

# Ecological, evolutionary, and societal impacts of invasions by emergent forest pathogens

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## 1. Introduction

Biological invasions, including those by forest pathogens, are regarded as one of the major causes for the loss of biodiversity at the planetary level (Simberloff et al., 2013), together with climate change (Bellard et al., 2012; Pautasso et al., 2012) and urbanization (DeFries et al., 2010). Notably, while comparing environmental impacts of invasions by alien plants, insects, and pathogens in protected riparian forests, it has been shown that pathogens, namely fungi, had significantly higher impacts than other invasive organisms (Lapin et al., 2021). Indeed, the vast majority of microbial invasions of terrestrial ecosystems is caused by alien plant pathogens (Lovett et al., 2016), many introduced through international trade (Liebhold et al., 2012; Santini et al., 2013). However, native pathogens may also become invasive due to ecosystem-level alterations such as practices associated with plantation forestry and the planting of exotic hosts (Edmonds, 2013; Garbelotto and Gonthier, 2013). Thus, in a broader sense, invasive pathogens include both those introduced by man and those whose range may be rapidly changing in association with rapid climate change or habitat transformation. Together, these two classes of invasive pathogens can be defined as emergent and can lead to the rise of novel plant diseases causing detrimental effects on affected ecosystems (Parker and Gilbert, 2004; Desprez-Loustau et al., 2007; Almeida and Nunney, 2015). In general terms, the shift in forest structure and species composition as a result of invasions by pathogens alters ecosystem functions such as productivity, nutrient cycling, and wildlife habitat. In urban and suburban areas, the loss of trees from streets, yards, and parks affects aesthetics, property values, shading, stormwater runoff, and human health (Lovett et al., 2016).

The main focus of this chapter is not to discuss disease and mortality caused by emergent tree pathogens on their main hosts, a topic discussed by a vast and readily available literature, but rather to summarize some of the other broader and less obvious effects. These include ecological effects on plant communities as a whole, on wildlife, on microbial communities, on soil structure and composition, on nutrient cycles, and on fire behavior. A second, less obvious, category of effects caused by invasions by tree pathogens can be identified as being evolutionary in nature. These evolutionary effects may be multiple and include (a) evolutionary shifts in the invasive pathogens themselves due to isolation of introduced populations, founder effects associated with the genetic bottlenecks inevitably occurring during the introduction process, adaptive selection in new environments including that caused by new viral pressures, and changes in reproductive strategies; (b) evolutionary shifts occurring in both invasive and related pathogen species because of genic introgression associated with interspecific hybridization and backcrossing; and (c) evolutionary shifts on the hosts affected by invasive pathogens, for instance, reduction of genetic diversity in tree populations decimated by novel diseases, phenotypic- or phenological-based selection caused by infection and mortality being more frequent in trees of a certain size or at a certain phenological stage, and genetic-based selection of trees carrying genes conferring tolerance or resistance to the novel diseases caused by the emergent pathogens. Finally, the emergence of novel expanding tree diseases can have profound effects on society because of the economic losses caused by tree diseases and of the cultural impacts tree loss may have, often resulting in a destabilization of local communities and in the abandonment of entire regions whose economy and/or culture was centered around trees and the resources associated with them. Table 7.1 summarizes the impacts of emergent forest diseases discussed in this chapter.

**TABLE 7.1** A list of the ecological, evolutionary, and societal impacts of a selected group of emergent tree diseases that is discussed in this chapter.

Pathogen	Disease and geography	Ecological impacts	Evolutionary impacts	Societal impacts
<i>Armillaria</i> spp.	Armillaria root disease (ARD) worldwide			Disease threatens both orchards and wine-producing areas and often originates from natural outbreaks
<i>Ceratocystis fagacearum</i>	Oak wilt in the United States		Selection of tree families with smaller wood vessels	Economic damage due to loss of amenity, urban and landscape trees
<i>Ceratocystis lukuohia</i> and <i>C. huliohia</i>	Rapid Ōhi'a Death (ROD) in Hawaii	Drastic reduction in range occupied by native Hawaiian tree species Change in bird populations: Some species will increase abundance, some others will decrease it		Economic damage due to loss of amenity, urban and landscape trees Cultural significance of host trees
<i>Ceratocystis platani</i>	Canker stain of plane trees in Europe		Reduced genetic variability in pathogen	Economic damage due to loss of amenity, urban and landscape trees
<i>Cronartium ribicola</i>	White pine blister rust (WPBR) in North America		Reduced genetic variability in pathogen Evolution of genetically distinct fungal populations due to isolations between source native and various introduced populations Adaptive fast evolution of pathogen to overcome resistance in host	Loss of revenues from timber sales Loss of resources (timber and nontimber) for native people Local reverse migration of workforce in wildlands in the attempt to eradicate <i>Ribes</i> spp., the alternate plant hosts of the pathogen Cultural significance of host trees
<i>Cryphonectria parasitica</i>	Chestnut blight in North America, Europe, and Turkey	Removal of adult chestnut trees Reduction of chestnut-dependent biodiversity Slight increase in biodiversity due to invasive plants Changes in tree species composition Reduced ectomycorrhizal efficiency in regeneration	Reduced genetic variability and increase in frequency of asexual reproduction in pathogen Viral infection in fungus in novel environments Dominance of a few pathogen genotypes Artificial crossing of different chestnut tree species shows genomes of resistant species will be selected for	Loss of revenue associated with loss of timber and of nontimber products Abandonment of chestnut producing areas resulting in migration and in depopulation of rural areas, which in turn resulted in a worsening of the health of chestnut trees
<i>Fusarium circinatum</i>	Pine pitch canker (PPC) worldwide	Increase in abundance of trees displaying systemic acquired resistance (SAR)	Reduced genetic variability in pathogen, loss of sexual reproduction	Loss of revenue associated with loss of timber Economic damage due to loss of amenity, urban and landscape trees

<i>Heterobasidion irregulare</i>	<i>Heterobasidion irregulare</i> root disease in Europe	Presence of non-native pathogen alters the molecular interplay between mycorrhizae and pines, at times reducing the benefits to the plant	Reduced genetic variability in pathogen Hybridization with Eurasian <i>Heterobasidion annosum</i> creates viable hybrid swarms and genic introgression of very specific adaptive alleles between the two species. Adaptive nuclear genes from <i>H. irregulare</i> and the entire <i>H. irregulare</i> mitochondrion confer an advantage to fungal genotypes and are expected to invade populations of <i>H. annosum</i>	Loss of revenues from timber sales Economic damage due to loss of amenity, urban and landscape trees Recreation is impacted as campsites and other tourist venues need to be closed down due to the hazard of tree failure Loss of pine nut production
<i>Heterobasidion</i> spp.	Heterobasidion root and butt rot in North America and Europe		In North America, interspecific hybridization resulting in a third yet undescribed species, sexually reproducing and with a novel host (Alpine larch)	Loss of revenues from timber sales Recreation is impacted as campsites and other tourist venues need to be closed down due to the hazard of tree failure
<i>Hymenoscyphus fraxineus</i>	Ash dieback in Europe	High risk of extinction of ash-dependent organisms, including invertebrates, bryophytes, lichens, and fungi Changes in four trophic levels of invertebrates		Loss of revenues from timber sales Economic damage due to loss of amenity, urban and landscape trees
<i>Neonectria</i> spp.	Beech bark disease (BBD) in the Eastern United States	Increase in litter decomposition, decrease in soil C:N ratio, and large increase in soil nitrates		
<i>Nothophaeocryptopus gaeumannii</i>	Swiss needle cast (SNC) of Douglas-fir on the West Coast of the United States	Lower functional mycorrhizal tips and decreased ectomycorrhizal species richness		
<i>Ophiostoma ulmi</i> and <i>Ophiostoma novo-ulmi</i>	Dutch elm disease (DED) in North America and Europe	Changes in populations and communities of both birds and wood-feeding insects	Viral infection in fungus in novel environments Hybridization and genic introgression between the two species have caused the rapid adaptive evolution of <i>O. novo-ulmi</i> . Likewise, adaptive introgression is now ongoing in between two subspecies of <i>O. novo-ulmi</i> Selection of tree genotypes with wood capable of producing secondary metabolites associated with resistance	Economic damage due to loss of amenity, urban and landscape trees
<i>Phytophthora cinnamomi</i>	Oak decline in Europe. <i>Phytophthora</i> dieback of <i>Banksia</i> in Australia	Shifts in populations of nematodes Changes in soil nutrients and in respiration of soil microbes Serious threat to some bird species but not to all birds in general		Pathogen is a major player in many crops, especially ornamental plants, Christmas trees, fruit orchards, and avocados Agroforestry in the Iberian Peninsula is threatened by the pathogen as well as <i>Banksia</i> in Australia
<i>Phytophthora plurivora</i>	n/a	Leaves more attractive to moth attacks		

Continued

**TABLE 7.1** A list of the ecological, evolutionary, and societal impacts of a selected group of emergent tree diseases that is discussed in this chapter— cont'd

