages: invasive alien species host stage (yellow), ecosystem stage (turquoise), and native host stage (vivid green) (following Sokolow et al. [6]). Actions that can be used to prevent spillover at every stage of its spread are demonstrated on the left, favorable conditions that support transmission are on the right.

The cryptic life of many fungi is one of the most difficult features to monitor, especially in the context of international plant phytosanitary monitoring. Endophytic fungi, settling tissues of plants, can alter their life strategy during their individual lifespan, activating features that enable them to initiate pathogenesis on the host plant [46–48]. They may do this, for instance, in response to changing environmental conditions, increased insolation, temperature, or exposure to other stressors [47,48]. The host plant's reaction to a potentially pathogenic fungal species also varies depending on the species/variety and the microbiome present, where antagonistic relationships between microorganisms can occur [49]. Therefore, potentially cryptic, unnoticed fungal species transferred to a new area may behave differently in relation to the non-native host plant, triggering the parasitic phase in its tissues. This makes the potential prevention of the invasive alien pathogens spread even more challenging and hard to assess. Another factor that can affect the live strategy shifts are changes in environmental conditions caused by climate changes. Increasing temperatures and insolation not only opens the natural passages for pathogens drift, like e.g., melting the glaciers on mountain ranges, which was important in *Biscogniauxia nummularia* (Bull.) Kuntze drift [50,51], but also can lead to initiation of the pathogenesis on the host plant [46–48] (Figure 3).

3.2. Transfer of Genes

The breakage of natural borders and barriers, like oceans and mountain ranges, can lead to the unprecedented meetings of related pathogen species, which had never shared the development or stayed in isolation for a long time, which let them to evolve in separation. These events may potentially lead to uncontrolled gene transfer through introgressive hybridization, asexual fusion, or horizontal transfer (Figure 3) [52], which can resolve in the emergence of virulent and potentially dangerous for our native flora and crops pathogens. A similar was recently observed in the Balkan Peninsula, where *B. nummularia* and *Biscogniauxia anceps* (Sacc.) J.D. Rogers, Y.M. Ju & Cand., underwent introgresive hybrydysation, resulting in the more virulent pathogen *Biscogniauxia destructive* Vujanovic, which causes dieback of beeches in Montenegro [50]. Introgressive hybridization has also substantially contributed to the successful spread of plant pathogens such as *Ophiostoma ulmi* (Buisman) Nannf. and *Ophiostoma novo-ulmi* Brasier, the causal agents of Dutch elm disease, and other tree pathogens such *Melampsora*, the primary cause of rust disease [53]. Also, other authors suggest the emergence of new pathogens that had evolved from interspecific hybridization between endemic and invading fungi, which raise the importance of the geographical barrier even more than before [52–56].

In sight of molecular plant pathology, it is worth concerning the number of "entry points" of the new invasive pathogens and the diversity of the IAS pathogens' population, to assess the possible scenarios of its development in new areas [57]. One of the best-documented example in the history of alien plant pathogens that led to the epidemy outbreak is *P. infestans*, which caused late blight of potatoes. The A1 clonal mating type initially spread from the Americas to Europe in 1845 but the second "entry point" of A2 mating types, which happened in 1980, let the previous clonal genotype to undergo sexual reproduction [58]. This increased the adaptability of the pathogen and provided a new life-cycle stage, oospores, enabling survival in the absence of host plant material between seasons [59]. A very similar situation occurred with myrtle rust in Florida [60,61]. Therefore, in early monitoring of invasive alien pathogens that were transferred with IAS, it is important to recognize the local genetical population diversity. This type of information could aid in decision-making and the establishment of phytosanitary politics.

3.3. Time Matters

When considering a potentially pathogenic fungus introduced with an IAS plant, it is essential to recognize that, upon crossing the geographical barrier, it may adopt an endophytic cryptogamous lifestyle but undergo changes in its characteristics over time. Additionally, the timing of its introduction into a new area should be taken into account. Facultative pathogens, or those with a wide host spectrum, may need time to fully develop, undergoing similar stages of invasion as plants and animals, making them a potential "time bomb". Unfortunately, removing the IAS host transmitting the pathogen might not be sufficient after introducing a new pathogen into the environment. Alien pathogens may survive even if their original hosts do not, as the spill of the pathogen into the external environment may have already occurred [62].

