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FOREST INVASIONS

Ecology of invasive forest pathogens

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Abstract Invasive forest pathogens are a major threat to forests worldwide, causing increasing damage. The knowledge of both the specific traits underlying the capacity of a pathogen to become invasive, and the attributes predisposing an environment to invasion are to be thoroughly understood in order to deal with forest invasions. This paper summarizes the historical knowledge on this subject. Many aspects of the ecological processes underlying alien forest pathogens invasions are still unknown, which raises several scientific issues that need further study. The introduction of invasive forest pathogens to areas where naïve hosts are found, is mainly due to global plant trade. Rapid transportation and reduced delivery times increase the chances of survival of pathogen propagules and of their successful establishment in new environments. In forest pathogens, the reproduction mode seems not to be a crucial determinant of invasiveness, as highly destructive pathogens have a variety of reproductive strategies. The most important drivers of forest pathogen invasions appear to be (a) great adaptability to new environmental conditions; (b) efficient dispersal over long and short distances, possibly assisted by the capacity to form novel associations with endemic and/or alien insect vectors; (c) the ability to exchange genetic material or hybridize with resident or alien species. Moreover, these features interact with some key traits of the invaded environment, e.g. environmental variability and biodiversity richness. Host resistance and natural enemies may occur as a result of rapid selection/ adaptation after the epidemic phase of invasion.

Keywords Disease spread · Economic impact · Invasibility · Invasion pathways · Invasiveness · Novel insect-fungus associations · Pathogen hybridization

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Introduction

Currently, emerging infective diseases of plants (plant EIDs) are one among the greatest threats to agriculture, forestry and biodiversity conservation (Anderson et al. 2004; Misra and Chaturvedi 2015). In the past century, plant EIDs mostly resulted from the accidental introduction of invasive alien pathogens to new geographic areas by global trade and transport (Bandyopadhyay and Frederiksen 1999; Brasier 2008; Liebhold et al. 2012; Roy et al. 2014; Santini et al. 2013; Xu et al. 2006). Well known cases of introduction of invasive forest pathogens are the entrance of *Cronartium ribicola*, the agent of white pine blister rust, from Europe to North America along with plant material; the import of *Cryphonectria parasitica*, the agent of chestnut blight, from Asia to North America through plant propagation material; and the arrival of the subspecies *americana* of the Dutch elm disease fungus *Ophiostoma novo-ulmi,* from North America to Europe with rock elm logs (Brasier and Gibbs 1973). The human-mediated extension of the distribution range of microbes also enabled the emergence of new pathogens through hybridization or horizontal gene transfer (HGT) between previously isolated species (Brasier 2000; Gluck-Thaler et al. 2015). In some cases, the epidemic emergence of native or introduced pathogens was caused by the establishment of novel associations with introduced or native arthropod vectors (Wingfield et al. 2016).

Quantifying the damage by invasive pathogens is complex and only a few studies have calculated the cost of multiple alien diseases either at regional or global scale. Pimentel et al. (2001) estimated that invasive diseases and pathogens caused a worldwide loss of US$ 426 billion in 1998. In the US, the losses and control costs due to plant diseases introduced from abroad annually reach about US$ 21 billion (Brownlie et al. 2006).

With regard to forest trees, the few available quantitative estimates indicate large economic impact by alien pathogens (Sache et al. 2011; Lovett et al. 2016). Pimentel et al. (2005) reported that approximately US$ 2.1 billion in forest products are lost each year to alien forest pathogens in the US. In Canada, past introductions of harmful invasive plant pests on agricultural crops and forestry cost US$5.7 billion per year (Environment Canada 2004).

Apart from production loss, the full economic costs of invasions include negative side effects on trade of forest products and plants, control expenses due to inspections, monitoring, prevention and response, and ecological and environmental impacts on ecosystems (Morse 2005). Recently, Bradshaw et al. (2016) performed a critical synthesis of the available information to estimate the global goods and services costs of invasive insects. The ten most harmful insects to agriculture and forestry cost US$35 billion annually (2014 values), a massive yet largely underestimated value due to the shortage of quality data at the regional or local scale, as highlighted by Bradshaw et al. (2016). Invasive pathogens have ecological and environmental effects at all organization levels, from genes to the whole ecosystem (Morse 2005; Loo 2009). They affect the gene level by, for instance, hybridizing with native microorganisms, a phenomenon that drives the fast emergence of new pathogens able to infect new host species (Brasier et al. 1999; Stukenbrock 2016). Epidemic outbreaks of alien disease agents may modify diversity, richness, composition and abundance of host and non-host species, and in turn affect ecosystem processes and biogeochemical cycles (Morse 2005; Lovett et al. 2016).

To identify both the specific traits that underlie invasiveness, i.e. the capacity of any introduced organism to become a serious pest, and the attributes predisposing an ecosystem to invasion, i.e. determining its invasibility, is crucial for understanding the dynamics of invasion by forest pathogens (Santini et al. 2013; Desprez-Loustau et al. 2016). Recently, Garcia-Guzman and Heil (2014) reviewed the studies that have identified life history traits of plants and of their pathogens predictive for emergence of new diseases in the tropics. They concluded that the only widely accepted predictive quality in plant-pathogen interactions is ‘host conservatism’, i.e. the probability that a pathogen with a compatible interaction with a given host will be able to infect another species decreases with the phylogenetic distance among the hosts (Gilbert and Webb 2007; Schulze-Lefert and Panstruga 2011). These authors also showed that plant life-history, in addition to determining genetic structure and evolution of parasite populations (Barrett et al. 2008; Giraud et al. 2010), influences disease incidence and the relative frequency of plant infection by fungal pathogens differing in life-history traits. As for other invasive organisms, fungal pathogens may become successful alien invaders thanks to pre-introduction traits conferring them the ability for easy/fast adaptation, such as relatively high phenotypic plasticity, i.e. the ability of individual genotypes to produce different phenotypes when exposed to different environmental conditions (Pigliucci et al. 2006), and a broad ecological niche; or to post-introduction changes in key life-history traits, which may favour host jump (Giraud et al. 2010; Gladieux et al. 2011, 2015). Changes may consist in increased aggressiveness, increased numbers of virulence traits, and the loss of sexual reproduction, which most probably results from adaptation than from genetic drift (Ali et al. 2010). Finally, the ability to adapt to novel abiotic stress factors is a crucial determinant of invasion success (Gladieux et al. 2015).

