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Drivers of Forest Pathogen Invasions: The Roles of Global Trade and Climate Change

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ABSTRACT

In the past 25 to 30 years, a marked increase has occurred in numbers of invasive alien pests and pathogens recorded, damaging agriculture, horticulture and forest environments. The reasons for this upsurge are clear: all involve human-driven factors, with, arguably, global trade as the most important component in the complex. Climate change is another major factor. Each plant transported through trade could carry cryptic pests or pathogens, which may be introduced into previously naïve environments and lead to major health issues on previously unaffected plants. Global trade in plants is a complex system, driven by a desire to use large plants in landscapes and demand for varied species for gardens. Examples of invasive alien pathogens causing wide-spread problems on a global scale currently include many *Phytophthora* species, Dothistroma needle blight of pines, and *Xylella fastidiosa* on a wide range of trees. A striking example recently was the spread of the Dutch elm disease pathogen, *Ophiostoma novo-ulmi*, in North America and Western Europe. Many invasive pathogens cause problems in localized regions, including *Ceratocystis platani*, killing *Platanus* in some European countries. Other examples include the threat of pine wilt nematode (*Bursaphelenchus xylophilus*), damage to *Cupressus* in Mediterranean landscapes caused by *Seiridium cardinale*, dieback of sweet chestnut (*Castanea*) caused by the canker pathogen *Cryphonectria parasitica*, and many others. In addition to global trade, climate change appears to be exacerbating the problems, with major influences on establishment and spread of alien invasive species. Hope lies in the enormous genetic 'power' of plants: humans could establish selection and breeding programmes that will ultimately enable us to plant trees with greater tolerance of changing climate and pests and pathogens, whether native or invasive.

Keywords: Invasive alien pathogens; Global trade; *Phytophthora*; *Ophiostoma*; *Dothistroma*; *Ceratocystis*; *Cryphonectria*

INTRODUCTION

In the past 25 to 30 years, there has been a marked increase in the numbers of alien invasive pests and pathogens of plants recorded in populated continents of earth, damaging agriculture, horticulture and the wider environment, including both natural and plantation forest ecosystems. The reasons for this upsurge are clear: all involve interacting human-driven factors, with, arguably, global trade as the most important component in the complex (DAISIE 2014, Brockerhoff and Liebhold 2017, Santini et al. 2018). Climate change also appears to be having an impact on the establishment and impact of invasive pests and pathogens (Jactel et al. 2020).

This review focuses on increased damage in forest ecosystems by invasive alien species (IAS), with focus on invasive pathogens, some of which have led to, or are threatening, near extinction events for several tree genera and species. This review is focused on some of the most damaging and significant IAS of pathogens that are present in European forests.

The History of Global Spread of Damaging Forest Pathogens

Forests are ecosystems of enormous biological productivity, a fraction of which is utilized by humans in commerce, in timber production, for example, or in non-timber forest products. It is a fact, however, that in all of these ecosystems, some productivity is lost to biotic agents and abiotic factors associated with the forests. The forests in Figure 1, for example, all look pristine, with no pests or diseases apparent. Despite the appearance, however, each tree in each image will be colonised in to some extent by fungi and bacteria which may, at some time in the future, begin to reduce the health of the individual plants, depending largely on environmental factors (e.g., Sieber 2007). The same is true for arthropods and other animal pests. These native pests and pathogens are normal components in forest ecosystems. Being long-lived organisms, trees have developed strategies during evolution to cope with most potential pests and pathogens (Pearce 1996, Ayles et al. 2010).

Different problems arise when damaging invasive alien species (IAS) establish in the forests, however, as there have been no evolutionary pressures for the local trees to adapt to the presence of these organisms (Paap et al. 2020). A potential consequence, therefore, is that trees within the ecosystem are badly affected, possibly even dying because of attacks by these invasive species. Many examples of IAS are known in Europe (e.g., Santini et al. 2013), some of the most dramatic of which are detailed in the examples given below.

The history of the spread of plant pests and pathogens is closely intertwined with the development of shipping during human history (Liebhold et al. 2012, Santini et al. 2018, Costello et al. 2022). The desire to migrate developed early in human existence presumably during evolution in Southern Africa, undoubtedly driven by the need to access good food and water supplies, although it is possible that discovering what was over the next horizon was an exciting prospect too. Presumably the first migrations were on foot, but crossing rivers and, eventually, large expanses of water proceeded with the crafting of simple boats. Following the addition of sails, simple vessels could be used in passing over rivers and lakes and, possibly, were even used in migrations as far as from Europe to North America (Bill 2008).

Shipping evolved slowly, from small, canoe/kayak-like craft to the harnessing of wind power with sails, developing into the faster, ocean-crossing vessels of Mediaeval and later times. Towards the end of the 18th and into the 19th century, sails were supplemented with steam engines, followed by diesel engines in the early 20th century (Paine

Figure 1. Healthy forest ecosystems. **a)** *Picea abies*-dominated forest with some *Larix decidua* in the Dolomitic Alps, Northern Italy; **b)** A view over Yosemite National Park in the Sierra Nevada, California; **c)** *Fagus sylvatica* canopy in spring (Austria); **d)** Mixed coniferous forest to the south of Kaș, Turkey.

2014). The need to raise cereal and other crop plants in newly colonised areas led these early migratory humans to carry seed with them as they travelled. As seed are well-known vectors of many pathogens (Shade et al. 2017, Cleary et al. 2019), the diseases were transported along with the crops (Stukenbrock and McDonald 2008).

Although tree seed are well-known sources of certain pathogens (Cleary et al. 2019, Franić et al. 2019) major changes in the impacts of pests and pathogens came to the fore with the development of more efficient shipping. Reducing times at sea from months to a few weeks and less meant live plants, rather than seed, could survive long journeys.