4. Gardening and Urban Areas as Crucial Hubs for the Spread of IAS-Associated Pathogens

4.1. Environmental Chances to Pathogen Spread and Survival

Last but not the least, the environment plays a crucial rule in plant disease development (Figure 3). This triangular relationship (host–pathogen–environment) is unique to phytopathology in comparison to veterinary and medical sciences because terrestrial plants possess little thermal storage capacity, and their immobility precludes escape from an inhospitable environment [63]. During discussions about plant pathogens development, we cannot forget about this factor, especially because of the predominance of fungi in phytopathology, which also are highly dependent on environment. To stress this point, invasive alien species serve as reservoirs for pathogens, with the second most common group of isolated pathogens being fungi belonging to *Ascomycota* (84 different species) [64]. The climatic condition that an introduced IAS pathogen encounters in the new area determines its chances of spreading and surviving (Figure 3). For example, the minimum or maximum temperatures of host and pathogen can differ (as it is in case of coffee rust [65]), limiting the pathogen range of occurrence. However, the same example shows how small fluctuations of temperatures, caused by global rise of temperature, can impact this subtle relation, leading to the expansion of *Hemileia vastatrix* Berk. & Broome in areas that were previously unsuitable for it [65–67]. In sight of pathogens' temperature preferences, there is concern about the impact of urban heat islands in IAS' pathogen establishment and survival, especially considering that urban areas are the first and most invaded areas [68].

4.2. Host Factor: Invasive Alien Plants in Urban Ecosystems

According to Hulme's estimates [69], up to 80% of neophytes in Europe initially arrived due to their decorative values, serving as ornamental plants. Thus, anthropogenic communities, as noted by Tokarska-Guzik et al. [4], harbor the highest number of invasive plants. Thus, urban areas are one of the first areas where the IAS breaks the geographical barrier and enters a new environment. It is estimated that as much as 67.8% of urban areas are invaded by alien plants, making it the environment with the highest occupancy of area by IAS. In comparison, 43.9% of forests and woodlands and 42.9% of croplands are invaded by alien plants [68]. Given that many IAS plants are overrepresented species used in horticulture (387 species, 51% of them being trees) across the world [70,71], this highlights the significant problem of phytopathogen transfer on invasive plants and their implications for global economy and sustainable agriculture development.

An important aspect to consider in sight of the uncontrolled transfer of IAS' pathogens is the botanical families to which alien invasive plants belong. Pathogens with medium specificity to the host often inhabit several plant species closely related to each other, typically within the same botanical family (ex. *Colletotrichum* family) [72]. Consequently, the affinity of invasive alien species with local taxa increases the risk of transmitting potential phytopathogens, which can adapt to new environments, spread to native plants, and pose threats to ornamental, orchard, or horticultural crops. A compelling example is the rose family, with Europe alone hosting 25 alien invasive species belonging to the *Rosaceae* family, including four in the *Cotoneaster* family, one in *Pyracantha*, one in *Rosa*, and four in *Rubus* [70,71]. Similarly, North America is a natural area of 25 species, including two in the *Cotoneaster* family, six in *Rosa*, and eight in *Rubus*. This family includes several economically significant orchard plants in the temperate regions of the northern hemisphere, such as apple trees, pear trees, quinces, chokeberries, wild strawberries, plums, and blackberries. Therefore, any spread of its pathogens can be devastating to local fruit production.