A comparative analysis of the differences in many phenotypic traits between source and invasive populations of *Seiridium cardinale*, the fungal agent of cypress canker, showed that phenotypic plasticity increases at first during invasion, possibly helping survival in novel habitats, and it decreases afterwards (Garbelotto et al. 2015). Moreover, in the same study, selection proved to be stronger on traits related to dispersal than on traits related to virulence.

The concepts of species invasiveness and community invasibility, and their relations have been extensively studied in the ecology of plant invasions (Richardson and Pysek 2006; Hui et al. 2016).

In forest trees, the primary cause of EIDs is the invasion by alien fungal and fungal-like pathogens (Anderson et al. 2004; Ghelardini et al. 2016). Fungal-like organisms (FLOs) are species that were recently moved from Fungi to the kingdom Chromista, *Phytophthora* species among them. Many pathogenic fungi and FLOs share typical traits (for instance, high virulence; high environmental persistence in the absence of the host due to sapronotic potential or durable inocula; large host range (generalist pathogens); highly dynamic genomes (high rate of macromutations); broad environmental envelope, i.e. the set of environments within which the species can persist, that may represent key features in invasiveness (Desprez-Loustau et al. 2007; Fisher et al. 2012). Traits linked to invasiveness and invasibility in fungal pathogens of temperate forests were investigated by several studies (Desprez-Loustau et al. 2010; Vacher et al. 2010; Philibert et al. 2011; Santini et al. 2013). However, many aspects of the ecological processes leading to invasion of forest ecosystems by introduced pathogenic fungi remain unknown. This paper summarizes the historical knowledge on this subject, examining each stage of the invasion process: transport, arrival, establishment, and spread as defined in Roy et al. (2016), but many issues remain open and need to be further investigated.

Transport and arrival

Critical events in human history and the technology progress applied to intercontinental transport had a huge impact on the spread of invasive forest pathogens. Until the end of World War I, the main pathway of emergence of new forest diseases in Europe was the transport of commodities among European countries. Afterwards, Europe became the first market of US products, and North America, as a consequence, the main source of new forest pathogens (Santini et al. 2013). Following the increase of commercial exchanges with the US, temperate regions of North America became the main source of alien pathogens also for China (Xu et al. 2006).

The number of introductions of invasive forest pathogens rapidly increased after World War II, when standardized containerization revolutionized international trade, dramatically reducing transport costs and shortening shipping time. Since the mid 1950s, when the first commercially successful container ships carried a few dozen containers between US destinations, the number of containers transported by a single ship has increased up to more than 19,000 units transported by the China Shipping Container Lines Globe, the world's largest container ship in 2014. Rapid transportation and reduced delivery times increase the survival of pathogen propagules, and increase their chances of successful establishment in the environment of arrival (Hulme 2009). Three among the most infamous alien pathogens of European trees, namely *S. cardinale*, *Ceratocystis platani*, and *Heterobasidion irregulare*, the agents of cypress canker, plane stain canker and Heterobasidion root rot, respectively, were introduced to Europe by the US army during WWII (Fig. 1). The fall of the Iron Curtain opened the doors to further globalization, leaving a world without strict borders and few, if any, areas sheltered from invasive species migrations. From the 1990s onwards Asia became, mainly because of cheaper labour costs, one of the world's most important producers of plants for planting and, therefore, a new source of invasive fungal pathogens of trees for Europe (Fig. 1).

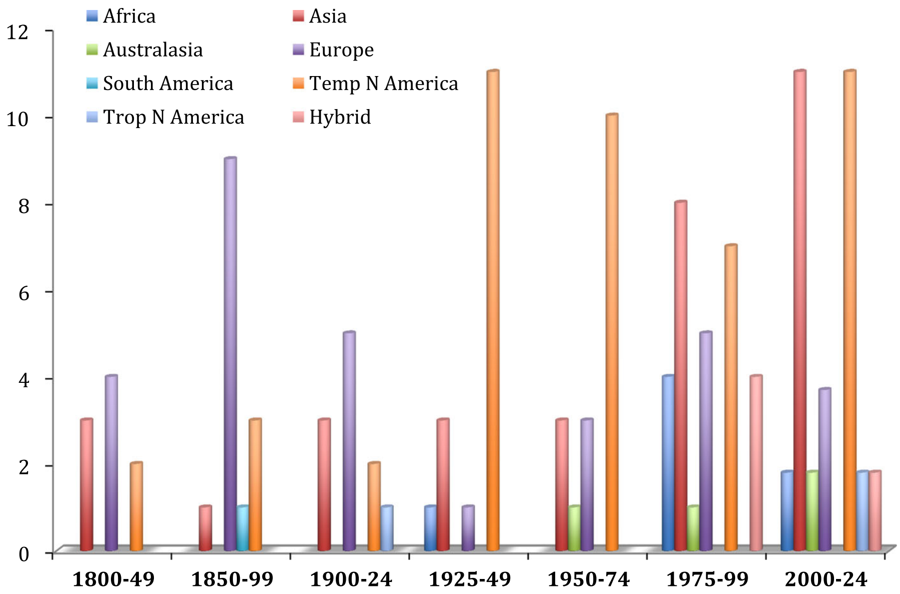

Fig. 1 Temporal changes in the origin of forest pathogens established in Europe (updated from Santini et al. 2013)