Pathogen	Disease and geography	Ecological impacts	Evolutionary impacts	Societal impacts
<i>Phytophthora ramorum</i>	Sudden oak death (SOD) on the West Coast of the United States	Change in size class (removal of adults) of oaks and tanoaks Decrease in population size of oaks Decimation and local extinction of tanoaks Tanoak pollinators at risk Oak-dependent birds will be affected causing large population size variations Increase in wood-boring insect populations Changes in forest plant composition Increase in populations of two tick species, both vectors of the Lyme disease pathogen ( <i>Borrelia burgdorferi</i> ), suggesting an increase in Lyme disease rates in humans Reduction of the hyphal component of tree-fungus ectomycorrhizal symbiosis in the soil Local decimation or disappearance of mycorrhizal fungi in symbiosis with tanoaks and oaks Increase in soil nitrates and in accumulation of coarse woody debris Changes in fire behavior: higher intensity, longer flames, higher frequency of hot spots, increased unpredictability of fires Fire-resistant redwoods are scorched and killed during fires in SOD-infested stands	Insurgence of resistance to fungicides in introduced pathogen populations Increased frequency of tree genotypes displaying disease resistance and/or tolerance	Matsutake mushroom decline lowers sources of income for migrant foragers, and such limitation puts native First Nation communities in contrast with migrants Disease is a major constraint to the ornamental plant industry due to the susceptibility of many ornamental plant species Costs of pathogen regulation occur both in natural settings and in the ornamental industry Economic damage due to loss of amenity, urban and landscape trees Cultural significance of host trees
<i>Phytophthora xalni</i>	Alder dieback in Europe	Direct reduction in soil nitrogen, shade, and bank stability, causing an indirect influence on food webs, both terrestrial and aquatic	Change in phenotypes, including host range, due to interspecific hybridization	
<i>Pseudocercospora ulei</i>	South American leaf blight (SALB)			Fostered rubber production in Asia and Africa while hampering it in Latin America Disease makes many regions of Latin America no longer productive, and the need to use resistant clones makes rubber a difficult crop for small landowners and local communities
<i>Raffaelea lauricola</i>	Laurel wilt in the Eastern United States	Invertebrates that are specialists on plants of the family Lauraceae are at risk Changes in forest plant composition	Selection of tree genotypes capable of altering volatile production responsible for attracting insect vectors	Impact on avocado industry
<i>Seiridium cardinale</i>	Cypress canker disease worldwide		Reduced genetic variability in pathogen, loss of sexual reproduction Evolution of genetically distinct fungal populations due to isolations between source native and various introduced populations Adaptive fast evolution on new fungal phenotypes characterized by different virulence and morphology Faster growing tree families may be at a disadvantage in the presence of the disease	Economic damage due to loss of amenity, urban and landscape trees Cultural significance of host trees

Only the main impacts are reported. The table omits the ecosystem services provided by the trees affected by emergent pathogens, given that all trees provide such services and that the quantification of such services is difficult. Most of the various costs associated with disease control strategies and regulations are also omitted.

## 2. Ecological effects

### 2.1 Effects on entire terrestrial communities

Emergent tree diseases can alter terrestrial ecosystems not only by causing significant tree mortality, but also by reducing fecundity or regeneration recruitment of host trees (Gilbert, 2002), or by causing, overtly or cryptically, a significant reduction in the competitive nature of infected plants (Holt and Bonsall, 2017). While the time frame of the impacts may differ—with direct tree mortality being more likely to cause a significant disturbance in the shorter time frame than disease-associated reductions in fecundity, recruitment, or vigor—the end effect of emergent diseases will be the removal or reduction in the size of host populations in infested areas. Emergent diseases can also cause dramatic shifts in the structure of terrestrial ecosystems, without necessarily eliminating a tree species, but shortening its life span, consequently reducing the proportion of adult host trees (see below). While, in general, reduced tree diversity may correlate with higher spread rates of emergent diseases, generalizations are not truly possible because all depends on the epidemiological role of surviving trees and on the overall ecological resilience of the affected ecosystem as explained below. The removal and/or the reduction in size and number of host trees will cause a number of cascading effects, the magnitude of which is correlated to the extent of the impact of the disease, the temporal frame of the impact (in turn depending on whether the disease is reversible or not), the ecological role played by the host tree, and the amount of biodiversity and of ecological redundancy of the affected ecosystems. One good example of the diverse impact that emergent tree diseases can have on terrestrial ecosystems, depending on the severity of the diseases they cause, is offered by sudden oak death (SOD) caused by the non-native introduced pathogen *Phytophthora ramorum* in California. The disease in California is prevalent in two different forest types: the redwood-tanoak forest characterized by the dominance of coastal redwoods (*Sequoia sempervirens*) with the codominance of tanoaks (*Notholithocarpus densiflorus*), and the mixed evergreen forest where the canopy cover is usually a mix of *Quercus* (particularly *Quercus agrifolia*, *Quercus parvula*, or *Quercus kelloggii*), Douglas-fir (*Pseudotsuga menziesii*), and California bay laurel (*Umbellularia californica*). In the first forest type, the main host lethally affected by the disease is tanoak, while in the second forest type, the main hosts killed by SOD are oak species. Tanoak, being itself infectious, requiring a low inoculum load to become infected, and with no known true disease resistance mechanisms, has witnessed mortality rates of adults approaching the 100% in areas climatically favorable to the pathogen (Goheen et al., 2017). Conversely, oaks are not infectious, require a high inoculum load to become infected, and display some resistance to the disease (Conrad et al., 2019). As a result, mortality of adult oaks is generally much lower than tanoak mortality, and only occasionally it approaches 70% (Brown and Allen-Diaz, 2009). Both tanoaks and oaks are regarded as keystone species in their respective forest types (Pavlik et al., 1991; French, 2017); hence, their removal is predicted to disproportionately affect the biodiversity and resilience of affected ecosystems. Because both tanoaks and oaks are easily infected before they reach the adult status, even if their regeneration is not as seriously threatened by the disease (Swiecki and Bernhardt, 2007; Ramage et al., 2011), adults of both species are being effectively and permanently removed from the system. However, the difference in mortality levels between tanoaks and oaks is significant both ecologically and evolutionary, given that adult tanoak populations may be completely removed, while adult oak populations will be only partially removed and thus will remain as significant components of the ecosystem and will ensure a future presence of the species even in SOD-affected woodlands. A comparable distinction can also be made for the same pathosystem (i.e., same host-pathogen combination) in sites that, being environmentally different, may support disease outbreaks of drastically different intensity. This happens because the environmental conditions that are optimal for the host and the pathogen may be different, resulting in areas where hosts are abundant but the pathogen either cannot survive or cannot spread efficiently. Once again, SOD provides an excellent example of a disease that becomes marginal in areas where tanoaks and oaks are present but rainfall is too low and temperatures are too high for sporulation of *P. ramorum* to occur, resulting in much slower disease spread, lower host mortality (Grünwald et al., 2019), and high reversal rates of trees from infected to uninfected (Lione et al., 2017).

SOD is just one of forest emergent diseases known to affect keystone tree species. Another striking example of the potential destructive effects on an entire terrestrial ecosystem caused by an emergent tree disease is that of Rapid Ōhi'a Death (ROD) in Hawaii. ROD results in high levels of tree mortality and is caused by two *Ceratocystis* species, *C. lukuohia* and *C. huliohia*, both recently introduced in the Hawaiian archipelago (Barnes et al., 2018). Ōhi'a is a native tree species regarded as one of the main keystone species of Hawaiian forest ecosystems. Many native plants are likely vulnerable to these types of large Ōhi'a mortality events, and it has been estimated that more than 60% of 234 endangered native plant species have more than 50% of their range in areas at risk of being infested by one or both ROD pathogens (Fortini et al., 2019).

We stated above that biodiversity and ecological redundancy may also have a significant impact on the overall end effects caused by emergent tree diseases. In this respect, the comparison of tanoak/SOD vs. the American chestnut (*Castanea dentata*)/chestnut blight caused by *Cryphonectria parasitica* is exemplary. In both cases, adult hosts are removed from the

ecosystem, but while no other tree species is available to fully replace tanoaks (Ramage and O'Hara, 2010), maples and oak species may be regarded as ecologically similar, at least in part, to American chestnuts, allowing for a functional recovery of forests following even extensive and prolonged disease outbreaks (McCormick and Platt, 1980). Likewise, although chestnut-dependent native organisms have disappeared, others have replaced them, resulting in an apparent increase and not in a reduction in biodiversity (Smith et al., 2009). Smith et al. (2009), however, also caution that comparisons may be difficult because they are often compounded by lack of comparable datasets for the same areas before and after an epidemic. Thus, even if levels of biodiversity may remain equal or even increase in ecosystems with significant levels of ecological redundancy, such as Appalachian forests once dominated by chestnuts (McCormick and Platt, 1980), some entire trophic webs characterized by host-specific organisms may be lost when the host is removed from an ecosystem by an emergent disease. This appears to be the case for ash dieback caused by *Hymenoscyphus fraxineus* triggering niche replacement of European ash (*Fraxinus excelsior*) (Díaz-Yáñez et al., 2020) and resulting in a high risk of extinction of organisms solely dependent on ash, including 48 invertebrates, 37 lichens, 19 bryophytes, and 11 fungi based on a study conducted in Sweden (Hultberg et al., 2020).

There are several studies regarding the effects of emergent tree diseases on the diversity of arthropods and of wildlife in general (Wright and Dodd, 2013; Riggins et al., 2019). Some of the results echo what is mentioned above, that is, host-dependent animals will be more at risk if their hosts are threatened by emergent diseases, but generalists may not be at a comparable risk level, and studies may fail to detect a loss in overall biodiversity in conjunction with infestation by emergent pathogens. The following examples deal with organisms characterized by varying levels of host specificity. A total of 178 native arthropod species could be impacted by widespread mortality of their lauraceous host plants due to laurel wilt caused by the non-native fungus *Raffaelea lauricola* and its primary vector, the redbay ambrosia beetle *Xyleborus glabratus*, in the Eastern United States. While species with multiple hosts, including some not affected by the disease, would only be moderately impacted, obligate Lauraceae specialists were predicted to be at high risk. This prediction was confirmed by a study on the abundance of a laurel obligate butterfly (*Papilio palamedes*), whose populations were found to have decreased sixfold in areas infested by laurel wilt (Riggins et al., 2019). Likewise, high mortality of tanoaks caused by SOD could detrimentally affect populations of tanoak pollinators (Wright and Dodd, 2013), and by using geocoded data, Monahan and Koenig (2006) showed that post-SOD bird populations would be 25%–68% smaller and 13%–49% more variable relative to pre-SOD estimates.