4.3. International Trade Market

The transfer of alien species, along with potentially pathogenic fungi, through seeds and nursery materials is inevitable [73,74] (Figure 3). Global and uncontrolled transfer of seedling caused the spread of many invasive alien pathogens, carried on the hosts tissues to the new areas. A good example is one of the most important pathogens of North America—*C. ribicola*—causing white pine blister rust, which lead to high mortality of western white pine, sugar pine, limber pine and whitebark pine across Canada and the United States [31,32]. In this particular case, the key to the survival of the pathogen was the natural occurrence of its alternative host, representatives of the *Ribes* family (currant and gooseberry), where the pathogen develops part of its lifecycle. It highlights the complexity of the relationships between pathogens, their hosts, and environment, which allows a new plant pathogen to establish itself in a new area. It is also important to note that in gardening, while seeking desirable consumer traits, many of these varieties lack crucial pathogen resistance genes, making them more susceptible to diseases [75] (Figure 3). This, in turn, has implications for the exchange of pathogens and genes between ornamental plants and their invasive relatives, particularly in urban environments, where anthropogenic alterations can weaken the host plant's ability to respond to pathogens [76–79], aiding the potential adaptation of pathogens to new hosts.

4.4. Gardening Strategies That Support Invasive Alien Plants' Pathogen Transfer

It is worth noting that urban centers, another form of anthropogenic environment, may also facilitate the dispersion of pathogens associated with IAS and their subsequent migration beyond metropolitan regions. This is primarily due to plant selection in urban gardening and the unique characteristics of these anthropogenic ecosystems. Unfortunately, IAS are still cultivated in urban centers, primarily due to their ease of cultivation, low environmental requirements, and their resistance to adverse abiotic factors. Notably, in a list of woody plants best adapted to the urban environment, provided by Yang et al. [76], many species with the highest adaptability scores are invasive alien species. This phenomenon can be attributed to the remarkable phenotypic plasticity of invasive alien species, which enables them to maintain productivity and vitality even under unfavorable conditions [80–82]. However, IAS plants are often planted in close proximity to native relatives in dense plantings in small urban areas, which promotes the sharing and drift of pathogens in between closely related species, for example alien and local species of maples, oaks, and coniferous trees (Figure 3). An example of shared pathogens is *Colletotrichum acericola* Patejuk, Piątek, Czachura & Baturo-Cieśniewska, which, in in vitro conditions, has shown the possibility of host jumping to native European maples [74] (unpublished data). The presence of invasive alien ornamental plants (e.g., *Lantana camara* L. and *Ochna serrulate* (Hochst.) Walp.) also facilitate spread and impact of myrtle rust (*A. psidii*) to native Australian and New Zealand *Myrtlaceae* plants, such as *Archirhodomyrtus beckleri* (F.Muell.) A.J.Scott, *Decaspermum humile* (G.Don) A.J.Scott, *Gossia hillii* (Benth.) N.Snow & Guymer, and *Rhodamnia maideniana* C.T.White [83].

Furthermore, urban conditions, characterized by limited water and nutrient availability and air pollution, pose challenges for plant growth. These conditions reduce the resistance of native plants to potentially new pathogens associated with IAS, facilitating their rapid adaptation to new hosts and thereby breaking down the resistance of native plants (Figure 3). Poor plant selection based solely on ornamental features can also expedite the spread of IAS pathogens. As a result, urban areas emerge as pivotal locations for the occurrence of the spillover phenomenon and serve as centers for the adaptation of IAS pathogens to potential new hosts.

5. Counteracting the Spread of Invasive Plants: Pathogens as "Green Agents" and Their Role in Long-Term Monitoring

5.1. Legislation and Programs Against Invasive Alien Plants' Pathogen Spread

The topic of counteracting the invasion of alien species is addressed by numerous legal acts and international agreements, including the Convention on Biological Diversity [1], as well as the EU Strategy for the Conservation of Biodiversity for the period up to 2020 [84]. They assume the identification and categorization of knowledge on the mechanisms that determine spread of IAS organisms, potential methods of IAS elimination, as well as the establishment of a comprehensive legal framework. So far, the mechanical removal of plants, chemical herbicide treatments (offshoot applications, injections, herbicide markers), the removal of the top layer of soil, deep plowing, liming, and limiting seed dispersal are commonly used [4]. Repeated mowing and soil screening (by sifting) are also used. These treatments are associated with huge costs and often require many years of repetition for the treatment to be highly effective [4,85,86]. One alternative method, which does not require such large expenditures, is the use of the IAS' natural enemies, such as fungal or bacterial pathogens, with commercial potential.