Establishment

Pathogen traits driving invasiveness

Life history traits

Reproduction in fungi is complex, and a species' life cycle may include asexual, sexual and/or parasexual stages (in the latter two cases novel genetic variation is produced by recombination). Fungi exhibit three different sexual compatibility systems: (1) hermaphroditic, i.e. a mycelium produces both female and male organs (self-fertile or not); (2) dioecious, i.e. a certain mycelium may only bear female or male organs (obligatory outcrossing); (3) sexually undifferentiated, i.e. sexual structures may act as male or female (Nieuwenhuis and Aanen 2012).

The reproductive strategy does not appear to be among the main determinants of invasiveness in forest pathogens, although it may be important for invasion management. In fact, the most destructive epidemics of forest trees were caused by invasive fungi with very different reproduction modes. For instance, *S. cardinale*, *Diplodia sapinea* and *C. platani* (for more details see "Box 1", "Box 2" and "Box 3" sections, respectively) spread clonally in the invaded range; the first two species reproduce by agamic and parasexual systems, while the third species reproduces agamically and by sexual mechanisms, being hermaphroditic and self-fertile. *Cronartium ribicola*, a rust fungus colonizing white pines, has a complex life cycle during which it produces 5 different spore types, requiring an alternative host (*Ribes* spp.) to produce basidiospores, i.e. sexual spores. The fungus is native to central Siberia (Leppik 1970) and became invasive in the mid 1800s on American white pine species in Europe, being accidentally introduced to North America and Asia after a few decades through infected nursery stock (Hummer 2000). In every part of the invaded range the fungus spread very rapidly, jumping to new hosts (*Pedicularis* and *Castilleja* spp.) (McDonald et al. 2006).

Ophiostoma novo-ulmi, the causal agent of Dutch elm disease and one of the most destructive forest pathogens ever known, reproduces both clonally and sexually. Once introduced into a new area, this fungus generally spreads at the epidemic front, with a single mating type exhibiting only one or a few vegetative compatibility groups. A few years after establishment, these genetically uniform invasive populations suddenly increase in genetic variability due to the appearance of the other mating type (Brasier 1988; Brasier et al. 2004).

Host specificity

In ecology, species confined to particular habitats because of their narrow environmental tolerances are defined specialist species, while species with a broader environmental tolerance enabling them to live in many and diverse habitats are defined as generalist species. Generalist parasites, as opposed to specialist parasites, are able to infect a wide range of hosts with varying severities (Holmes 1979). Observed host ranges of parasites often include only part of the potential hosts because of limitations to dispersal (Poulin 2011). In Europe, generalist invasive pathogens of trees tended to spread over a larger area than specialist pathogens (Santini et al. 2013). The ability of generalist species to become successful invaders is probably due to their capacity to infect novel hosts, persist in a wide range of environmental conditions, and to spread over longer distances (Brown and Hovmøller 2002; Evangelista et al. 2008). The unspecialized pathogen *Phytophthora ramorum* probably became a successful invader in the UK, causing huge damages to the Japanese larch *Larix kaempferi* (Lamb.) Carr., by virtue of the pathogen's capacity to quickly adapt to a naïve host, grown in uniform plantations and highly susceptible through lack of coevolution (Brasier and Webber 2010). In generalist pathogens, the ability to live on many host species probably helps the maintenance of high within-population genetic variation, which increases their evolutionary potential (Kassen 2002). Nevertheless, among forest pathogens there are also striking examples of successful invaders with high host specificity, as *Hymenoscyphus fraxineus*, the agent of European ash dieback (Kräutler and Kirisits 2012), and obligate pathogens, for instance rusts (Prospero and Cleary 2017). However, highly specialized pathogens frequently experienced local extinction, especially when the host population's range was discontinuous (Barrett et al. 2008). Other specialized pathogens, as *O. ulmi* s.l. and *C. parasitica*, which have nearly destroyed their hosts in two continents, underwent less extreme boom and bust population cycles possibly because they share with other fungal pathogens the capacity to survive as a saprophyte on plant debris between successive epidemic outbreaks (Webber et al. 1987; Baird 1991; Prospero et al. 2006; Rigling and Prospero 2017).

Hybridization

The 1990s and early 2000s were characterized by the discovery of an exceptional number of hybrid forest pathogens (reviewed in Brasier 2000 and Ghelardini et al. 2016). Again, the cause of this phenomenon is probably the accidental transfer of micro-organisms through global transport and trade, which increased the chances of contact between species that were previously isolated by distance. Once established in a new area, invasive pathogens come into contact with native and possibly related pathogens, some of which may have similar hosts or vectors. Thus it is more likely that hybridization will occur between immigrant species and an endemic species belonging to the same genus because allopatric species are less likely to have evolved strong barriers to hybridization (Brasier 2000). Other factors influencing the probability of hybridization are the likelihood of niche contact between the two species, and the fitness of any recombinant hybrids relative to that of the parent species (Brasier 2000). However, there is sound evidence that hybrid plant pathogens may display increased virulence or enlarged host range when compared with their parental lineages, which provides them with a great potential for invasion and epidemic outbreak (Depotter et al. 2016; Stukenbrock 2016). With regard to forest pathogens, Paoletti et al. (2006) demonstrated selective acquisition of mating type (*Mat)* and vegetative incompatibility (*vic)* genes by *O. novo-ulmi* from *O. ulmi*. Brasier and Kirk (2010) provided evidence for emergence of a hybrid swarm of the *O. novo ulmi* subspecies across Europe with an increased level of pathogenic fitness. Dhillon et al. (2015) provided evidence that *Mycosphaerella populorum*, the Septoria canker of poplars, acquired the capacity to infect, colonize, and cause mortality on poplar woody stems through horizontal transfer of the necessary gene battery from ascomycete fungi associated with wood decay and from prokaryotes. On hybridization see also Wingfield et al. (2017a).