In the past 70 years, shipping efficiency for goods has increased massively through the wide-spread adoption of containerisation. As containerised transport became more accepted, ships were built to carry larger numbers of containers on each trip. Currently, the largest container ship on the oceans is The Mediterranean Shipping Company (MSC) Gülsen, launched in 2019, with a capacity of nearly 24,000 standardised containers.

Although it is unlikely in practice, each container on a ship could include live plant materials. Within plant batches, each plant could potentially carry one or more cryptic pest or pathogen infestations. Many plants with compost may include more than one potential pathogen within the compost, possibly infecting the plant or simply living saprotrophically or as viable inoculum in the compost itself. Recent work suggested that individual plants can harbour multiple Oomycetes in the rhizosphere without any symptoms being visible (Puertolas et al. 2021). Imported plants are often grown on further in nurseries in the receiving state, before sale for landscaping or garden use. When the contaminated stock is planted out, the pathogens are introduced into a previously naïve environment, where they may establish on suitable host species in the newly invaded area, ultimately leading to major health issues on those plants and in those ecosystems (Jung et al. 2016).

Global trade in plants is a very complex system (see Santini et al. 2018), driven by the need for plants in landscapes and demand for different plants for gardens. Plant production systems in horticulture have also advanced greatly in the past 50 years (e.g., Davies et al. 2017). Currently, many woody plants are reproduced clonally by specialist growers outside Europe (for example; see FAO 2012). The young, rooted cuttings are then imported by European nurseries, where they are grown on, in pots of increasing size, before sale to the end users (Santini et al. 2018). Not all plants are produced in this manner: many native trees, for example, are raised in other specialist nurseries in Europe, sometimes for several years and either sold as root-balled specimens or raised into very large pots, before sale to end-users (e.g., Newman and Hayden-Smith 2014).

Examples of Serious IAS Causing Damage to Forest Ecosystems

There are many examples of tree pathogens causing wide-spread problems on a global scale. It can take several years following the likely introduction of the IAS for the problem to be noticed (e.g., Wylder et al. 2019). This period is the establishment phase for the IAS: it arrives as inoculum, and subsequently the population gradually builds up on the local plants it is able to colonise and reproduce from.

In the following section a number of these invasive pathogen problems are detailed, particularly those affecting forestry in Europe, but many others are described in the literature (e.g. Santini et al. 2013, Ghelardini et al. 2017). The choice of species was based on the extent of damage already caused and the potential to cause further damage with wider dissemination and climate change.

Phytophthora Species

Oomycota in genera including *Phytophthora, Pythium, Phytopythium*, *Saprolegnia Leptolegnia, Aphanomyces* and *Achlya*, are notorious pathogens of plants and animals, causing massive losses globally in agriculture, horticulture, aquaculture and natural ecosystems (Mendoza and Vilela 2013, Van West and Beakes 2014). Several species of *Phytophthora* are causing ongoing epidemics affecting trees in various regions of the world, with the most well-known species overall arguably being *Phytophthora cinnamomi* Rands and *Phytophthora ramorum* S. Werres, A.W.A.M. de Cook & W.A. Man in't Veld (Hansen 2015). There are at least 140 species of *Phytophthora* that are fully described in the literature (Scott et al. 2013, Jung et al. 2015), but it has been predicted that there could be at least 400-600 species in total (Brasier 2009). It is well established that *Phytophthora* and other plant pathogenic oomycetes are commonly transported in the 'plants for planting pathway'; recently published work demonstrated that individual hardy woody ornamental plants traded in garden centres and online almost all include one or more potentially pathogenic oomycetes on the plants or in the accompanying compost (Puertolas et al. 2021).

Phytophthora cinnamomi is rated as one of the worst plant pathogens known (Burgess et al. 2017), with a host list including over 1,000 plants. Serious problems can arise anywhere the pathogen is known, but hot spots of activity occur, some of which are associated with regions of high overall biodiversity. The pathogen probably evolved in Celebes, possibly including Taiwan (Ko et al. 1978), and was first discovered in the 1920s when cinnamon trees planted in Papua New Guinea began to die (Rands 1922, Shepherd 1975, Arentz and Simpson 1986). Some evidence suggests that *P. cinnamomi* had already been spread from its centre of origin before it was first isolated and described (e.g. Santini et al. 2013). Phytophthora dieback, caused by both *P. cinnamomi* and *P. x cambivora* (Petri) Buisman is a well-known problem on *Castanea sativa* Mill. in Europe, but *P. cinnamomi* also causes dieback and mortality on *Quercus* species (Figure 2a). The pathogen is considered to cause epidemics on *C. sativa* and *Quercus suber* L. throughout the Mediterranean region, with particular hot spots in Italy (Vannini and Vettraino 2001, Scanu et al. 2013), Spain (Rodríguez-Molina et al. 2005), Portugal (Brasier et al. 1993, Moreira and Martins 2005) and Turkey (Balcı and Halmschlager, 2003, Akıllı et al. 2012).

There is particular concern over the activity of *P. cinnamomi* and other *Phytophthora* species in UNESCO biodiversity communities in South-Western Australia (Figure 2b) and in the Fynbos, South Africa, with extensive dieback of the woody flora, particularly on disturbed sites (Engelbrecht and Van den Berg 2013, Reeksting et al. 2014). In the past, *P. cinnamomi* caused an epidemic of little leaf disease on pines planted on nutrient depleted, former cotton growing sites in the southern USA (Copeland 1952, Roth 1954).