When non-native or generalist animals are considered, instead, results may be different. For instance, when comparing birds' diversity pre- and post-ROD in Hawaiian lowland forests, an overall increase in species diversity was identified, with a couple of species observed for the first time only post-ROD, due to the novel conditions (i.e., increase in shrubs and more open habitats) generated by the disease. However, populations of two bird species, the Hawaii Amakihi (*Chlorodrepanis virens*), and the non-native Japanese white-eye (*Zosterops japonicus*), decreased significantly, of which the first one is notoriously associated with healthy Ōhi'a stands (Camp et al., 2019). Likewise, bird community composition in Southwestern Australia differed significantly between healthy Banksia sites and sites infested by the soil-borne pathogen *Phytophthora cinnamomi*, but bird abundance, species richness, and foraging guilds did not, suggesting that this pathogen is potentially a serious threat to some species but not to all birds in general (Davis et al., 2014).

There are some shifts in the abundance of tree-dependent organisms that, although associated with outbreaks of emergent tree diseases, may only be cyclical and simply associated with the availability of appropriate reproductive and/or feeding habitats in dying or dead trees. Changes in avian communities often follow large-scale mortality of forest canopy species: For instance, elm (*Ulmus* spp.) mortality following the introduction and spread of Dutch elm disease (DED) caused by *Ophiostoma* spp. in the United Kingdom and North America led to significant changes in bird populations and communities (Osborne, 1983). An increase in saproxylic insects and tree cavities as a result of DED-triggered mortality has been reported to support more woodpeckers, and, as forest canopies opened up, understory bird species have been observed to increase in abundance (Canterbury and Blockstein, 1997). Similarly, ambrosia beetle populations were shown to increase significantly in association with SOD outbreaks; however, it could not be determined if this increase was solely an effect of the increase of ambrosia beetle habitat offered by dying and recently dead trees, or if larger ambrosia beetle populations could also hasten the speed and rate of tree mortality (Beh et al., 2014).

While post-disease recovery of an ecosystem is in part facilitated by higher levels of biodiversity and by the presence of biological or ecological redundancy, recovery may also occur if host populations respond to infection either by adaptive selection of disease-resistant individuals or through systemic acquired resistance (SAR). SAR is a mechanism by which plants may respond to initial pathogen challenge through the activation of inducible defense responses, thereby increasing resistance to subsequent infection attempts (Bonello et al., 2001). In spite of the potential trade-off costs associated with the induction of resistance triggered by infection, a combination of experiments and simulations have convincingly shown that in the case of SAR induced by the pine pitch canker (PPC) pathogen *Fusarium circinatum*, tree growth is not significantly

affected (Reynolds et al., 2016) and the cost associated with SAR is less than that associated with infection, so that trees with SAR will dominate a population in the presence of the disease (Reynolds et al., 2019). However, infection by emergent pathogens may have physiological effects on the host other than SAR, with different implications and outcomes. For instance, root infections by the emergent pathogen *Phytophthora plurivora* increase the attractiveness of red oak leaves to the moth *Lymantria dispar*, probably because of higher nitrogen and water content observed in the leaves of infected trees (Milanović et al., 2015).

We recognize that tree diseases in general are explained by the classic theory of the disease triangle, which postulates that disease will increase with increasing susceptibility levels of the host, virulence levels of the pathogen, and permissivity of the environment, and we also believe that disease itself may become a disturbance factor further affecting the outcome of the disease triangle (Garbelotto and Gonthier, 2017). Until here, this chapter has focused on disease interpreted as the outcome of this triple interaction; hence, the consequences of the disease on host-dependent organisms can all be viewed as a direct effect of the level of mortality or disease explainable with the disease triangle. The picture, however, becomes more complex when one pathogen can affect multiple hosts in the same forest ecosystem, because of the complex feedback processes initiated by disease in ecologically distinct hosts, and in plants and other organisms interconnected in different trophic webs. This is the case for multi-host forest pathogens such as *P. cinnamomi*, *P. ramorum*, or *R. lauricola*, which can infect multiple dominant, codominant, and understory species (Hardham and Blackman, 2018; Garbelotto et al., 2020; Olatinwo et al., 2021).

The removal of tree species caused by emergent diseases can also have extremely complex and cascading damaging effects on the overall integrity of ecosystems. The case of the dieback of riparian alder (*Alnus* spp.) in Europe, caused by the newly emerged hybrid taxon *Phytophthora ×alni*, is emblematic. Alders are in fact nitrogen-fixing plants, and their decline and mortality caused by *P. ×alni* have been documented to have multiple effects on affected ecosystems, including a direct reduction in soil nitrogen, an indirect influence on food webs—both terrestrial and aquatic—by reducing the input of nitrogen-rich leaf litter, a reduction in shade, a loss of habitat for wildlife, and a substantial negative effect on river bank stability (Bjelke et al., 2016). Hence, the removal of a tree species affects an ecosystem at various levels, in both the physical sense and biological sense.

Food webs, plant-microbe associations, and nutrient cycles are of great importance for the functioning of natural ecosystems, and their disruption is probably one of the most important, yet least understood, effects on the ecology of forest ecosystems caused by emergent forest disease outbreaks. The three cases below are good examples of such complex and often cascading effects. The ash dieback pathogen *H. fraxineus* affected four trophic levels (plant-herbivore-coleopteran intermediate predator-top predator web-building spiders) and simplified the web-building spider-prey food webs in plantations, representing a threat to biodiversity and ecosystem functioning (Michalko et al., 2021). Canopy thinning and mortality of cork oak (*Quercus suber*) caused by *P. cinnamomi* altered the nematode trophic structure, resulting in an increase in the abundance of lower trophic levels (sores, fungivores, and herbivores) and in a decrease in the abundance of higher levels (predators and omnivores) with lasting effects on biogeochemical processes (Domínguez-Begines et al., 2019). Forest disturbance caused by SOD was associated with an increase in populations of two important animal hosts of nymphs of the tick *Ixodes pacificus*, the vector of the Lyme disease pathogen (*Borrelia burgdorferi*) in California. One of the two hosts is also known as a reservoir of the bacterium. A third tick host, instead, was negatively affected by SOD, and a fourth host was not affected at all. The effect of SOD on the frequency of infected tick nymphs was confounded by tick-vector and tick-predator relationships, but the overall density of tick nymphs was positively associated with forest gaps due to SOD-induced oak mortality, suggesting that the presence of SOD may increase disease rates in humans (Swei et al., 2011).

## 2.2 Effects on microbes intimately associated with hosts of emergent pathogens

Microbial interactions are key to the functioning and survival of forest ecosystems. Plenty of evidence indicates that mycorrhizal and endophytic associations directly affect the vigor of trees as well as their resilience during biotic and abiotic disturbances. Mycorrhizal networks have been identified to be population-level drivers of resilience and growth of multiple individual trees and even of multiple interconnected species that coexist in a single location. Some of the early literature on the effects of emergent diseases on microbes simply reported declines in microbial organisms that were associated with declines in the hosts affected by emergent diseases and with the habitat such hosts define (Watson et al., 1988). However, a few studies have investigated the more dynamic relationship between emergent diseases and mycorrhizal associations. Douglas-firs defoliated by Swiss needle cast (SNC) caused by *Nothophaeocryptopus gaeumannii* have been reported to have lower functional mycorrhizal tips and a decreased ectomycorrhizal species richness (Luoma and Eberhart, 2014). Bauman et al. (2018), by working on American chestnut affected by *C. parasitica*, reported instead that ectomycorrhizal frequency in diseased trees was statistically comparable to that of healthy trees; however, seedlings growing near diseased

trees were smaller and had the lowest survival rate (56%), while ectomycorrhizal root colonization was significantly lower on seedlings neighboring dead chestnut trees. Although the results of the above studies are partially contrasting, the incongruences are likely to have been determined by differences in the systems studied or by different experimental designs. Bergemann and Garbelotto (2006) first described a rich ectomycorrhizal community in pure tanoak stands, and then, they selected three of the most abundant taxa to study the effect of mechanical cambial and xylem girdling, simulating SOD-caused girdling, on the abundance of mycorrhizal tips and of hyphae in the soil. Six months after girdling, girdled tanoaks showed canopy symptoms similar to those caused by SOD, and while the abundance of ectomycorrhizal tips of the three target taxa was not affected by the girdling, the abundance of fungal mycorrhizal DNA in the soil near girdled trees was significantly lower than that near ungirdled trees (Bergemann et al., 2013). These results suggest that the first effect of SOD is to lower the soil hyphal component of the mycorrhizal association, a component that is essential for the sequestration of nutrients by the mycorrhizal network, while maintaining the actual fungus-root tip mycorrhizal symbiosis. The authors speculated on three possible end scenarios: (a) Disease will kill tanoaks leading to a loss of the mycorrhizal symbiosis, given that other plants in the forest studied were not associated with ectomycorrhizae; (b) trees will recover and the soil mycorrhizal network and its essential function will be re-established; and (c) trees will survive in a diseased state and will further suffer from a significant loss of ectomycorrhizal function, given the significant reduction of the soil component of the mycorrhizal network. Unfortunately, given the virulence of the SOD pathogen, a and c were deemed the most likely long-term outcomes. Finally, by working on cork oak infected by *P. cinnamomi*, Gómez-Aparicio et al. (2022) showed that tree decline and mortality of host trees caused not only an increase in the diversity of both bacteria and fungi in the soil, but also a drastic reduction of tree-symbiotic fungi and Proteobacteria, both known to play a positive role on plant growth and disease suppression.

Even if the examples above imply an effect of emergent tree diseases on a symbiotic interaction, the effects measured on the mycorrhizal association are likely to be mediated by the altered physiology of diseased trees. This has to be the case for the SOD-tanoak study, in which mechanical girdling was used as a proxy for disease. Zampieri et al. (2017) used the model system comprising Italian stone pine (*Pinus pinea*), its ectomycorrhizal symbiont *Tuber borchii*, and the non-native and native pathogens *Heterobasidion irregulare* and *H. annosum*, respectively, to test whether the impact of forest pathogens on ectomycorrhizae may differ for non-native/invasive and native pathogens. The two pathogens induced the same morphological reaction in the plant-symbiont complex, with mycorrhizal density increasing exponentially with pathogen colonization. However, thanks to gene expression analyses, the results of this study suggested that host-microbe interactions at the molecular and transcriptome levels may be dramatically different when the pathogen involved is non-native. Hence, altered host-microbe interactions in association with infection by emergent pathogens may be not simply determined by the altered host physiology caused by the disease, but also by novel molecular protective interactions between noncoevolved genomes.