Environmental and host species features driving invasibility

Climatic variability, biodiversity and human activity

The pattern of invasion by forest pathogens depends on the environmental variability and biodiversity of the invaded region, in addition to the magnitude of human activities and commercial exchanges (Santini et al. 2013). Consistently with the 'environmental heterogeneity hypothesis of invasions' (Melbourne et al. 2007), a high environmental diversity allows the establishment of many forest pathogens with different ecological niches. Regions with high diversity may display environmental conditions suitable for numerous alien species and function as 'invasion hotspots' (O'Donnell et al. 2012). For example, Italy and France, having high environmental and biological diversity among European countries, suffered historically the highest number of invasions by forest pathogens in Europe (Santini et al. 2013; Roy et al. 2014). However, part of the observed differences in the frequency of introductions/invasions is probably due to non-uniform biosecurity regulation or ineffective application of common rules (Eschen et al. 2015; Klapwijk et al. 2016). In addition, human activities, which can be represented by various economical indices, as the volume of imports (Desprez-Loustau et al. 2010) or the gross domestic product (GDP) (Santini et al. 2013; Roy et al. 2014), or by human presence as measured by total population (Desprez-Loustau et al. 2010) or population density (Santini et al. 2013), influence the frequency and pattern of invasion. For instance, the high incidence of forest invasions in Italy probably depends on the synergistic effect of biogeographical diversity, concentrated human activities, and intense prolonged commerce (Santini et al. 2013). This is consistent with the 'species-energy theory', which posits that the stability of a host-pathogen system and the ecosystem's pathogen-carrying capacity are higher in regions with a higher biomass productivity (Wright 1983).

In the near future, the countries at the highest risk of invasion by forest pathogens are probably those that have been commercially isolated in the recent past, and those with a low Human Development Index (HDI), previously limited and currently expanding international trade/GDP, and fragile economy with no resources to invest in prevention/control of alien invasions (Early et al. 2016; Roy et al. 2014). Biodiversity hotspots in their territories will probably be vulnerable to relatively low-impact invasive (pathogen) species (Early et al. 2016; Li et al. 2016).

Europe is the continent with the highest number of invasive forest pathogen species, i.e. there are about four and five times as many reports as in China and North America, respectively (Fig. 2). Since plant trade is the major source of plant pathogens' introduction, a possible explanation is that Europe has one of the most open phytosanitary systems among highly developed countries (Brasier 2008; Eschen et al. 2015), i.e. any plant that is not specifically regulated can be imported. Brasier (2008) highlights in particular (1) that many of the introduced threat organisms were previously unknown to science; (2) the European reliance on named organisms; (3) risk of rapid evolution via hybridization; (4) the danger of the 'open border' basis of plant biosecurity protocol within Europe. Plant trade is currently a huge business in Europe and North America, therefore the risk of further invasion remains very high even in regions that suffered many invasions in the past.

Climate change may alter ecosystem functioning and change species' richness and abundance, enhance the fitness of pathogens and drive their range-expansion, weaken host plants, i.e. predispose them to infection, eventually promoting the establishment of new invasive alien plant, animal and pathogen species (Scherm and Coakley 2003; Theoharides and Dukes 2007; Eastburn et al. 2011). According to Early et al. (2016) the continuous climate change disturbance expected for the near future will increase the invasion threat in Eastern North America, Northern Europe, Central and Southern Asia, and Northern Australia.

Spatial structure of host populations

Besides the host's life-style and mode of reproduction, abundance and spatial distribution of the host's populations also significantly influence a pathogen's population dynamics, invasion success, and disease impact (Real and Biek 2007). Therefore, the capacity of a tree species to form pure forests or on the contrary, its tendency to grow scattered in mixed forests, together with the host's tendency to reproduce sexually or clonally, might favor a pathogen or another depending on their requirements and features. As an extreme example, genetically uniform populations on large areas, such as planted forests, represent a

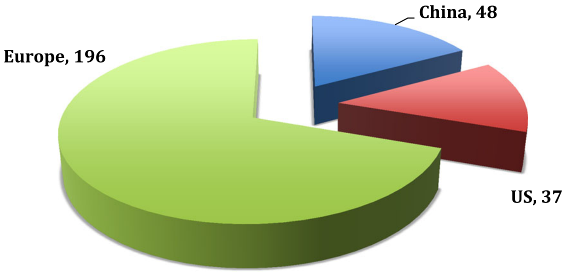

Fig. 2 Number of invasive forest pathogens (data modified and updated from Xu et al. 2012; Liebhold et al. 2012; Santini et al. 2013)

uniform and continuous carbon source, and an empty niche, readily available for pathogens, whether they be introduced species, against which there is usually a lack of natural resistance, or native species, which may, in such conditions, be subjected to fast adaptive selection. In this case, a pathogen's population may undergo massive size growth, and only afterwards, when the population size is stable again, new genetic variation usually appears (Barrett et al. 2008). In wild tree populations of smaller size, patchily distributed or isolated, the populations of invasive pathogens remain usually smaller, have limited genetic variability, and are commonly subjected to near-extinction events, in which drift and gene flow play a significant role (Barrett et al. 2008).