Warm temperatures of 25°C+, i.e., a Mediterranean climate, favour disease, particularly when associated with intermittent rainfall and droughts (e.g., Burgess et al. 2017).

a)

b)

Figure 2. Impacts of *Phytophthora cinnamomi* infection on: **a)** *Quercus suber* in Sardinia (photo: T. Jung); **b)** *Eucalyptus marginata* in Western Australia.

Canker of Sweet Chestnut

In the early 20th Century, serious dieback of the American chestnut, *Castanea dentata* (Marsh.) Borkh. was observed in the Bronx Zoological Garden, New York. The disease symptoms included formation of sunken cankers where the pathogen killed host tissues, with shoots distal to the infection dying; in many infections, the roots of the tree remain alive, but the top of the tree dies back completely, resulting in repeated regrowth from stump sprouts (Anagnostakis 1987). Investigations showed that the problem was caused by a fungal pathogen; the fungus was first named *Diaporthe parasitica* Murrill. (Murrill 1904, 1908) but later placed in the genus *Endothia* (Anderson and Anderson 1912). Subsequently the pathogen was reclassified as *Cryphonectria parasitica* (Barr 1978). Infections resulted in the formation of severe cankers on branches and the main stem (Figure 3), leading to dieback and mortality. In 1912-14, expeditions were launched to find the source of the pathogen and the same fungus was quickly discovered causing mild symptoms on *Castanea* species native to Japan and China, such as *C. mollissima* Blume and *C. seguinii* Dode (e.g., Fairchild 1923) from where infected chestnut timber was exported to North America (Anagostakis 1987).

The speed of spread of *Cryphonectria parasitica* in North America was alarming. The native chestnut there, *Castanea dentata*, occurred naturally throughout the Appalachian Mountains and in small pockets of woodland further south. It was a very important, multi-purpose tree species, with excellent timber qualities for many uses from fine furniture to railway sleepers, a durable bark which was used for roofing and, of course, the chestnuts themselves, which as with the Europe sweet chestnut, were highly valued for culinary purposes and also consumed by many wild animals in the native forests (Rigling and Prospero 2018). Within 40 years of *Cryphonectria parasitica* being recorded in the Bronx Zoological Gardens, New York, the pathogen had spread throughout the native range of *Castanea dentata*, killing most trees or reducing them to small shrubs (Anagostakis 1987).

In the last ten years, chestnut trees, derived by hybridising *C. dentata* with *Castanea* species from Far East Asia which showed good levels of resistance to the pathogen, are now being planted out in the Eastern USA (Clark et al. 2019). A major objective of the breeding programme was to produce trees that had a growth habit as close to *C. dentata* as possible. A recovery programme is now underway in the Appalachians, but it took over 100 years to reach that point from the time the disease was first noticed.

The situation in Europe differed from that in North America, however. The presence of *Cryphonectria parasitica* was first recorded in Italy in 1938 (Biraghi 1946), with observations of dieback of the European sweet chestnut, *Castanea sativa*. Regular surveys for the disease were made after World War II and, in the early 1950s Biraghi (1953) reported that cankers recorded in previous surveys appeared to be reducing in size, enabling trees to partially recover from the infections. It took over 10 years to prove that this effect was due to the presence of a virus-like infection in *Cryphonectria parasitica*, causing hypovirulence (low virulence) in infected strains of the pathogen (Grente

Figure 3. Symptoms of *Cryphonectria parasitica* attacking *Castanea sativa*: **a)** well-formed canker on stem of *C. sativa* in north-east Turkey; **b)** canker on branch; **c)** canker caused by virus-infected hypovirulent strain of *C. parasitica*; **d)** early symptoms of canker, causing death of branches (photos c and d: Kiril Sotirovski).

1965). This hypovirulence has been exploited in many European countries and in Turkey (see Rigling and Prospero 2018) to reduce the impacts of chestnut canker in nut and timber-producing regions. Hypovirulence works well in Europe and Eurasia, where genetic diversity in the pathogen is low, compared to the higher relative diversity in North America (MacDonald and Fulbright 1991, Liu et al. 1996). Many European countries have used extended programmes to investigate the efficacy, longevity and non-target impacts of hypovirulent strains of the pathogen (Robin et al. 2000, Krstin et al. 2017, Diamandis 2018). There have also been trials of new formulations and delivery systems for the hypovirulence factor (Kunova et al. 2016). Currently, the disease continues to spread in Europe, including into the UK (Hunter et al. 2013), with attempts to use hypovirulence as the major management tool widespread in affected parts of the continent.

Dutch Elm Disease

A striking example of the potentially catastrophic impacts of invasive alien pathogens on tree populations in recent history was the spread of the Dutch elm disease pathogen, *Ophiostoma novo-ulmi* Brasier, firstly in the 1930s in North America, then from the early 1960s in Western Europe (Brasier and Gibbs 1973). There was a previous epidemic of Dutch elm disease in northern Europe in the early 20th Century, which caused considerable dieback in the *Ulmus* populations and led to mortality in approximately 30% of the elms present at the time (Peace 1962). The pathogen was defined as *Ceratocystis ulmi* (Buism.) (later: *Ophiostoma ulmi* (Buism.) Melin & Nannf. [1934]) (Gemma 1984). By the 1950s, however, that epidemic had run its course (Peace 1962); but within a few years, it was noted that elms in parts of England were dying. Mapping of the outbreak showed that deaths were focused around major ports in England