The presence of a genetically driven process is also plausible in the case of altered endophytic communities in trees affected by emergent diseases. This is supported by recent studies that indicate that the nature of tree endophytic relationships is not simply the outcome of a specific physical environment in a tree (e.g., an increase in the gaseous phase within the xylem) (Boddy, 2001), but the result of a fine-tuned symbiosis of endophytes existing in a “cell wall-less” protoplast state within the cytoplasm of hosts’ cells (Atsatt and Whiteside, 2014). Once again, although not all studies report a change in the endophytic community of trees associated with infection by emergent pathogens (Schlegel et al., 2018), some do. For example, elms displaying resistance to DED are characterized by a different endophytic community in the xylem, but not in the cambium or the leaves (Martín et al., 2013). Similarly, the endophytic community in leaves of the invasive plant *Miconia calvescens* differs significantly between plants that are either resistant or susceptible to the invasive biocontrol pathogenic agent *Colletotrichum gloeosporioides* (Garbelotto et al., 2019). In both of these examples above, a feedback tripartite process is in play among the emergent pathogen, the host, and the endophytic community. Thus, the composition of the endophytic community may determine the success or failure of infection by the pathogen. Likewise, by working on the model system comprising Scots pine (*P. sylvestris*), *H. irregulare*, and *H. annosum*, it was showed that the European ectomycorrhizal fungus *Suillus luteus* reduced the level of host susceptibility only to infections operated by the native *H. annosum* and not to those by the non-native *H. irregulare*, suggesting that the protective role of ectomycorrhizae on hosts may fail in the case of emergent diseases (Gonthier et al., 2019). The mechanisms underlying this complex tripartite interaction still need to be elucidated.

### 2.3 Effects on nutrient cycling

Changes in nutrient availability probably cause—together with effects on tree growth rates, shifts in forest composition, and forest structure—major long-term effects of biological invaders on C stocks and C sequestration in forests (reviewed in Peltzer et al., 2010). Several are the examples of changes in nutrient availability and composition associated with tree



mortality and tree species replacement caused by emergent pathogens. Beech bark disease (BBD), caused on beech (*Fagus* spp.) by two bark-cankering fungi of the genus *Neonectria* infecting trees wounded by the beech scale *Cryptococcus fagisuga*, has been reported to cause an increase in litter decomposition, a decrease in soil C:N ratio, and an increase in soil nitrates at a scale larger than that caused by climate change or air pollution, indicating emergent diseases are major disturbance agents at the planetary level (Lovett et al., 2010). By studying the effects of the invasive pathogen *P. cinnamomi* in oak woodlands in the Iberian Peninsula, Avila et al. (2019) detected significant changes in nutrient availability in soils associated with the presence of the pathogen, but the magnitude of such changes was site-specific and dependent on soil texture. Interestingly, the same study further determined that such changes were associated with changes in microbial respiration even in the absence of measurable changes in microbial biomass and diversity. Cobb et al. (2013) determined that soil litter accumulation and litter chemistry were significantly affected by SOD, not in relation to tree mortality, but rather because of the different symptoms the disease causes on different sympatric hosts. In SOD-infested stands, California bay laurels—infectious but unharmed by the disease—increase their abundance, while tanoak representation decreases due to high SOD-induced mortality. Increased bay laurel foliage in the litter and SOD-caused tanoak mortality both contribute to an increase in soil nitrates. This increase is positively correlated to the intensity of SOD outbreaks, which in turn is correlated to the density of California bay laurels, the host tree most responsible for disease transmission in California woodlands (Garbelotto et al., 2003). Besides litterfall, the accumulation of coarse woody debris (CWD) is one of the major drivers of nutrient cycles in forest soils (Harmon et al., 1986). Invasive forest diseases can increase CWD by one order of magnitude. Cobb et al. (2012) showed that in the case of SOD, the increase of CWD on the forest floor was positively correlated to the disease incidence and pre-disease tanoak biomass.

## 2.4 Effects on wildfires and on resilience of ecosystems to wildfires

CWD on the forest floor is not only the intermediate biomass state in between standing plant biomass and soil biomass, but it is also an important driver of wildfire dynamics in forests (Brown, 2003). Several articles report that SOD increases the amount of fuels on the forest floor and can change fire behavior by increasing flame lengths, rates of spread, and surface fire intensity in diseased stands (Valachovic et al., 2011; Forrestel et al., 2015). However, emergent diseases do not only alter the amount and quality of fuels on the forest floor, but are also likely to cause reduction in moisture content in the stem and canopy of diseased trees. Kuljian and Varner (2010) demonstrated that foliar moisture content in SOD-diseased tanoaks was significantly lower than that of healthy tanoaks and that the foliar moisture content of dead trees was as low as 5.8% and undistinguishable from that of the surface litter. Models have shown that standing trees with low moisture content such as tanoaks affected by SOD are likely to generate fire hot spots of very high intensity due to so-called torching of individual trees (Kuljian and Varner, 2013). These hot spots have been described by managers in SOD-infested areas and have been reported to increase fire spread rates and to heighten the unpredictability of fire behavior, causing serious complications in fire-fighting operations (Valachovic et al., 2011).

Such significant modifications of fire attributes and fire behavior caused by emergent diseases have been reported in several forests affected by emergent pests or pathogens (Dickman and Cook, 1989; Hummel and Agee, 2003; Jenkins et al., 2012), but one of the most interesting and unexpected outcomes of such modifications is that reported by Metz et al. (2013) for SOD-infested redwood (*S. sempervirens*) forests. In the above paper, the authors stated: “The dominant tree, coast redwood (fire resistant without negative disease impacts), experienced unexpected synergistic increases in mortality when fire and disease [SOD] co-occurred. The increased mortality risk, more than fourfold at the peak of the effect, was not predictable from impacts of either disturbance alone.” This relevant ecological impact of an invasive forest pathogen was unpredictable and well exemplifies how profoundly emergent disease can alter the ecology and resilience of forests. The results are bound to change the textbooks about the ecology of redwoods and redwood forests, often referred to as the supreme fire-resistant tree (Starker, 1934).

## 3. Evolutionary effects of the emergence or introduction of tree pathogens

### 3.1 Direct effects on the pathogens

As it inevitably occurs for all biological invasions, the genetic bottleneck caused by the long-distance movement of a limited number of founder individuals responsible for the establishment of an alien population of a tree pathogen in a non-native setting will cause a reduction in the overall genetic diversity of the pathogen that had been transported. In fact, reduced genetic diversity and strong deviations from Hardy-Weinberg equilibrium due to inbreeding or fixed heterozygosity are generally used to support the notion that some emergent pathogens are non-native (Gladieux et al., 2015). The examples of reduced genetic variability of introduced vs. native populations of forest pathogens are several and encompass

the seminal early research on the chestnut blight fungus *C. parasitica* (Milgroom et al., 1992), as well as many others, including *Ceratocystis platani*, the agent of canker stain of plane trees (Engelbrecht et al., 2004), the cypress canker pathogen *Seiridium cardinale* (Della Rocca et al., 2011), and the PPC pathogen *F. circinatum* (Wikler and Gordon, 2000). In the case of the root rot pathogen *H. irregulare* introduced from North America in Italy, population genetic analyses were able to confirm not only that the Italian population was indeed introduced and exhibited lower genetic variability than native populations, but also to identify the most likely site in Italy where the pathogen had been originally introduced (Garbelotto et al., 2013).

The genetic bottlenecks associated with introduction events will completely change the evolutionary trajectory of exotic populations isolated from their parent populations. This has been shown convincingly for quite a few forest pathogens. A study by Brar et al. (2015) confirmed that different introduction events, being associated with different founding individuals, will result in genetically differentiated populations of the same species if the introduced populations are geographically isolated. The authors provide convincing evidence about this outcome by studying the geographically isolated Western and Eastern North American populations of the white pine blister rust (WPBR) pathogen *Cronartium ribicola*, which were started by genotypes belonging to genetically distinct populations of the same species. The same study also showed that the Eastern North American population of the pathogen, being derived from multiple introductions, is characterized by higher genetic diversity but is overall homogeneous because of abundant regional gene flow, while the Western North American population, although overall genetically less diverse, is diversified into genetically distinct local populations, because of restricted gene flow due to the rugged topography and spotty host distribution in Western North America. Likewise, it has been shown that European, New Zealand, and North American populations of the cypress canker fungus *S. cardinale* are now genetically distinct, after less than 100 years of isolation from one another (Della Rocca et al., 2019).

There are two additional significant and interconnected implications of the genetic bottlenecks experienced by non-native introduced forest pathogens. The first is the likelihood that only a single mating type will be introduced or that mating type ratio in the non-native population may be strongly skewed in favor of one type, lowering the rates of sexual reproduction. These scenarios normally result in a switch from a mixed reproductive strategy (sexual and clonal) to an exclusive or quasi-exclusive clonal reproductive strategy, as evidenced by several studies on forest pathogens including *C. parasitica*, *S. cardinale*, and *P. cinnamomi* (Milgroom et al., 1992; Dobrowolski et al., 2003; Della Rocca et al., 2011). Clonal reproduction may lead to the emergence of fit dominant genotypes that can be further spread around the globe as shown, for instance, by Mehl et al. (2017) for *Lasiodiplodia theobromae*, by Marsberg et al. (2017) for *Botryosphaeria dothidea*, and by Socorro et al. (2019) for *P. cinnamomi*. The case of *P. cinnamomi* is also very interesting because infestations by this pathogen in most regions of the world outside of the Asian-Papuan region, where the pathogen is presumed to be native (Arentz and Simpson, 1986), are characterized by the presence of a single mating type, and there is strong evidence that the two mating types of this species are evolutionarily and phenotypically extremely divergent (Arentz, 2017).