Preventing the spread of invasive alien species requires a comprehensive understanding of invasion dynamics and acquiring specialized knowledge about each species and its interactions with the environment [4,87]. In this regard, various international programs have been initiated to collect data and raise awareness about the subject. Examples include the European programs DAISIE (Delivering Alien Invasive Species Inventories for Europe) [88], HARMONIA+, and PANDORA+ [89–91]. Updated databases on invasive species are also accessible, such as NOBANIS [92], containing information about alien species in Central and Northern Europe, and the Polish database "Alien species in Poland" [93].

Alien invasive species vary in factors that determine their invasiveness. To enable an objective assessment of the harmfulness of a given taxon, various metrics have been developed to classify specific characteristics of such species, including the extent of their establishment on a national or regional scale. Tokarska-Guzik et al. [4] listed four categories of invasive species that allowed for a preliminary evaluation of their impact on the environment. The assessment considered features of the taxon, such as the degree of its establishment, population size and dynamics, the type of colonized habitats, and the economic, environmental, and social threats posed by the alien species.

Recognizing the complexity of the invasion issue, recent projects like PANDORA+ have taken into account the significance of pathogen transfer by non-native species and the impact of local pathogens on plant health [90]. Pathogens have been incorporated into the Species Invasiveness Analysis Survey, conducted for each taxon classified as invasive [93–95], with consideration of both economic and sanitary aspects. The European and Mediterranean Plant Protection Organization website [96] provides a partial list of pathogens and pests associated with invasive species.

Developing a global database of pathogens accompanying invasive alien plants and regular monitoring of their health status become crucial in the context of threats posed by the spillover and spillback phenomena. Rapid identification of potential threats and establishing protocols for quick responses can significantly reduce these phenomena and prevent their spread across continents. Historical cases have demonstrated that the spread of foreign pathogens can lead to the near extinction of native or cultivated species, as seen with Dutch elm disease, ash dieback, dogwood anthracnose, chestnut blight, white pine blister rust, potato blight, and banana dieback [97–99]. According to Mułenko et al. [100], these types of parasitic fungi (alien and fast spreading) meet the criteria for invasive organisms, making them a group of organisms that requires constant monitoring of their spread, similar to plants and animals, legislated as obligatory by many countries.

The most important aspects are the prevention and rigorous control of plant material transported across borders. Countries with valuable and vulnerable ecosystems, such as New Zealand or Australia, have implemented strict phytosanitary regulations to prevent the transmission of invasive plants and their pathogens. However, research indicates that many parts of the world do not prioritize this issue, as evidenced by studies showing the scale of transfer of foreign fungi colonizing seeds of non-native plants purchased from commercial stores [73]. There is currently no monitoring or rapid warning system for the transfer of potentially dangerous species on the surface of invasive plants, which could limit their spread. Controlling everything that crosses borders would be extremely difficult if not impossible, but there are some of the most dangerous species that should be investigated. Such species have been identified for Poland and Europe [64]. Similar meta-analyses can be performed for other countries or areas. Perhaps, considering adding pathogens of invasive alien species to international quarantine lists could facilitate data collection, education, and implementation of procedures to prevent the movement of these pathogens to new areas along with their host plants.

5.2. IAS Pathogen on Service: "Green Agents"

Another concerning and contentious topic related to pathogens of invasive alien plants is the concept of creating so-called "green agents," which involves the intentional introduction of natural enemies of invasive alien plants to control them. This approach is often more economically viable than mechanical removal or the use of strong herbicides. Understanding the mycobiota inhabiting neophytes may be particularly useful in the context of developing and utilizing mycoherbicides, which could serve as natural remedies to slow down the expansion of certain invasive species [101–105]. Extensive research on this subject has been carried out in Poland, particularly in the Wigry National Park [57,106], the Drawa National Park [57], and Tatra National Park [107], where long-term monitoring of the health condition of invasive alien plants is combined with mycological analysis. However, only isolated cases of finding pathogenic species associated with invasive plants are known [108,109].