and Wales, and an investigation of *Ulmus thomasii* Sarg. logs imported from Canada into southern England demonstrated the presence of the Dutch elm disease pathogen, along with North America elm bark beetles, *Hylurgopinus rufipes* (Eichhoff) (Strobel and Lanier 1981) (Coleoptera: Scolytidae) in the timber consignments (Brasier and Gibbs 1973). Bark beetles are vectors of the Dutch elm disease pathogens; in Europe, the vectors include several species of *Scolytus*, mainly *Scolytus scolytus* Fabr. (Coleoptera: Curculionidae) but replaced by *Scolytus multistriatus* (Marsham 1802) (Coleoptera: Curculionidae) in more northerly latitudes (Santini and Faccioli 2015). In depth analyses showed that the second outbreak of Dutch elm disease was caused by a previously unknown species, subsequently named *O. novo-ulmi* (Brasier 1991, 2000). There is an interesting phenomenon occurring: into the late 1970s, it was relatively easy to isolate *O. ulmi*, the pathogen which caused the early 20th century outbreak of Dutch elm disease from stands of elm where dieback was occurring. More recently, however, it has become rare to find *O. ulmi* in isolations from similar niches. It appears that the causal agent of the later Dutch elm disease outbreak has replaced the original pathogen, possibly driving it to extinction (Brasier 2000).

European and North America species of *Ulmus* are all highly susceptible to infection by *O. novo-ulmi* (Brasier 2000). The disease cycle is heavily reliant on the elm bark beetle vector, on which the spores of the pathogen adhere to the beetle exoskeleton (Webber 2000, Santini and Faccioli 2015). Elm bark beetles target trees in decline for egg laying (Webber and Brasier 1984). Following mating, the females bore a brood gallery into bark on declining elms, laying eggs at regular intervals along the gallery. When the eggs hatch, the larvae consume the nutritious secondary phloem of the inner bark tissues, with the pattern of galleries formed varying between *Scolytus* species (Figure 4a). Following pupation, the newly emerged beetles exit the dead bark tissues, but before mating must carry out maturation feeding, usually on bark in the upper parts of a healthy elm crown, often in branch crotches (Webber and Brasier 1984; Figure 4b). When emerging from the old bark tissues, the young beetles are in an environment that is perfect, in terms of temperature and humidity, for the pathogen to produce large numbers of coremia (fused conidiophores) covered in sticky masses of asexual spores. These spores adhere to the beetle exoskeleton and, when the beetles begin maturation feeding, the spores are introduced into the wounds formed, gaining entry to the host vascular tissues (Figure 4d). The tree is then infected: brown staining in the xylem tissues, typical of vascular wilt diseases, forms as the tree responds to the damage. Toxins produced by the fungus, however, cause severe disruption to the tree water balance, causing stomata to stay open and tyloses to form in the xylem vessels, even those that are not directly infected by *O. novo-ulmi*. The tree wilts and, eventually, dies. Bark beetles are attracted to the dying trees, lay their eggs in the bark tissues, and the disease cycle begins again (Webber and Brasier 1984).

Xylella fastidiosa

The problems caused by *Xylella fastidiosa* Wells et al. 1987, a xylem-limited bacterium, were recognised in North America in the late 19th Century, when a severe problem arose on grapevines planted for viticulture in California (Jeger and Bragard 2018). The US Department of Agriculture sent a 'special agent' to investigate the problem: Newton B. Pierce became the first professional plant pathologist working in California, and demonstrated that the unknown cause of the disease on grapevines was transmitted by sap sucking insects. The agent responsible, however, remained unknown until the early 1970s, when an unculturable species of xylem-limited bacterium was suggested as the cause (Goheen et al. 1973, Hopkins and Mollenhauer 1973). The causal agent was partially described from grapevines (Davis et al. 1978) and fully described as *X. fastidiosa* by Wells et al. (1987).

Subsequently, it was shown that at least four, possibly six, distinct sub-species of *X. fastidiosa* occur, with differing host ranges (Nunney et al. 2010, 2012), including *X. fastidiosa* subsp. *fastidiosa*, *X. fastidiosa* subsp. *multiplex*, *X. fastidiosa* subsp. *pauca* and *X. fastidiosa* subsp. *sandyi:* all subspecies are native to the American continents.

Collectively, *X. fastidiosa* sub-species cause dieback and mortality on a very wide range of woody plants, with, so far, almost 600 hosts known to be infected (European Food Safety Authority 2020). Most *X. fastidiosa* disease reports are from North and South America, usually in tropical and sub-tropical climates (Desprez-Loustau et al. 2021), although there are reports from Canada (Goodwin and Zhang 1997). According to the EFSA database, 15 forest tree species common in European forests are known hosts of *X. fastidiosa*, of which nine have been recorded as infected in Europe. Some affected plants that are widely planted in Europe, such as *A. platanoides* L. and *Q. rubra*, have not yet been confirmed to be infected. *Xylella fastidiosa* is currently restricted to Mediterranean Europe, where these species are uncommon (Desprez-Loustau et al. 2021). A current notable problem of relevance to south-eastern Europe and beyond is that of 'olive quick decline syndrome' occurring in olive groves in Apulia, Southern Italy (Elbeaino et al. 2014, Loconsole et al. 2014). Spread from the infected area is considered highly likely, threatening a disastrous impact on olive production throughout the Mediterranean basin. Further identifications of *X. fastidiosa* in Europe in recent years suggest that several invasive events have occurred (Baldi and La Porta 2017). It is feared that further spread of the *X. fastidiosa* strains now known to be present in Europe could lead to serious problems on many other species of woody plants, in horticultural production, in gardens and in forests and woodlands (Jeger and Bragard 2019, Morelli et al. 2021).