One additional evolutionary consequence associated with isolated populations of introduced forest pathogens in novel world regions does not involve the genome of the pathogen itself, but rather the acquisition of viral infections upon exposure to novel viruses in the new environments being explored during the invasion process (Brasier, 1990; Springer et al., 2013). Viral transmission has been shown to be facilitated in alien forest pathogen populations given that their decreased genetic variability facilitates cytoplasmic contact and viral infection among individuals (Liu and Milgroom, 1996; Choi et al., 2012; Bryner et al., 2014). Viral infection has been shown to affect the virulence of forest pathogens with obvious consequences on their evolution (Rigling and Prospero, 2018), including exerting a significant selection pressure that has been shown to have accelerated evolutionary processes through genic introgression of adaptive traits (Buck et al., 2003).

As Gladioux et al. (2015) discussed in their review on the subject, alien fungal populations with limited genetic variability need to be able to adapt to the challenges posed by novel ecosystems. Adaptation may be faster for sexually reproducing invasive pathogens, and one of the best examples of rapid adaptive evolution of an exotic forest pathogen in a novel range is that of *C. ribicola* in a forest stand entirely replanted with pines carrying a major gene for resistance to the pathogen. *Cronartium ribicola* in fact is an obligate biotrophic parasite that can only survive in its hosts, and when a novel race of the fungus capable of bypassing host resistance emerged in that site, it quickly became dominant locally, while it remained absent in at least five other forest sites included in the same study (Richardson et al., 2008). The emergence of clonal lineages that may be particularly fit in novel environments has been well-demonstrated—although indirectly—by the fact that the same genotype of a tree pathogen dominates certain environments or is present in multiple continents (see references above). The case of *C. parasitica* is particularly interesting as it shows that both in North America and in Europe, multiple introductions from different sources established distinct lineages, some of which were able to dominate new environments (Dutech et al., 2012). This finding showed that multiple introductions are always beneficial to invasions by forest pathogens, as postulated by the general theory of biological invasions (Dlugosch and Parker, 2008). Furthermore, the finding also showed an intriguing shift in reproductive strategy associated with the presence of dominant genotypes, likely to have

been triggered by the necessity to survive and spread in a novel environment. In fact, in spite of the fact that *C. parasitica* is a sexual outcrossing organism, it appears to be also selfing in its introduced “wild” range, most likely to preserve the benefits offered by the insurgence and maintenance of fit dominant lineages (Marra et al., 2004). In this example, thus, the advantages provided by highly fit lineages exert a strong selection against outcrossing, a phenomenon that is in contrast to the normal evolution of a sexual outcrossing organism.

Two recent examples of evolution associated with introductions of clonally reproducing forest pathogens show that introduced populations have evolved more rapidly than expected by drift alone: These may be some of the best examples of rapid adaptive evolutionary consequences associated with the introduction of non-native forest pathogens. In a comparative study of invasive and source populations of the pathogen *S. cardinale*, Garbelotto et al. (2015) showed that invasive Italian populations of the fungus were characterized by smaller spores, lower growth rate, and higher overall sporulation rates than native source Californian populations. In the same study, the authors also provided evidence that plasticity is essential to the successful invasion, albeit only in the first stages of the invasion process. Introduction of tree pathogens often follows a systematic pathway: For instance, many *Phytophthora* species have been introduced in natural ecosystems because of the sale of infected plant stocks (Grünwald et al., 2012; Garbelotto et al., 2018). Thus, our second example of a unique evolutionary trajectory unreported in natural populations of the same pathogen species is that of the insurgence of resistance to fungicides in genotypes of *Phytophthora* introduced in natural ecosystems (Sims et al., 2019). This resistance has been identified in multiple introduced *Phytophthora* species and has been hypothesized to have evolved when these pathogens were transitioning in infected plants grown in commercial or ornamental production nurseries where fungicides were being used (Hunter et al., 2018).

### 3.2 Effects on emerging and native pathogens mediated by interspecific hybridization and genic introgression

An additional evolutionary consequence of the introduction of tree pathogens on the evolution of pathogens themselves is the outcome of interspecific hybridization events that may occur when an introduced and invasive tree pathogen encounters a sexually compatible, related, and usually congeneric species. As long as the first-generation  $F_1$  hybrids are viable (even if only temporarily), the combination of two distinct genomes can give rise in a single generation to drastically distinct pathogens, both genetically and phenotypically. In some cases, backcrossing of hybrids with parental genotypes can deeply alter the evolutionary trajectory of the parental species. Already in 2000, a surge in fungal hybridization reports had been observed, often in conjunction with the introduction of tree pathogens (Brasier, 2000).

There are four cases that exemplify this phenomenon, and only one has been studied extensively.

- (1) The establishment of the North American tree pathogen *Phytophthora uniformis* in European nurseries has led to mating with the congeneric species *P. multiformis*, resulting in the generation of a third hybrid species named *Phytophthora* × *alni*. Hybridization events were multiple and occurred in different locations between different genotypes belonging to the two parental species, giving rise to genetically distinct hybrids, some of them exhibiting higher fitness and becoming dominant at the local and/or regional scales (Aguayo et al., 2016). Aguayo et al. (2016) further determined that the distribution of genotypes of the invasive species *P. uniformis* was a major determinant of the genetics (and possibly phenotype) of hybrid individuals. In general, the hybrid species *P.* × *alni* displays higher virulence on alder species than the parental species, and because of repeated hybridization events and of spread of dominant genotypes through the planting of infected alder plants, it has decimated *Alnus* spp. in European riparian ecosystems, causing the emergence of alder decline at the continental level in Europe (Bjelke et al., 2016).
- (2) The root and butt rot pathogen *Heterobasidion occidentale* is common in true fir (*Abies* spp.) stands in Western North America and is known to be partially interfertile with the root rot congeneric species *H. irregulare*, a pathogen of pines, junipers (*Juniperus* spp.), and incense cedars (*Calocedrus decurrens*) (Garbelotto and Gonthier, 2013). Even if sympatric at the broad geographic scale, the two species are characterized by a strong host preference that normally negates a true fine-scale sympatry of the two species (Worrall et al., 1983). Until recently, co-infection by the two species had only been reported for freshly cut pine stumps (Otrosina et al., 1992) and, in one case, co-infection of a stump had resulted in a *H. irregulare* × *H. occidentale*  $F_1$  hybrid genotype capable of infecting and killing pine and juniper trees in proximity of the stump itself, without any detectable further consequences on the ecosystem (Garbelotto et al., 1996). A thorough genomic analysis, however, confirmed that the hybrid genotype was diploid (rather than dikaryotic as all *Heterobasidion* species are), and this finding suggested hybrids could be viable and could backcross with parental genotypes (Garbelotto et al., 2004). Backcrossing was also suggested by the identification of DNA insertions introgressed from one species into the other (Garbelotto et al., 1996; Linzer et al., 2008). In California, with the exception of stumps, there are no host trees that are equally susceptible to both *Heterobasidion* species, but in 2014, a hybrid

*Heterobasidion* genotype in a high elevation alpine larch (*Larix lyallii*) stand was identified in Montana (Lockman et al., 2014). An in-depth genetic analysis of multiple fungal genotypes from the same stand determined that all genotypes from larches were hybrid and none of them was an F<sub>1</sub> generation hybrid, but rather the result of multiple backcrossing events of F<sub>1</sub> hybrid individuals with *H. occidentale*, the species that is locally dominant on subalpine fir (*A. lasiocarpa*) (Sillo et al., 2019). As a result, *Heterobasidion* hybrid genotypes from larch comprise one nucleus that is clearly *H. occidentale* and one nucleus that is the result of hybridization between the two parental species and can no longer be assigned to either one (Sillo et al., 2019). Spores contained either one of the two genomes, and the isolation of one haploid spore solely containing the novel genome proved we are dealing with a third species, one that unlike the parental ones is an excellent pathogen of alpine larch (Sillo et al., 2019). Hybridization was postulated to be the result of the documented local emergence of *H. irregulare* at mid-elevations on pine stumps, leading to a newly found zone of sympatry between the two species, once isolated by a strong elevation gradient combined with significant geographic separation.