However, creating green agents is a challenging and controversial task. Monitoring invasive plants allows for the identification of suitable pathogens that have already been established in a new area alongside their host plant. This can help in selecting genotypes with satisfactory virulence and effectiveness for developing mycoherbicides. It was tested, for example, on *Puccinia komarovii* var. *glandulifera* R.A. Tanner, C.A. Ellison, L. Kiss & H.C. Evans rust, infecting *Impatiens glandulifera* Royle in England [103]. However, most green agents are foreign to the local environment, raising concerns about the spillover phenomenon, where introduced species can become invasive themselves. Arguments often cited in this discussion include the escape of the Asian ladybug from greenhouses that becomes invasive in Europe [110], or cane toads in Australia that were used to control the native grey-backed cane beetle (*Dermolepida albohirtum* C.O.Waterhouse) [111] and French's beetle (*Lepidiota frenchi* Blackburn) [112]. Nevertheless, current research and procedures accompanying the creation of new green agents are much more refined. CABI (Centre for Agriculture and Bioscience International) is a prominent organization in the world dealing with research and the creation of such biological preparations, and it has achieved numerous successes in this field [112]. Examples of successful green agents include the usage of rust fungus *Maravalia cryptostegiae* (Vestergr.) Y. Ono against invasive alien rubbervine *Cryptostegia grandiflora* R.Br. in Australia [113] and the usage of *Aphthona* flea beetle to successfully control *Euphorbia esula* L., an alien and invasive plant in North America [114]. Currently, ongoing projects are exploring biocontrol methods for the Madagascar rubbervine (*Cryptostegia madagascariensis* Bojer ex Decne.), which threatens Brazil's biodiversity. A promising candidate for this is the rust fungus *Uredo cryptostegiae* Vestergr. [115]. Efforts are also underway to control invasive blackberry on the Galápagos Islands, with promising results from two rust species belonging to the genus *Phragmidium* and two insect species: a leaf-rolling weevil and a sawfly [116]. Additionally, trials are being conducted with three species of weevils to manage garlic mustard in North America [117].

However, green agents face numerous legislative problems. In the light of current European laws [118], the introduction of a pathogen of foreign origin into the environment is considered equivalent to introducing an invasive alien organism and is therefore illegal. This legal stance also hinders research into alien species that are already present in the environment. Despite the procedures accompanying the development of green agents, which prioritize testing in vitro and in vivo infection tests on closely and distantly related native plants, the new legislation has completely halted the progress of these studies in Europe [119,120].

6. Conclusions

The topic of pathogens colonizing the invasive plants is complex, multifaceted, and requires a comprehensive perspective encompassing phytopathology, botany, ecology, and economics to gain a full understanding. Observing the adaptation of plants to new environments and the reciprocal changes in the environment, due to the introduction of invasive species, allows us to be a witness the gradual evolution of both components and its far-reaching consequences. From a nature protection standpoint, the negative impacts of introducing invasive plants of foreign origin are evident. The scientific community, along with activists and educators, has been taking actions to control invasive alien species for years, but still there is still much to be done.

The research supports the notion that while pathogens can act as natural checks on invasive species over time, they also pose significant risks to native ecosystems and agricultural practices. The cryptic lifestyles of many fungal pathogens, combined with the potential for genetic transfer and shifts in life strategy, further complicate the challenge of managing these biological invasions. The role of urban and anthropogenic environments in fostering the establishment and spread of invasive species and their pathogens requires special attention, given their status as hubs for pathogen adaptation and spillover phenomena.

Future management strategies should prioritize an integrated approach that includes rigorous phytosanitary controls, ongoing monitoring, and the development of global pathogen databases. While the use of pathogens as biological control agents presents a promising avenue for mitigating invasions, it requires careful consideration of ecological risks and legislative constraints. Expanding research into the mechanisms underlying plant-pathogen interactions and the impacts of environmental changes, such as climate warming, will be essential for improving our ability to predict, monitor, and mitigate the effects of invasive alien plants and their associated pathogens.

Ultimately, combating the challenges posed by invasive alien plants and their pathogens will demand enhanced international collaboration, comprehensive legislative frameworks, and adaptive management strategies that balance ecological, economic, and societal considerations. By addressing these challenges proactively, we can better safeguard biodiversity, ecosystem services, and human well-being from the multifaceted threats of biological invasions.

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