Ash Dieback

The pathogen causing dieback of ash (*Fraxinus* spp.) in Europe, *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya,, is native in east Asia, including Japan and the far eastern regions of China and Russia, where it is considered a saprotroph on species of *Fraxinus* native in that region (Gross et al. 2014, Zhao et al. 2012). The first indication of serious problems on ash in Europe came in the early 1990s, when a progressive dieback was noted on *Fraxinus excelsior* L. in the north east of Poland and the south west of Lithuania (Przybył 2002, Gil et al. 2006, Kowalski 2006). The problem

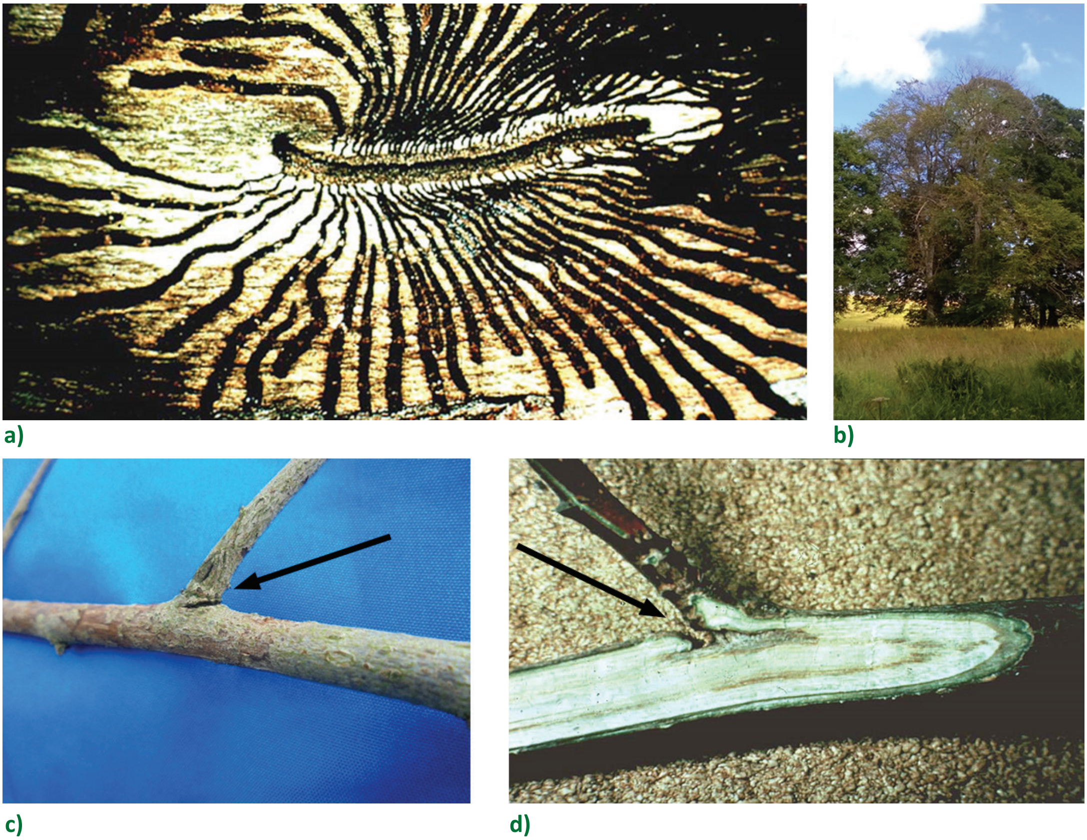

Figure 4. Typical symptoms of Dutch elm disease: **a)** underside of bark removed from the lower stem of *Ulmus minor* with breeding gallery of one of the vector beetles, *Scolytus scolytus*; **b)** large *U glabra* trees in a field boundary dying of *O. novo-ulmi* infection; **c)** notch (arrowed) created during maturation feeding by the vector beetle; **d)** typical staining in the xylem of a twig, following maturation feeding by *S. scolytus* (photos a and d, courtesy of Don Barrett).

had spread more widely in Europe before the causal agent was identified definitively in the mid-2000s (Baral et al. 2014), when it had already caused great amounts of damage in eastern and central Europe, and into western Europe. The pathogen appears to infect all *F. excelsior* (Figure 5) and *Fraxinus angustifolia* Vahl. trees, although individual host genotypes vary greatly in the symptoms shown (Krautler and Kirisits 2012). A third *Fraxinus* species native in Europe, common in the Balkans, *Fraxinus ornus* L. may be infected but shows limited symptoms, compared with *F. excelsior* and *F. angustifolia* (Kirisits and Schwanda 2015). *Fraxinus* spp. from Far East Asia are considered resistant to the disease, although foliage is infected: it appears that a difference between the two highly susceptible European ash and those in the Far East of Asia is that the fungus fails to grow from the leaf petioles and in to the twigs and branches of the Asian species (Cleary et al. 2016). The mechanisms underlying this difference are under investigation.

Box Blight

Box (boxwood) blight was first reported from infected samples in England in 1994 (Henricot and Culham 2002, Henricot 2006), causing dieback of ornamental *Buxus sempervirens* L. clones, since when the problem has been reported from all over the world where the plant is used extensively in amenity and garden plantings (see Leblanc et al. 2018). Apart from ornamental settings, the disease is killing *B. sempervirens* (and the putative species, *B. colchica*) in the wild in some European and Eurasian countries. In Turkey, for example, where *B. sempervirens* is the dominant understory species in forests of the north-eastern Black Sea region, as many as 90% of certain box populations lost all foliage within 12 months of the first report of the disease occurrence (Figure 6; Akilli et al. 2012, Mirabolfathy et al. 2013, Lehtijärvi et al. 2014, 2017). Conditions in the Black Sea region of Turkey and neighbouring Georgia, with high humidity most of the time, are perfect for disease development and spread of the spores.

The first report of the disease in the USA was in 2011, but by 2018 it was known in 25 states (LeBlanc et al. 2018).