- (3) The North American root pathogen *H. irregulare* was introduced in Italy, near Rome, presumably by the US Army during World War II (Gonthier et al., 2004). *Heterobasidion irregulare* is now sympatric with the congeneric Eurasian species *H. annosum*, with which it is almost completely interfertile (Gonthier et al., 2007). Not unexpectedly, wild populations of *Heterobasidion* in woodlands near Rome were later discovered to include a very large proportion (up to 25% of the sampled individuals) of interspecific hybrids (Gonthier and Garbelotto, 2011). These hybrids were the result of a variable number of genetic backcrosses with parental species, indicating they were fully viable and fertile; in other words, they represented a true hybrid swarm (Gonthier and Garbelotto, 2011). In its zone of infestation in Italy, *H. irregulare* was clearly dominant over *H. annosum* (Gonthier et al., 2014) and may even be able to infest habitats unavailable to its native congener like pure oak stands (Gonthier et al., 2012). In addition, it has been recently reported that *H. irregulare* is replacing *H. annosum* in Italy (Garbelotto et al., 2022). A series of field and greenhouse experiments suggested that the North American species had become dominant in Italy not because of its higher virulence or because of higher susceptibility of Italian hosts (Garbelotto et al., 2010), but because of its greater saprobic ability and higher sporulation potential (Giordano et al., 2014). A comparative analysis of the entire genome of the two species confirmed that genes involved in virulence and pathogenicity are conserved between the two, while genes involved in wood decay, cellular communication, and nucleus-mitochondrial interplay were more divergent than expected by drift alone (Sillo et al., 2015). Based on these findings, it was hypothesized that genes involved in wood decay and mitonuclear interactions would have been positively selected for and be introgressed from the invasive into the native *Heterobasidion* species. A full genome analysis of natural hybrids and parental genotypes indeed showed that various nuclear genes of *H. irregulare* involved in wood decay processes and in mitochondrial communication were detectable in *H. annosum* genotypes and that their frequency was higher than that expected by chance alone (Sillo et al., 2021). Finally, an experiment measuring the fitness and genic expression of artificial hybrids characterized by the same nuclei, but different mitochondrial genomes, showed that hybrids with the native *H. annosum* mitochondrion were significantly less fit than hybrids with the non-native *H. irregulare* mitochondrion, due to a large deviation from the norm in the expression level of nuclear genes involved in nucleus-mitochondrion communication (e.g., genes were strongly over- or under-expressed in these chimeric genotypes) (Giordano et al., 2018). Together, these results indicate that *H. irregulare* genes will selectively be introgressed into *H. annosum* and “contaminate” its genome, making *H. annosum* a better saprobe and a greater sporulator. Likewise, the non-native *H. irregulare* mitochondrion will be favored in hybrid genotypes. These data show that a potentially more insidious invasion is occurring in Italy besides that of the alien *H. irregulare*: The invasion of superior alien *H. irregulare* genes that will increase the fitness and the destructive potential of the native *H. annosum*.
- (4) The fourth and best studied example of the evolutionary consequences of interspecific hybridization between two tree pathogens does not involve an alien and a native pathogen. Rather, interspecific hybridization and genic introgression through backcrossing occurred originally in Europe between two introduced pathogens, namely *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*, the two agents responsible for DED. Additionally, in this particular system, first-generation hybrids were not generally competitive when compared to the parental genotypes, but did and still do backcross with them, allowing for a genetic exchange between the two species. An increase in vegetative compatibility (vc) diversity occurred in *O. novo-ulmi* in Europe, probably in response to the presence of significant viral populations. Vegetative compatibility is a multigenic system that regulates the recognition of self: When alleles at all vc loci are identical, fungal hyphae of two ramets will fuse and share their cytoplasm and any viral element the cytoplasm may contain; when alleles at vc loci differ, cytoplasmic fusion does not occur or is incomplete, blocking or slowing down viral spread. Likewise, the MAT-1 mating-type idiomorph and other alleles and/or genes such as those associated with pathogenicity, regulating the production of the toxin cerato-ulmin and growth responses to temperature, were introgressed from

*O. ulmi* into *O. novo-ulmi* (reviewed in [Brasier et al., 2021](#)). A similar process of genic introgression also occurred in North America as evidenced by the presence of the *O. ulmi* MAT-1 idiomorph in *O. novo-ulmi* and by evidence of mitochondrial recombinants. However, due to the lack of strong viral pressure in North America, there was no adaptive introgression of *vc* loci, and therefore, *vc* diversity was not increased. As a result of the lack of viral pressure, a few dominant genotypes of *O. novo-ulmi* have long persisted in North America, thanks also to their strong saprobic growth potential and to the high susceptibility of North American elms (reviewed in [Brasier et al., 2021](#)). More recently, a third wave of hybridization is occurring in parts of Europe, this time between the North American (SSAM) and the European (SSNU) subspecies of *O. novo-ulmi*. Hybrids between the two subspecies are viable, and thus, further hybridization is creating hybrid swarms. These swarms have furthered the introgression of *vc* loci and of the MAT-1 idiomorph into *O. novo-ulmi*, significantly and permanently lowering viral infection in *O. novo-ulmi* to endemic levels that should not negatively affect the fitness of the fungal pathogen. In concert, hybrids tend to show an enrichment of other adaptive traits such as increased pathogenicity (normally the SSAM phenotype, that is either preserved or introgressed into hybrid populations) and greater growth rates, often as an additive effect of traits gained from both parental species. In conclusion, DED provides the most egregious example of how the emergence of tree pathogens can trigger an accelerated evolutionary process, with adaptive consequences because of hybridization-mediated genic introgression. Although all pathogenic taxa involved in the system are alien, their ability to accelerate their evolution and adapt by sharing genes is bound to increase the overall negative effects of these pathogens on affected trees and ecosystems (see [Brasier et al., 2021](#)).

### 3.3 Effects on the hosts of emerging pathogens

This section on the evolutionary effects of emergent tree pathogens would not be complete if we did not mention some of the evolutionary effects such pathogens may have on the hosts themselves. Here, we do not focus on system-level effects such as changes in stand composition or on cascading effects on other forest-dwelling organisms, as both of those effects have already been discussed previously in this chapter; rather, we limit our discussion to direct evolutionary effects that emergent pathogens may have on the tree hosts they infect. One of the major effects of an emergent disease is the removal of the most susceptible tree genotypes, with a local increase in the percentage of less susceptible individuals. This shift toward increased disease resistance or tolerance has been documented at least in two studies comparing oaks in stands naturally exposed to SOD with oaks in stands unexposed to the disease ([Dodd et al., 2008](#); [Conrad et al., 2019](#)). Similarly, when planting half-sib tanoak seedlings in common gardens in a SOD-infested forest, the survival of seedlings from putatively disease-tolerant families was significantly higher than the average survival of seedlings ([Hayden et al., 2013](#)). It is not always clear whether the selection for resistance-associated traits will decrease the overall genetic diversity of tree populations. For instance, it has been shown that if trees can resprout easily, genetic diversity can be maintained, even if adult trees have been decimated ([Dagleish et al., 2016](#); [Martín et al., 2019](#)). However, in the absence of viable resprouting, as expected, populations of trees post-epidemics are characterized by a lower level of genetic diversity and by stronger deviations from Hardy-Weinberg equilibrium ([McDonald et al., 1998](#)).

When polygenic disease resistance in host trees has been obtained by the artificial hybridization of different tree species, the level of resistance is proportional to the amount of the genome inherited from the more resistant tree species ([Westbrook et al., 2019](#)). Hence, under disease pressure, the expectation is that both the resistant genome and genotypes bearing the highest percentage of such genome will be positively selected. As a result, evolutionarily speaking, the genomes of native susceptible trees will progressively diminish their presence in ecosystems affected by emergent diseases when reforestation programs employ artificial tree crosses, resulting in a significant loss of endemic genetic diversity ([Westbrook et al., 2019](#)).

There are several reports of disease incidence being positively associated with tree size ([McPherson et al., 2005](#); [Shields et al., 2011](#); [Dagleish et al., 2016](#); [Martín et al., 2019](#)). While it is clear that these diseases will have strong ecological effects by removing the larger individuals thus drastically altering the structure of a forest, the evolutionary implications of this size preference are unclear, although it is possible that faster growing families may be negatively selected ([Ismael et al., 2021](#)).

Finally, many traits are positively or negatively associated with disease incidence or severity. These include greater size of wood vessels, net CO<sub>2</sub> assimilation, stomatal water conductance, transpiration, water use efficiency, xylem sap flow rates, and the production of specific volatile compounds which may attract insect vectors ([Pouzoulet et al., 2014](#); [Ploetz et al., 2015](#); [Conrad et al., 2017](#); [Martini et al., 2017](#)). However, the heritability of these traits is not always known, and our understanding of the genetic structure of the tree host population is often unknown: Long-distance gene flow through pollen from uninfested areas may in fact lower the heritability of the traits below the threshold necessary to detect an evolutionary significant shift in the frequency of the traits in question.

#### 4. Societal effects caused by the emergence of tree diseases

Emergent tree diseases may cause significant damage to local human communities. If the affected trees have a clear economic importance, the magnitude of the impact on the local economies may be estimated directly by determining the current and future losses in revenue associated with tree mortality, reduction in their growth rates, lower reproductive potential, and inferior quality and quantity of timber or flower/fruit or other tree products. Because tree products have a commercial value (see [FRA, 2010](#)), the estimates of the financial impact of tree disease outbreaks have mostly focused on the loss of marketable commodities provided by trees ([Ayres and Lombardero, 2000](#); [Aukema et al., 2011](#)). These direct economic impacts apply to primary, secondary, and planted forests, because they are inextricably due to the loss of a revenue. Other economic impacts that are not directly associated with the loss of timber and of forest products, but that are caused by the loss of ecosystem services provided by trees affected by emergent diseases are discussed further below.

Historical, yet still ongoing, cases of emergent diseases causing large-scale direct losses of timber and tree products include the following examples. Annosus root rots caused by *Heterobasidion* spp. were estimated to cause a yearly damage of about 800 million Euros to the European timber industry, primarily by decaying the wood and/or killing infected trees (reviewed in [Garbelotto and Gonthier, 2013](#)). Although the *Heterobasidion* spp. leading to these losses are native to Europe (with the exception of the North American *H. irregulare*, to date only present in the Latium Region of Italy), they should be regarded as being emergent and invasive because both disease incidence and severity increase every time a forest stand is logged (reviewed in [Garbelotto and Gonthier, 2013](#)). The establishment and spread of these diseases are in fact greatly facilitated by stumps generated during logging and by wounds inflicted on standing trees during tree harvest operations. Both stumps and wounds can easily be infected by *Heterobasidion* spp., which then can grow in the roots of stumps and wounded trees and infect multiple neighboring trees.