Host resistance

The interactions between host plants and pathogens enhanced ecosystem diversity during evolution (Thompson 1998). Every ecosystem is shaped by different interactions between plants and herbivores including pests and pathogens, which result in the selection of useful genes both in prey and predator, enabling a long-standing association between the involved species. Flor's gene-for-gene hypothesis (Flor 1971) and the "zig-zag model" by Jones and Dangl (2006) best explain parasite-host interactions in obligate pathogens. They proposed that for each gene that conditions reaction in the host (i.e., a resistance- or R-gene) there is a corresponding gene in the parasite (i.e., an avirulence- or Avr-gene) that conditions pathogenicity. According to this model plants detect microbial/pathogen–associated molecular patterns (MAMPs, PAMPs) via receptors triggering an immunity response. Pathogens may evolve new effectors that enable them to overcome plant immunity. Plants may in turn evolve new receptors able to recognize those new effectors, triggering immunity again.

In this way, host plants and their pathogens establish a dynamic equilibrium in a continuous process of co-evolution. The assemblages of plants and pathogens have mostly evolved in a condition of genetic isolation because of geographical barriers. When these barriers are broken, most frequently because of human activities, and exotic pathogens are introduced into new environments, they may find naïve hosts lacking specific resistance genes targeting them, and a favorable environment, i.e. conditions that increase pathogen aggressiveness and possibly result in disease outbreak (Brasier 2001)

Host phenology and disease avoidance

Avoidance can be defined as a mean of disease resistance, encompassing mechanisms under the genetic control of the host, taking place whenever susceptible plants do not become infected because the factors necessary for disease development (susceptible host, virulent pathogen, and favorable environment) do not coincide and interact at the proper time or for a sufficient period of time (Ghelardini and Santini 2009). The variation in the timing of the host's life stages and phenological phases characterized by different degrees of susceptibility, i.e. the transitory presence of plant tissues or organs susceptible to infection, change host availability, making it possible for a tree to resist infection, therefore altering disease epidemiology (Dantec et al. 2015). For example, in the European field elm (*Ulmus minor* Mill.) plants that open their vegetative buds earlier in spring are less susceptible to Dutch elm disease than late flushing plants (Santini et al. 2005). Early flushing may function as a mechanism of disease avoidance inasmuch it causes a temporal mismatch between the time of maximum susceptibility, which is linked to the host's phase of growth, and the appearance of the *Scolytus* insects vectoring the infection. Rhythm of leaf expansion, rate of height and diameter growth, seasonal changes in wood anatomy, and seasonal variation in secondary metabolism are likely involved in the seasonal variation of susceptibility in elms and in disease avoidance by early flushing genotypes (Solla et al. 2005; Ghelardini and Santini 2009). The variation of host susceptibility in the course of time may however exert a strong selective pressure, which might be able to promote fast adaptation in pathogens or vectors.

Enemy release

The traditional explanation for the success of alien species as invaders in new regions is that they do not have enemies in the non-native range (Wolfe 2002) and/or they attack non-coevolved hosts, which lack specific defenses against them (Morrison and Hay 2011). However, at least in the case of invasive plants, the enemy release hypothesis has been questioned

(Heard et al. 2006; Liu and Stiling 2006; Parker and Gilbert 2007). As regards invasive forest pathogens, the effect of a temporary lapse of enemies in the new environment has never been tested. However, there is circumstantial evidence for either delayed adaptation or acquisition of natural enemies in the invaded range at least for two alien invasive pathogens in Europe, i.e. the appearance of virus mediated hypovirulence in *Cryphonectria parasitica* (Grente 1965) and of deleterious d-factor viruses in *Ophiostoma ulmi* s.l. (Brasier 1983; Buck et al. 2002).

Novel associations

Once established in a new area, invasive alien pests or pathogens may replace endemic species in local insect-fungus associations. The establishment of a novel association may increase dispersal and/or transmission efficiency of the involved alien pests or diseases resulting in epidemic outbreaks (Wingfield et al. 2016).

An illustrative case is represented by the replacement of the non-aggressive fungus *Pestalotiopsis funerea* (Desm.) Stey, which is endemic in Europe, by the aggressive alien invasive pathogen *Seiridium cardinale* (Wag.) Sutton and Gibson, the causal agent of cypress canker, in the ancient symbiotic association with the cypress seed bug *Orsillus maculatus* in the Mediterranean Basin. *P. funerea* and *O. maculatus* had co-evolved with the Italian cypress (*Cupressus sempervirens* L.), and only caused negligible damage in the native range (Santini and Di Lonardo 2000). Once introduced into Europe and North Africa, *S. cardinale* was rapidly spread by the bug with disastrous consequences for the survival of *C. sempervirens* (Battisti et al. 1999).

Another illustrative example is the association between the introduced *O. ulmi* and *O. novo-ulmi* (collectively *Ophiostoma ulmi* s.l.) and endemic elm bark beetles in the subfamily Scolytinae in the invaded range. The spread of the two fungi is mainly operated by these beetles (Fransen and Buisman 1935; Webber and Brasier 1984), and disease transmission to suitable hosts is effective since the life cycles of the host-trees, the pathogen(s) and the beetles are synchronized (Webber 2004; Ghelardini 2007; Ghelardini and Santini 2009). Before DED, elm bark beetles in Europe probably had a mutualistic ectosymbiosis with the indigenous saprophytic fungus *O. quercus* (previously known as the hardwood biological species group, or OPH group, of *O. piceae)* (Brasier 1990). In the past century, the introduction of *O. ulmi* s.l., a species with similar niche requirements to *O. quercus* but pathogenic on *Ulmus* spp., has resulted in the replacement of this endemic congeneric species on elm. The new bark beetle/fungus association resulted in a highly effective transmission pathway with devastating consequences for the survival of elms (Brasier 1982; Santini and Faccoli 2015).