The disease is caused by two similar species, *Calonectria pseudonaviculata* L. and *Calonectria henricotiae* sp. nov., first classified as *Cylindrocladium*. The origins of these fungi are unknown, but it is believed that they are spread by human

a) **b)**

Figure 5. Symptoms of ash dieback caused by *Hymenoscyphus fraxineus*: **a)** Young ash tree with severe dieback on many branches; **b)** Typical premature death of severely infected foliage, which remains attached to the tree for some time.

activities, particularly through the transport of live plants (LeBlanc et al. 2018). Coupled with the activities of the box moth, *Cydalima perpectalis* (Walker, 1859), inadvertently imported into Europe and Eurasia from Asia (Leuthardt et al. 2010, Nacambo et al. 2014, Bras et al. 2019), the future of *B. sempervirens* in both native forest areas and in ornamental plantings is in serious doubt.

Canker Stain of *Platanus*

The pathogen, *Ceratocystis platani* (Walter) Engelbrecht & Harrington, causing this lethal disease of oriental and hybrid plane in Europe is probably native to the southeast of North America (Engelbrecht et al. 2004) but was accidentally introduced into Europe during World War II (Panconesi 1999). The western plane, *Platanus occidentalis* L., is susceptible to infection by *C. platani*, but the disease caused is a more mild, often trivial, dieback than occurs on *Platanus* x *hispanica* Mill. or *Platanus orientalis* L. The common clones of *P.* x *hispanica* are, almost without exception, very susceptible to infection and will die within months, regardless of tree size (Ferrari and Pichenot 1976, Panconesi 1999). The plane species native in parts of south-east Europe and Turkey, *P. orientalis*, is highly susceptible and infection invariably leads to death. With *P. orientalis* being a major component of riparian ecosystems in the eastern Mediterranean region, as well as a very important urban shade tree, the threat posed by the canker stain pathogen is enormous (Tsopelas et al. 2017).

To date, problems caused by *C. platani* are reported in Italy (Panconesi 1972), Switzerland (Panconesi 1999), France

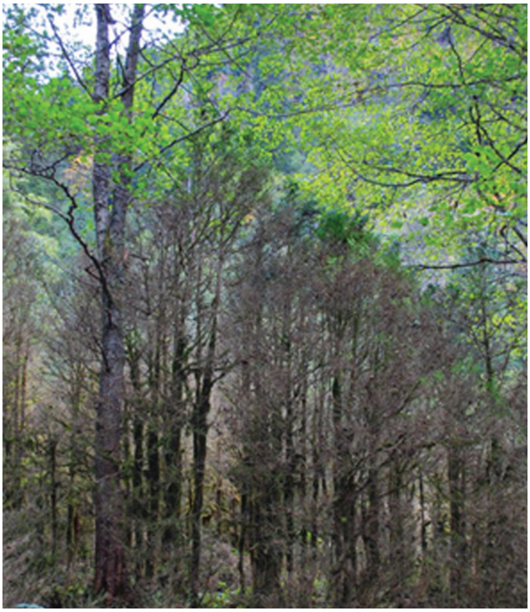

Figure 6. *Buxus sempervirens* trees forming the main understory of natural forests in The Black Sea region of Turkey. The trees are dying due to severe blight attack: note the very tops of the trees remain green, in a niche that is better ventilated than nearer the ground. (Photo: Asko Lehtijarvi).

(Ferrari and Pichenot 1974, 1976, Vigouroux 1986), Greece (Tsopelas and Angelopoulos 2004), Albania (Tsopelas et al. 2015) and Turkey (Lehtijarvi et al. 2018). After entering Italy, the problem was first noted when urban *Platanus* trees, mostly *P.* x *hispanica*, began dying, spoiling the aesthetic qualities of major avenues (Figure 7) comprised entirely of plane (Panconesi 1999). Subsequently, the pathogen spread into south-east France before migrating northwards, extending as far as Switzerland. With a few possible exceptions, all of the trees affected in Italy, France and Switzerland were planted: the only native stands of plane (*P. orientalis*) in Italy were restricted to a few small sites in Sicily (Tutin 1964).

In the early 2000s, a serious dieback and death of *P. orientalis* began in native stands in Greece and was discovered to be caused *C. platani* (Tsopelas and Angelopoulos 2004, Tsopelas and Soulioti 2011). It is thought that the pathogen was inadvertently taken into Greece on plane trees imported from nurseries in Italy. Subsequently, the disease was also found in the south of Albania, near to the border with Greece (Tsopelas et al. 2015). Currently, the disease appears to have spread throughout much of Albania and is killing *P. orientalis* in river valleys towards the eastern border with North Macedonia (Woodward and Doğmuş, personal observations, September 2021). Canker stain is also killing *Platanus* trees in Istanbul, where the hybrid and *P. orientalis* are iconic features of the landscape and constitute major proportions of the urban tree population (Lehtijarvi et al. 2018). An additional complication is that a second lineage of *C. platani* now appears to be in the Mediterranean region, possibly leading to changes in virulence and further loss of *Platanus* trees (N. Soulioti, personal communication, April 2022).

Canker stain of plane resembles a wilt disease: the pathogen enters the tree through wounds, often caused by pruning in urban areas, and grows rapidly in the xylem of hosts. Toxins released by the growing fungus have a catastrophic impact on water balance in the infected trees, causing rapid water loss through open stomata, wilting, dieback and death (Panconesi 1981). Due to routine pruning activities in urban areas, the pathogen can spread rapidly from tree-to-tree, leading to serious impacts on the aesthetics of street and park plantings.