Nine North American white pine species are susceptible to white pine blister rust (WPBR) caused by *C. ribicola* that was introduced multiple times in North America at the beginning of the 20th century ([Geils et al., 2010](#)). At least two species, namely *Pinus strobus* in Eastern North America and *Pinus lambertiana* in the Western part of the continent, have been of great commercial importance and have been decimated by WPBR to the point that these pines are no longer planted in sites conducive to the disease ([Schoettle et al., 2019](#)). The economic importance of these two species was notable: The soft but durable wood and nutritious seeds of Eastern white pines were important to native people and early colonizers of the American continent ([Abrams, 2001](#)). *Pinus strobus* was the pine of choice for the construction of ships' masts in the 1600s and fostered at first the British colonization of New England and Canada ([Albion, 1926](#)) and then the American independence from Britain ([Carroll, 1973](#)). *Pinus lambertiana* in California, instead, became one of the main construction timbers to support the burgeoning growth of the State starting with the 1849's gold rush ([Cermak, 1996](#)). Although hazard mapping of sites not to be planted with white pines and the use of resistant stocks has in part alleviated the constraints on the growth of commercially valuable white pines, the effects of WPBR are still particularly sizeable in the West, due to the co-occurrence of the disease with large-scale insect outbreaks and fires, combined with the insurgence of fungal races of *C. ribicola* capable of circumventing host genetic resistance ([Geils et al., 2010](#)).

American (*C. dentata*) and European chestnut (*C. sativa*) trees were a staple of local economies in Eastern North America and Europe, respectively, due to the value of their nuts, timbers, and tannins ([Bounous and Beccaro, 2020](#)). Both species were at first impacted by ink disease caused by *Phytophthora cambivora* and/or *P. cinnamomi*, and then, they were further affected by chestnut blight caused by the Asian invasive fungus *C. parasitica* ([Gonthier and Robin, 2020](#)). Consequences of chestnut blight during the 1900s for the American chestnut, a majestic and dominant tree species along the Appalachian range, were particularly dramatic. Billions of trees were killed by the pathogen in a 30-year period, shattering the local timber industry ([Bounous and Beccaro, 2020](#)). The loss of revenue associated with the disappearance of chestnut trees was a major destabilizing force ([Prospero and Rigling, 2013](#)). In fact, in the United States, misguided policy and scientific testing aimed at preserving chestnuts may actually have hastened its demise, with scientists favoring the spread of the disease in uninfested areas and recommendations being sent out to local residents to cut down chestnuts and cash in before the arrival of chestnut blight in their communities ([Freinkel, 2007](#)). In Europe, the decline of chestnut trees associated with pests and diseases, including both ink disease and chestnut blight, accelerated social change, pushing populations out of rural areas into cities and to the Americas ([Swanson et al., 2021](#)). Additionally, synergistic feedback processes between tree disease and society have been reported in Europe. Abandonment of chestnut-producing orchards led to an accumulation of vegetation in the understory that negatively affected chestnut recruitment compounding the effects of chestnut blight ([Zlatanov et al., 2013](#)) and favoring high-intensity wildfires further accelerating the replacement of chestnut trees by fire-tolerant tree species ([Swanson et al., 2021](#)). Another interesting example of the worldwide effects of an emergent tree fungal pathogen is that of *Pseudocercospora ulei* causing South American leaf blight (SALB) of rubber trees (*Hevea* spp.). Although the pathogen and the rubber tree are both native to South America, the emergence of SALB has greatly

hampered the development of rubber cultivation on the American continent, while favoring rubber production elsewhere, particularly in Africa and Asia, with the latter now responsible for over 90% of the world production. Within Latin America, entire communities lost a major source of revenue, because rubber plantations can only be profitable in areas that, although suboptimal for rubber production, are less conducive to SALB outbreaks. Additionally, the need to use *Hevea* spp. clones with increased resistance to SALB no longer makes this crop suitable for small growers and native communities (reviewed in [Guyot and Le Guen, 2018](#)).

Interestingly, there are also examples in which the onset of emergent forest diseases caused temporary migratory fluxes into rural and forested areas, thanks to jobs being offered in the attempt to curtail the further spread of such diseases. The most famous and sizeable of such example of what could be defined as “inverse migration” is that of the “Ribes eradication” camps set up in the United States, especially in the West, during the depression to slow down the spread of WPBR ([Geils et al., 2010](#)). Ribes (commonly known as currant or gooseberry) is the major obligate alternate host for the WPBR pathogen *C. ribicola*, and consequently, it was assumed its removal would have stopped the spread of WPBR. However, it should be noted that the thorough removal of Ribes was close to impossible in the rugged Western landscapes, strongly reducing the efficacy of this disease management strategy ([Maloy, 1997](#)).

Trees are also key elements of entire economies that are not based per se on the trees themselves. For instance, the foraging of mushrooms, honey production, hunting and fishing, agroforestry practices in general, and some types of cattle grazing all depend more or less strictly on the presence of healthy trees. These tree-dependent economies in part referred to as renewable nontimber forest resources will also suffer significantly with the onset of tree disease outbreaks. The extent of this more indirect economic damage caused by emergent forest diseases can also be estimated, although with much greater uncertainty, due to the yearly and seasonal fluctuations in yield and due to “niche” or “specialty” narrow markets that nonetheless can be affected by global supply and demand mechanisms. One of the best examples of renewable nontimber forest resources is that of matsutake mushrooms: These mushrooms are very important to the Japanese cuisine and to the Japanese culture as a whole. They are ectomycorrhizal obligate tree symbionts, and, in the last decades, the local Japanese production has crashed due to the demise of one of the main tree symbionts of the fungus, the Japanese red pine (*Pinus densiflora*) in part driven by the spread in Japanese forests of the non-native pinewood nematode (*Bursaphelenchus xylophilus*). The high demand for this mushroom by the Japanese market has generated an escalation of prices, and mushrooms can be sold for up to USD 10,000/Kg. This price in turn has triggered the creation of a global network of buyers who will purchase the mushrooms from local collectors in other parts of the world and quickly ship them to the Tokyo’s wholesale market ([Faier, 2011](#)). The mushrooms cannot be easily cultivated, so they are mostly collected during forays either by local residents or by migrant workers ([Tsing and Satsuka, 2008](#)). In California, matsutakes have become a staple commodity of subsistence for harvesters, mostly migrants of Southeastern Asian or Latin American origin or belonging to native First Nations ([Richards and Creasy, 1996](#)). The spread of SOD in coastal California has locally decimated tanoaks, one of the main tree symbionts of matsutakes, causing significant changes in the seasonal movement of migrant mushroom collectors, dwarfing one of their major sources of income, and putting them in competition with native First Nation people ([Bowcutt, 2015](#)).

One additional indirect economic impact of emergent forest diseases, one of significant magnitude, occurs when tree pathogens are also pathogens of cultivated crops. Major examples of this additional indirect economic impact are provided by laurel wilt, SOD, Armillaria root rot caused by *Armillaria* spp., and by *Phytophthora cinnamomi*, with each case representing a substantially different scenario. The laurel wilt pathogen *R. lauricola*, originally introduced in North American wild settings, is now threatening commercial avocado orchards in the Eastern United States, thus increasing the overall economic damage associated with the disease ([Olatinwo et al., 2021](#)). Conversely, the SOD pathogen *P. ramorum* was first introduced in North America in the ornamental plant industry, and subsequently, it escaped into the wild from infected ornamental plants located in private gardens and in plant production or resale facilities ([Grünwald et al., 2012](#)). However, extremely high tanoak and oak mortality in coastal forests prompted a serious and costly set of regulations of the ornamental plant industry worldwide to avoid the further spread of this pathogen ([Frankel, 2008](#); [Grünwald et al., 2008](#)). Thus, the huge costs associated with the design, testing, and implementation of regulations for the ornamental plant industry are a consequence of the spread of SOD in the wild. Armillaria root rot is an emergent disease in California associated with native species of the fungus and native forest types ([Baumgartner and Rizzo, 2001](#)). The emergence of the disease is associated with land use changes, both historical ([Rizzo and Slaughter, 2001](#)) and more recent ([Baumgartner, 2004](#)), in which a change in forest cover or a shift from native forest to agricultural cultivation has occurred without elimination of fungal inoculum in the soil. In turn, *Armillaria* infestations can circle back into wild or semi-wild settings adjacent to cultivated sites; hence, the costs of disease management in both forests ([Shaw and Roth, 1978](#)) and agricultural settings ([Fox, 2003](#)) can be ascribed to the emergence of these pathogens at the wild-urban-agricultural interfaces. Finally, a very complex and global example of cascading economic effects of an emergent forest disease is represented by *P. cinnamomi*, probably one of the first plant pathogens to have emerged because of its transfer from native settings to agriculture, followed by multiple

introductions of the pathogen in the wild originating from different infected crops in different parts of the world (Hardham and Blackman, 2018). For instance, the pathogen has been recently released on various native hosts from various agricultural commodities in both California and Mexico (Socorro et al., 2019). Although, to our knowledge, there are no known reports of re-infection of agricultural commodities from infested wild sites, these are likely to be happening, and the global scale of interconnectivity of natural and agricultural settings in the case of *P. cinnamomi* and its combined economic impact in both settings deserves to be mentioned in this chapter.

The direct and indirect effects of emergent forest diseases on society discussed above can in part be estimated using strictly monetary values. However, there are intrinsic values associated with trees that are not easily (and maybe should not be) estimated using only a monetary metric. These include the value of the ecosystem services that trees provide including the value that trees add to the landscape and the cultural significance of trees in cultures all over the world. These aspects, requiring a complex analysis that is beyond the scope of this chapter, have at least to be mentioned. Ecosystem services provided by trees are too many to be listed exhaustively and include climate regulation, carbon storage and sequestration (Canadell and Raupach, 2008; Luysaert et al., 2008), flood control, and water purification (Bonan, 2008). Emergent diseases target one or multiple components of forest ecosystems, and the severity of these is normally greater when the biodiversity and ecological redundancy of the system affected are lower (Boyd et al., 2013). For this reason, forest systems dominated by one or a few keystone species that become hosts of an emergent disease, forests in colder climates, transitional ecosystems (mangrove stands, riverine habitats), and even urban landscapes can be more at risk of being degraded when a single tree species is affected by an emergent disease (Garbelotto and Pautasso, 2012).