The Western conifer seed bug *Leptoglossus occidentalis* Heidemann (*Heteroptera*, *Coreidae*), which seriously impairs seed production of conifer species in Europe (Roversi et al. 2011; Tamburini et al. 2012; Lesieur et al. 2014), was introduced in the late 1990s and in just a decade invaded large parts of the continent (Taylor et al. 2001; Fent and Kment 2011). In Italy, *L. occidentalis* is the vector of *Diplodia sapinea* (Fr.) Fuckel Nassau (Luchi et al. 2012), a cosmopolitan fungal pathogen of conifers, probably native to Southern Europe. As a result of this new association, *D. sapinea* is today dispersed much faster and reaches a higher number of susceptible trees of the genera *Cedrus*, *Juniperus*, *Picea* and *Pseudotsuga*, which rarely were attacked by the fungus in natural conditions before (Stanosz et al. 1999). In addition, in the last 25 years, milder winters have allowed *D. sapinea* to expand its distribution range towards Northern Europe, threatening an even greater number of conifer species (Hanso and Drenkhan 2009; Oliva et al. 2013).

Several new interesting associations between ophiostomatoid fungi, insects and tree hosts are also described by Wingfield et al. (2017b in this issue) and the possible reasons of a recent increase in emergence of the disease due to these associations were also discussed.

Spread

Domestic invasion pathways

Pathogens may be transported by human travel and trade as hitchhikers or contaminants on different goods or in soil. The intercontinental trade of live plants for planting is the major pathway for the spread of non-native plant pathogens globally. The commerce of live plants also plays a major role in the dispersal of invasive forest pathogens at the regional and local scale (Jones and Baker 2007), confirming the importance of human-mediated jump-dispersal in determining invasion dynamics subsequent to introduction or establishment (Suarez et al. 2001).

In addition, pathogens may be dispersed through wind-, water-, and animal-borne propagules. Dispersal at the continental scale by means of wind-borne structures has long been documented in species infecting crop plants (Brown and Hovmøller 2002) as in forest tree pathogens (Close et al. 1978). When a pathogen is introduced by humans to non-native areas populated by naïve hosts, a largely wind-borne epidemic is possible, as it happened with chestnut blight in North America (also assisted by occasional dispersal by insects and animals) or, more recently, in the case of ash dieback in Europe (Anagnostakis 2012; Gross et al. 2014). A recent analysis of a newly compiled global database of invasive tree pathogens suggests that wind-dispersed fungi may be overrepresented among invasive tree pathogens worldwide (Ghelardini et al. unpublished).

Medium- to short-distance dispersal is likely to be crucial for the successful establishment of a pathogen in the invasion range, greatly affecting an epidemic's development, and disease dynamics and persistence. At the local scale, rain splash-dispersed pathogens are those with the shortest spreading distance, while airborne pathogens have the widest spreading area. In between these two extremes there are vector-borne pathogens. Very efficient incidental vectors of invasive forest pathogens can be animals, and humans among them, with or without fitness benefit, as respectively symbiotic insects, e.g. beetles and ambrosia fungi, and squirrels (Panconesi 1999; Lieutier et al. 2004). *Ceratocystis platani* (see "Box 3" section) and *Cryphonectria parasitica* provide good examples of lethal wound pathogens possessing multiple short-distance dispersal means, i.e. wind, vertebrate and invertebrate animals, and water. However in some pathogens, as in *C. platani,* the most important dispersal route to short- and medium-distance is represented by pruning tools and terracing machinery, just showing how crucial human activities can be in spreading alien pests. Root anastomosis is an important mean of spread invasive pathogens attacking trees grown in lines as in city avenues, or in monospecific plantations, as shown by the examples of *O. ulmi* s.l. (Gibbs 1978), *Heterobasidion irregulare* (Garbelotto and Gonthier 2013) and *C. platani* (Tsopelas et al. 2017).

Impact

The economic and environmental impacts of alien forest pathogens on natural ecosystems have only recently, and in a limited number of studies, been assessed in-depth (Lovett et al. 2006; Pimentel et al. 2000). The removal costs of infected trees were used as an estimate of the economic damage caused by invasive forest pathogens (Pimentel et al. 2000; Haight et al. 2011). For instance, the removal cost was estimated at about US$100 million per year for the elms killed by DED in North America (Campbell and Schlarbaum 1994) and at roughly US$250 per tree killed by oak wilt (Haight et al. 2011). Pimentel et al. (2000) estimated the loss of forest products caused by plant pathogens in about 9% of the total production, or US$7 billion, per year.

Forests provide qualitative and long-term services which are difficult to monetize. The introduction and spread of invasive pathogens may change tree species abundance and diversity, altering the structure of forest ecosystems, their productivity, nutrient uptake, carbon and nitrogen cycles, and soil organic uptake and turnover (Lovett et al. 2006, 2010). The epidemic of chestnut blight due to the introduction of *C. parasitica* caused dramatic changes in the forests of eastern North America. In 1934 *Castanea dentata* (Marsh.) Borkh. was present in 98% of the forests in the Coweeta Basin, in the Southern Appalachian Mountains of North Carolina, contributing 22% of the total density and 36% of the total basal area (Elliott and Swank 2008). As the epidemic progressed, *C. dentata* was replaced by different species along environmental gradients, which produced a general increase in species diversity (Elliott and Swank 2008). Davis et al. (2014) showed that plant richness, cover at all strata and flowering are reduced at sites infested by *Phytophthora cinnamomi* in Western Australia, causing a drastic change in the bird community composition. In Oregon and California, *Phytophthora ramorum* modified the structure of forests so that the number of ecological niches suitable for two of the vertebrates' host of the Lyme disease pathogen and its vector, the tick *Ixodes pacificus,* resulted increased (Swei et al. 2011). The disturbance due to the invasion by *P. ramorum* indirectly increased the survival and abundance of ticks at the nymph stage, which is most likely to bite humans, consequently increasing the risk of exposure to the Lyme disease.