Figure 7. Symptoms of *Ceratocystis platani* infections on *Platanus* trees: **a)** infected *P.* x *hispanica* dying in a street in Firenze, with an apparently healthy tree to the left and a symptomatic tree to the right; **b)** avenue of *Platanus* dying on a major road in Istanbul; **c)** young, riparian *P. orientalis* dying from infections; **d)** cross-section through a stem showing typical internal staining of the wood following infection. (photo b: Asko Lehtijarvi; d: Panghiotis Tsopelas/Nikoleta Soulioti).

Dothistroma Needle Blight (DNB)

Dothistroma species have been recognised pathogens impacting on growth of most species of *Pinus* for many years, with the first record dating back to 1910, in the north-west of Russia (Doroguine 1911, Drenkhan et al. 2016). Plantations of *P. radiata* D. Don. in East Africa were devastated by the disease in the 1950s and 1960s, making planting pines in that region almost hopeless (Gibson 1974). *Pinus radiata* plantations in New Zealand were also very badly damaged around the same time, but techniques for reducing the damaging effects were heavily researched and put in place to maintain the stock of *P. radiata* which, diseases notwithstanding, grows exceptionally well in the region (Rogers 2002). Until the 1990s, therefore, DNB was considered a problem in plantation pines in the southern hemisphere. In the early 1990s, however, natural pinewoods and plantations in Europe and North America were attacked by DNB, causing massive losses in several *Pinus* spp. (see Drenkhan et al. 2016). Research in South Africa showed that what was considered a single pathogen, *Dothistroma pini*, was, in fact, two cryptic species, *D. pini* Hulbary and *D. septosporum* (Dorog.) Morelet (Barnes et al. 2004), of which *D. septosporum* seemed to be the more common globally and the species responsible for the large DNB outbreaks in pine forests of much of the Northern Hemisphere. Species of pine particularly badly damaged in their natural habitats by *D. septosporum* and *D. pini* include most sub-species of *P. nigra*, certain provenances of *P. contorta* Douglas and *P. brutia* Ten. and *P. jeffreyi* Balf. Climate plays a large part in determining the disease severity, however, resulting in sporadic epidemics (Woods et al. 2005). Dothistroma species are known to infect 109 hosts, 95 of which are in the genus *Pinus*. *Dothistroma septosporum* has also been recorded infecting species of *Abies, Cedrus, Larix, Picea* and *Pseudostuga*, all genera within the Pinaceae (Drenkhan et al. 2016).

The massive upsurge in incidence and severity of Dothistroma needle blight recognized from the early 1990s onwards, differs from the changes in invasive alien pathogens described for the other selected pathogens because it is possible that the causal agents, *D. septosporum* and *D. pini*, were widespread in North America and Northern Europe prior to the epidemic outbreaks we are now witnessing (Drenkhan et al. 2016). Although the centres of evolution of the pathogens are currently unknown, recent work demonstrated that there is great genetic diversity in *D. septosporum* populations in Turkey (Oskay et al. 2020b), suggesting that this region could be amongst the centres of evolution for this pathogen. As a region bridging Europe and Asia, although in the absence of large numbers of isolates of the pathogen from Asia for use in comparisons, it is difficult to assess fully this hypothesis. Spread of different genotypes of the pathogen also plays a role in the increased Dothistroma damage seen in Europe (Ennos et al. 2020).

As the common name suggests, DNB causes lesions on the needles (Figure 8), sometimes leading to defoliation and death. The common name prior to the upsurge in the epidemic was 'Red Band Needle Blight', referring to a symptom on infected needles, mainly of *P. radiata* (Gibson 1972); the red banding does not appear on all species of pine, or even on all infected individuals within a species hence the change in common name from the late 1990s onwards. A notable effect of the disease on surviving trees was the significant reduction in the number of years foliage retained on affected pines (Drenkhan et al. 2016), resulting in the trees having much thinner crowns than prior to the 1990s.

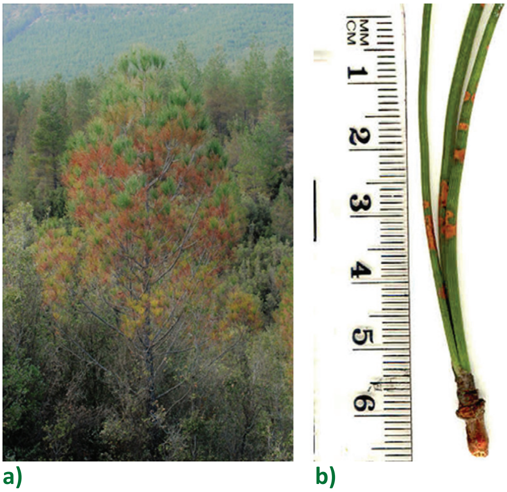

Figure 8. Symptoms of Dothistroma needle blight on: **a)** *Pinus brutia* in western Turkey; **b)** needles of *Pinus jeffreyi*. (photo a: Asko Lehtijarvi).

Brown Spot Needle Blight of Pines

Lecanosticta acicola (Thüm.) Syd. (syn. *Scirrhia acicola*; *Mycosphaerella dearnesii*) causes brown spot needle disease of *Pinus* spp., and can be particularly problematic in Christmas tree plantations. Disease symptoms include brown lesions on infected needles (Figure 9a), which can lead to early loss of foliage and, in severe or repeated cases, death of the affected tree (Figure 9b). The pathogen is widespread in North America, where it is believed to be native, but has spread into Central and South America, the Far East of Asia, Europe and Turkey (https://gd.eppo.int/taxon/SCIRAC/distribution). Infections have been confirmed on over 40 *Pinus* species (see: van der Nest et al. 2019), plus several sub-species and hybrids, along with *Cedrus libani* (Oskay et al. 2020a).