Recreation uses of forested lands and the aesthetic value of landscape or amenity trees can be included in a broader concept of ecosystem services provided by trees. It has been shown that people living in greener environments live healthier and longer (Turner-Skoff and Cavender, 2019). In this sense, the decline of elms, ashes, plane trees (*Platanus* spp.), Italian cypresses (*Cupressus sempervirens*) and oaks (*Quercus* spp.) caused by DED, ash dieback, canker stain of plane trees, cypress canker, and oak wilt, all emergent diseases caused by invasive non-native pathogens, has had important societal consequences by changing the landscapes familiar to a majority of citizens both rural and urban (Potter et al., 2011; Danti et al., 2013; Harrington, 2013; Tsopelas et al., 2017; Petuccio et al., 2020). However, the effects of emergent diseases can be significant also on a smaller scale. This is the case, for instance, when the disease affects recreational areas rendering them unsafe because of windthrows favored by pathogens (West, 1989). Likewise, the presence of trees killed or affected by emergent infectious diseases can significantly lower the value of real property, even if the magnitude of the effect may change in time. In California, for instance, the presence of infected or dead oaks because of SOD has been shown to lower house values by 3%–6% in the long term and by 8%–16% in the short term, e.g., in the window of time when oaks are dying or dead and have not been removed (Kovacs et al., 2011a).

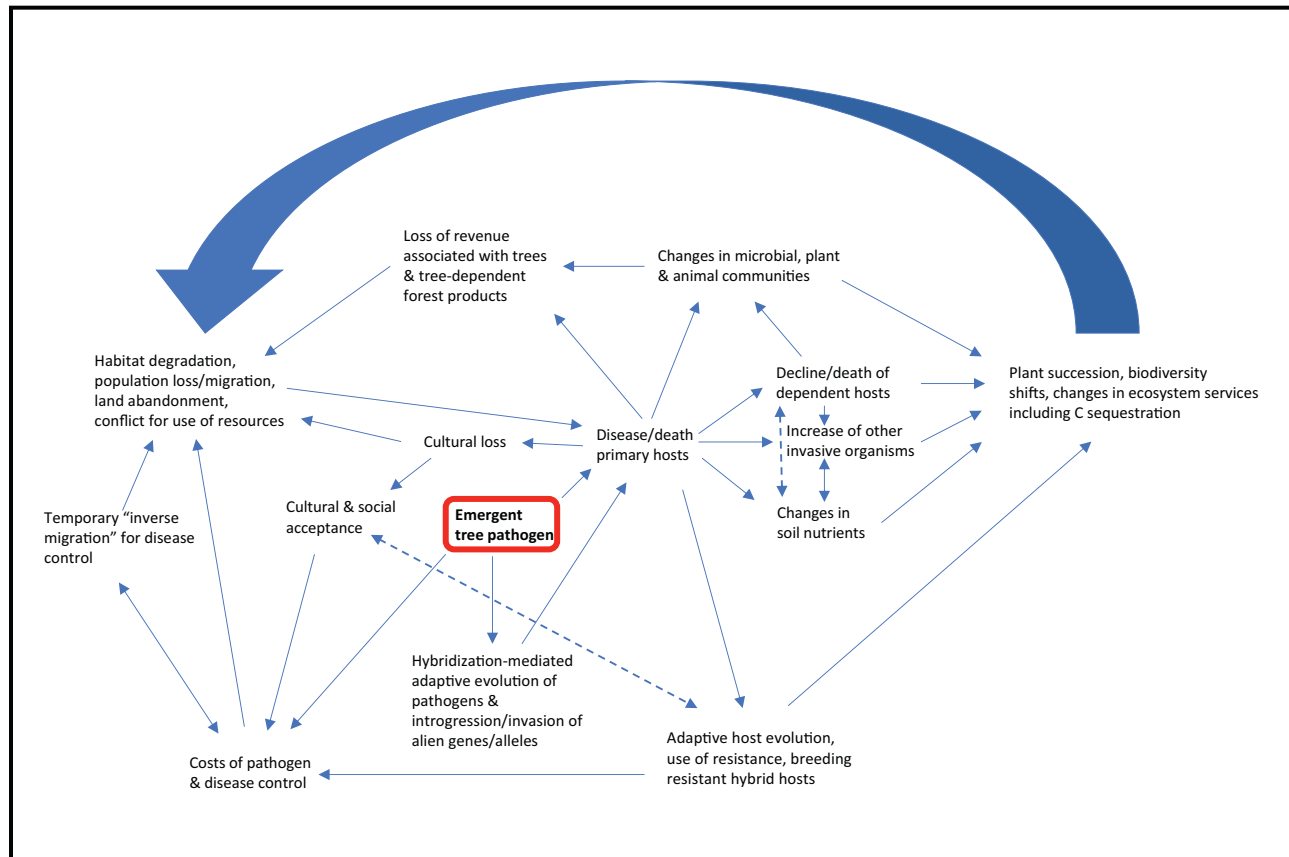
Thus, homes, cities, and recreational sites, i.e., the places that define the lives of individuals, families, and communities, may be negatively impacted by tree mortality and decline caused by emergent tree diseases. However, trees hold a much greater significance in almost every culture on earth, being seemingly timeless points of reference in a changing world and a keystone of both the natural and the human dimensions, connecting us with our past and/or with our beliefs. The removal of personally, historically, or culturally significant trees represents a fracture with one's past and a fracture with the culture, the history, and the beliefs of a community. Here, we cite only a few examples: tanoak trees for coastal native Californians in areas infested by SOD (Bowcutt, 2013), Eastern white pine (*P. strobus*) for native Quebec First Nations in areas infested by WPBR (Uprey et al., 2013), Ōhi'a for Hawaiian communities witnessing ROD (Martinez et al., 2020), and Italian cypress for people inhabiting the Mediterranean regions affected by cypress canker (Graniti, 1998).

## 5. Conclusions

Given the economic, social, and cultural importance of trees and forests on top of their biological and ecological significance, it is not surprising that their demise, in part associated with the emergence of invasive tree diseases, has spurred a call to reduce their frequency and impact through specific policies and regulations (Roy et al., 2014; Klapwijk et al., 2016).

We believe that science-based, culturally sensitive, historically informed, and fair policies are needed to curtail the introduction of non-native tree pathogens and to slow down their spread once introduced. We also acknowledge that the costs associated with these efforts should be accounted as an additional economic impact of emergent tree diseases that can be extremely significant overall, as exemplified by the £ 14.8 billion estimated for ash dieback in the United Kingdom alone (Hill et al., 2019). These costs may include costs for tree removal for sanitation and restoration purposes as reported, for instance, for oak wilt (Haight et al., 2011) and SOD (Kovacs et al., 2011b); pathogen eradication costs as those reported or hypothesized for SOD and estimated for DED (Cunniffe et al., 2016; Ganley and Bulman, 2016; Goheen et al., 2017); and general disease management costs including those incurred in the past or being currently





**FIG. 7.1** Schematic representation of the complexity of interacting and cascading impacts set in motion by emergent tree diseases. Note how large-scale, long-term ecological alterations of terrestrial ecosystems triggered by the emergence of tree diseases are interconnected with societal well-being and migratory fluxes through a series of feedbacks and processes that are not only ecological, but also evolutionary and societal in nature.

incurred to control emergent diseases such as DED, chestnut blight, and laurel wilt (Harwood et al., 2011; Rigling and Prospero, 2018; Olatinwo et al., 2021). The limitation of tree and tree product movement (Mabbett, 2017), the efforts associated with changes in silvicultural strategies such as the treatment of stumps where *Heterobasidion* spp. are emerging (Gonthier et al., 2014), severing root connections where DED or other vascular diseases are present (Campana and Stipes, 1981), or the use of disease-resistant tree genotypes and hybrids (Jacobs, 2007) also come at a cost and further require societal acceptance. While acceptance of various control strategies may be more easily granted if communities are economically impacted by a disease and thus knowledgeable about the issues (Okan et al., 2017), a longer and more involved dialogue among stakeholders may be required to reach social acceptance of certain disease control strategies and of their costs (ecological, evolutionary, and societal) (Martín et al., 2019). One notable example of the controversial acceptance of disease control methods is that of the use in nature of genetically modified strains of the chestnut blight fungus, in lieu of the naturally occurring mycoviruses (Griffin, 2000). This last point further highlights the interconnectivity among ecological, evolutionary, economic, social, and cultural aspects of tree diseases caused by emergent pathogens (Fig. 7.1).

## 6. Study questions

- (1) What is an emerging plant pathogen and what are the factors making plant pathogens emergent?
- (2) Discuss the ecological consequences of forest pathogen invasions.
- (3) Discuss the evolutionary consequences of forest pathogen invasions.
- (4) Do the economic and societal impacts strictly overlap? Discuss the issue.
- (5) Emergent forest pathogens may be impactful based on more than one perspective (ecological, evolutionary, economic, and societal): By providing examples, discuss the cascading impacts determined by those pathogens.

## Glossary

- Bacterivore** Organism that obtains energy and nutrients from the consumption of bacteria.
- Biotrophic** Quality of an obligate parasite living in a plant in intimate association with its cytoplasm.
- Dikaryotic** Stage of the life cycle of a fungus characterized by cells having two genetically distinct haploid nuclei.
- Diploid** Cell or organism that has paired chromosomes, one from each parent.
- Endophyte** Organism occurring in a living plant.
- Fungivore** Organism consuming fungi.
- Genic introgression** Transfer of genetic material from one species into the gene pool of another by the repeated backcrossing of an interspecific hybrid with one of its parent species.
- Hardy-Weinberg equilibrium** A law of population genetics stating that allele and genotype frequencies in a population will remain constant from generation to generation in the absence of other evolutionary influences.
- Interfertile** Capable of interbreeding.
- Pathosystem** Subsystem of an ecosystem defined by the phenomenon of parasitism, i.e., interaction between a host and a parasite feeding on that host and causing disease.
- Resprout** To develop sprouts or shoots again.
- Sympatry** **Species or populations occurring in the same place at the same time.**

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