The impact of *S. cardinale* on the Italian cypress, the iconic landscape tree of Tuscany, was tentatively assessed in the Project MED Operational Programme "CypFire" (see "Box 1" section). In order to evaluate the loss of landscape/ornamental value caused by cypress canker, about 600 tourists on holidays in Tuscany were interviewed according to a previously designed questionnaire. The questionnaire was based on two assessment methods: (1) the "Landscape components evaluation" (Tempesta 1997; Giau 1999), a non-monetary estimate of the importance of cypress in the Tuscan landscape; and (2) the "Willingness to pay", a contingent monetary method (Stellin and Rosato 1998; Notaro et al. 2005) based on people's willingness to pay for a service, i.e. in this case for preserving the Tuscan landscape from the disappearance of cypresses.

The results showed that landscape is one of the main attractions for tourists visiting Tuscany; that cypress is considered a quintessential component of the landscape of Tuscany; and that the disappearance of cypress would render the Tuscan landscape far less attractive and reduce the motivation for visiting the region. The persons interviewed expressed their willingness to pay a maximum of 11.2 Euros per capita on the average for protecting cypress from canker disease. Since each year between 460.000 and 550.000 tourists spend their holidays in farmhouses in Tuscany, the estimated total willingness to pay approaches 5–6 million Euros per year. This provides a rough estimate of the yearly impact of cypress canker on tourism, the economy and the landscape.

Conclusions

This paper summarizes some aspects of the ecological process leading to invasion by forest pathogens. Despite the worldwide importance and impact of forest invasions, invasion ecology of forest pathogens is a young research field, where much remains to be understood (Lugo 2015). The introduction of alien pathogens usually leads to novel host–pathogen or pathogen–pathogen combinations with no previous co-evolution history and complex outcome (Slippers et al. 2005; Dunn and Hatcher 2015). Many introduced pathogens responsible for severe disease epidemics of trees were not considered serious pathogens or were not even known before they attacked new hosts in the invaded range (Brasier 2008). Microbial hitchhikers, and latent or cryptic pathogens, living as endophytes, epiphytes or weak pathogens on their native and co-evolved host plants, once introduced into new regions may undergo host shifts and move onto native plants, changing their behaviour from mutualistic associates to aggressive pathogens (Burgess et al. 2016; Roy et al. 2016). The genomes of closely associated plant microorganisms (including mutualists and pathogens), recently referred to as the 'second-genome' (Grice and Segre 2012; Turner et al. 2013; Berg et al. 2014), have a crucial role in evolutionary mechanisms associated to biological invasion (Blackburn et al. 2011; Zenni et al. 2017). Because of post-invasion host jump and limited knowledge of the many steps and different components involved the invasion process, predicting which species might become invasive forest pathogens once introduced to new areas seems very difficult if not unrealistic in many cases. The unpredictable nature of biological invasion as well as the limitation posed to current predictions by inadequate scientific knowledge, has been recently analysed and discussed in detail elsewhere (Roy et al. 2016). There is no doubt that investment in research, possibly coordinated within an interdisciplinary framework (Wingfield et al. 2017a, b), and in-depth elaboration on the ecology of forest invasions (Desprez-Loustau et al. 2016) is the only option to strengthen the holistic interpretation of the phenomenon, develop well-grounded predictive approaches and possibly conceive the countermeasures for facing the constant attack perpetrated by invasive forest pathogens.

Box 1

Seiridium cardinale

Seiridium canker, or bark canker of cypress, is a pandemic disease due to three pathogenic fungi, i.e. *Seiridium cardinale* (Wagener) Sutton and Gibson, *Seiridium cupressi* (Guba) Boesew., and *Seiridium unicorne* (Cooke and Ellis) Sutton, causing stem and branch necrosis, dieback, and tree mortality in most Cupressaceae species. *Seiridium cardinale*, the most widespread and aggressive species, was first reported in California in 1928, where in a few years it destroyed the plantations of the inland districts (Wagener 1939). During the following decades, the disease progressively spread over the five continents and became pandemic, reaching in succession New Zealand, France, Chile, Italy, Argentina, Greece and other Mediterranean countries, Central and Northern Europe, Canada, South Africa and Australia (Danti et al. 2013a). *Seiridium cardinale* infects various species of *Cupressus, Chamaecyparis, Cryptomeria, Juniperus, Thuja* and x *Cupressocyparis leylandii* (Graniti 1998). Population genetic studies suggest the pathogen to be native or long naturalized in California, which is the source region of the Mediterranean population (Della Rocca et al. 2011, 2013). In the Mediterranean region, the fungus reproduces only clonally, although variation is likely to be ensured by occurrence and accumulation of mutations or mitotic recombinations, as expected in a parasexual life cycle (Della Rocca et al. 2011, 2013). Movement of infected cypress plants is thought to be responsible for the global spread of the pathogen since identical genotypes of the fungus were identified at large distances (Della Rocca et al. 2011, 2013). In the Mediterranean basin, the extensive presence of susceptible hosts, in combination with climatic conditions conducive to the development of the pathogen, has promoted its rapid spread. Cypress canker reached an incidence as high as 70% in Central Italy and Greece during the 1980s and severely affected the local cypress and other introduced cypress species (Panconesi 1990; Xenopoulos and Diamandis 1985). The epidemics killed millions of trees, spoiled the landscape, and produced severe damage in the woods, ornamental plantations, and nurseries (Graniti 1998; Panconesi 1990), with consequently high costs. Cypress canker has gradually reached an endemic phase in Central Italy, helped by extensive sanitation measures and the breeding of resistant cypress cultivars (Danti et al. 2006, 2013b).

Box 2

Diplodia sapinea

Diplodia sapinea (*Sphaeropsis sapinea*) is a haploid fungus species with worldwide distribution as well as an opportunistic plant pathogen of many conifers. The pathogen is widespread in Europe, South Africa and the United States, where it causes serious damage especially to pine species both in natural forests and commercial plantations (Stanosz et al. 1996; de Wet et al. 2000; Luchi et al. 2014). The fungal spores are dispersed by wind, water, animals, and human activities, and germinate on young elongating needles. Penetration occurs through the stomata, or through wounds caused by hail, insects, or pruning. *Diplodia sapinea* is thought to reproduce only by asexual mitospores, as no sexual stage has ever been observed (Burgess et al. 2001).

The taxonomy of this species has been under constant revision. The species included two morphotypes, A and B, until the latter was elevated to species level and named as *Diplodia scrobiculata* (J. de Wet, B. Slippers and M.J. Wingfield) (de Wet et al. 2003). These pathogens share the same habitat, but *D. sapinea* is much more aggressive and produces more pycnidia than *D. scorbiculata* (Luchi et al. 2007; Blodgett and Bonello 2003). Therefore, *D. sapinea* has spread faster and more efficiently in the northern hemisphere than *D. scrobiculata,* which remained confined to a smaller number of host species and maintained a scattered distribution (Bihon et al. 2011; Linaldeddu et al. 2010).

A key factor for understanding the invasion ecology of these species is the latency period, during which the pathogen lives asymptomatically in the host's tissues until a biotic or abiotic stress factors, for instance water stress, modifies the equilibrium of the plant-endophyte interaction, driving an epidemic outbreak of the disease (Stanosz et al. 2001; Fabre et al. 2011). In this respect, the current poleward spread of *D. sapinea* is representative of the effects of climate change-related stressors on disease emergence (Adamson et al. 2015). Moreover, *D. sapinea* well illustrates the case, probably quite common, in which the presence of a possibly long latency period, when apparently healthy plants carry the pathogen inside their tissues, helps spreading a disease to new geographic areas through commercial trade of asymptomatic plants. *D. sapinea* and *D. scrobiculata* were probably introduced to the southern hemisphere through the import of asymptomatically infected pine seedlings for plantations (Burgess et al. 2001). The presence of a common allele between the populations of *D. scrobiculata* from South Africa and California confirms the introduction of the fungus from the US, probably through infected *P. radiata* seedlings (Bihon et al. 2011).

Box 3

Ceratocystis platani

Ceratocystis platani (Walter) Engelbrecht et Harrington causes mainly a vascular wilt disease of *Platanus* spp. but it is also able to cause cankers on the bark, which is the reason why the common and accepted name of the disease, even if misleading, is canker stain disease (CSD). The fungus, probably native to North America (Walter et al. 1952; Engelbrecht et al. 2004), was accidentally introduced during World War II into Europe (Cristinzio et al. 1973; Panconesi 1999) where it spread as a single clone (Santini and Capretti 2000; Ocasio-Morales et al. 2007). The fungus is self-fertile and reproduction is ensured by ascospores and by three different forms of asexual conidia. *C. platani* penetrates the host through wounds or other injuries caused by biotic or abiotic agents in the branches, the trunk, or the roots (Vigouroux and Stojadinovic 1990). It is mainly spread by means of pruning tools, terracing machinery and root anastomosis, and in the second place by wind, animals, and water (Panconesi 1999; Luchi et al. 2013). All spore types of the fungus produce infections on freshly wounded tissues. After spore germination, the mycelium colonizes the exposed tissues, advances into the xylem of the underlying sapwood, and it develops both longitudinally and tangentially (Tsopelas et al. 2017). CDS is a devastating disease that may kill an adult tree in a single growing season and a monumental tree in a just few years (Tsopelas et al. 2017). Mortality rates due to *C. platani* are extremely high. Many trees have been killed throughout the invaded range in city parks and avenues, including plants of great aesthetic value. The spread of the disease out of the urban environment threatens plane tree survival in natural forests.

Although often overlooked in forest pathology reviews, in Southern Europe CSD has an impact comparable to that of notorious tree diseases such as DED, chestnut blight or ash dieback (Walter et al. 1952; Brasier and Kirk 2001; Kowalski 2006; Ocasio-Morales et al. 2007; Anagnostakis 2012). The pathogen, reported also in Switzerland and Spain (Panconesi 1999; Vigouroux 2013; EPPO 2014), caused widespread mortality of London plane (*Platanus x acerifolia* (Ait.) Willd) in Italy and France. But the most dramatic impact of the disease concerns the natural stands of oriental plane (*Platanus orientalis* L.) in Greece (Ocasio-Morales et al. 2007; Tsopelas and Soulioti 2011, 2014) where CSD killed and is currently killing each year thousands of trees that do not exhibit any sign of resistance. More recently *C. platani* was recorded for the first time in Albania (Tsopelas et al. 2015). There are unconfirmed reports for the presence of *C. platani* in Armenia (Simonian and Mamikonyan 1982) and Iran (Salari et al. 2006), and there is unpublished evidence that the fungus is present in other parts of Western Asia (Dogmus Lehtijarvi pers. comm.). Therefore, the pathogen seems to continue spreading in the natural range of *P. orientalis* in Western Asia with apparently no constraints.

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