It appears that *L. acicola* has spread rapidly in Europe over the last 15 – 20 years, with many reports from different countries in the region (Van der Nest et al. 2019), although to date, it has not been reported from the southern Balkans. With multiple threats to pine vigour and productivity, *L. acicola* presents a further worrying disease affecting this important genus of trees.

Cypress Canker and Dieback

The first epidemic of cypress canker and dieback disease caused by *Seiridium cardinale* (W.W. Wagener) B. Sutton & I.A.S. Gibson. *Seiridium cardinale* was reported on *Cupressus macrocarpa* Hartw. on the Monterey Peninsula, California (Wagener 1928), but the disease subsequently spread in the early to mid-twentieth century

Figure 9. Symptoms of brown spot needle blight caused by *Lecanosticta acicula*: **a)** needles of *Pinus nigra* subsp. *nigra* showing characteristic spots; **b)** *P. nigra* subsp. *pallasiana var. pallasiana* f. *şeneriana,* taken in the Atatürk Arboretum, Istanbul in 2018; within two years, this ornamental tree was dead. (photos: Funda Oskay).

to Australia and New Zealand, Europe and South America, via movement of infected plant material (Birch 1933, Barthelet and Vinot 1944, Grasso 1951, Saravi-Cisneos 1953, Anastassiadis 1963, Mujica et al. 1980, Torres 1969, Funk 1974, Caetano et al. 1991, Wingfield and Swart 1988, Danti et al. 2009). The disease has been reported on species of *Cupressus, Chamaecyparis, Cryptomeria, Juniperus, Thuja* and *×Cupressocyparis* (Anastassiadis 1963, Graniti 1998).

This disease problem was first recognised in Europe when an outbreak occurred in Italy in the 1930s (Graniti 1998). Once in southern Europe, however, *Cupressus sempervirens* L., an iconic tree species in Mediterranean landscapes proved highly susceptible to infection and damage from *S. cardinale* (Figure 10). In many regions now, the relatively non-susceptible species, *Cupressus arizonica* Greene is used as a replacement tree with similar environmental tolerance, although there is no obvious substitute for the fastigiate form of *C. sempervirens* (Beresford and Mulholland 1982, Saos et al 2001).

A number of other invasive pathogens are present in Europe, although spread to date has been limited. Examples include pine pitch canker, caused by *Fusarium circinatum* Nirenberg & O'Donnell, which is established in Portugal and Spain: outbreaks in France and Italy are considered to be eradicated (Wingfield et al. 2008, Drenkhan et al. 2020). The pine wilt nematode *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle, is native to North America, but established in China and Japan early in the 20th Century and was diagnosed causing death of *Pinus pinaster* in Portugal in the late 20th Century (Mota et al. 1999). Any further spread and establishment of these highly damaging problematic organisms from the Iberian Peninsula to other parts of Europe will result in extensive damage to pines and blocks trade in pine timber from invaded territories.

Influence of Climate Change

Although global trade is undoubtedly the main factor in the increasing invasions of forests and ornamental plantings by damaging alien pests and pathogens (Santini et al. 2018, Pyšek et al. 2020), climate change is also having a major influence on establishment and spread of these organisms, affecting pest and pathogen activities and life cycles, host plant physiology and the outcomes of interactions between pests and pathogens and the plants (Tubby and Webber 2010). Climate change, as suggested above for Dothistroma needle blight, is also altering the latitudes at which endemic pathogens are causing problems in forests (La Porta et al. 2008). Much of the climate effect is due to changing temperatures and humidities, altering the extent and timing of previous seasonal effects. Increasing frequencies of storm events and droughts also will have large effects on many pathogen life cycles (La Porta et al. 2008, Sturrock et al. 2011, Garrett et al. 2021).

Modelling has been carried out and published for several of the examples of invasive alien pathogens given

Figure 10. Symptoms of *Seiridium cardinale* infection on *Cupressus sempervirens*: **a)** top-dieback of a mature tree outside the centre of Firenze, Italy; **b)** flagging of smaller branches on a tree in an avenue in Italy.

above (e.g., Guerina et al. 2001, Harwood et al. 2011, Watt et al. 2011, Burgess et al. 2017, Danti and Della Rocca 2017, Möykkynen et al. 2017, White et al. 2017, Chumanová et al. 2019, Daughtrey 2019, Mesanza et al. 2021): below, we present summaries of the published models for two of the pathogens, *P. cinnamomi* and for *D. septosporum*, for which considerable information is available.

Phytophthora cinnamomi: This pathogen causes root and collar rot in many woody plant species resulting in a disease known as *Phytophthora* dieback (Cahill et al. 2008). As one of the most significant and damaging plant pathogens known (Kamoun et al. 2015, Hardham and Blackman 2018), the potential impact of predicted climate change on the distribution and activity of *P. cinnamomi* has been the subject of considerable attention (Brasier and Scott 1994, Bergot et al. 2004, Desprez-Loustau et al. 2007, Thompson et al. 2014, Duque-Lazo et al. 2016, Burgess et al. 2017). In the latest of these publications, Burgess et al. (2017) based the models on the known extensive global distribution of *P. cinnamomi*, utilizing the CLIMEX approach to climate change modelling. CLIMEX enables users to produce a likely scenario for pathogen (or pest) activity, given information on current knowledge of the distribution and environmental requirements of the organism; different climate change models can then be incorporated, enabling predictions of pest/pathogen distribution in the future.

Good conditions for the establishment of *P. cinnamomi* include the presence of suitable host plants and conducive soils and a climate that includes alternating warm, wet winters with dry summers (Hardham and Blackman 2018), as found in regions with Mediterranean climate types globally. Predictions for climate change suggest that some of the regions currently affected by *P. cinnamomi* may, with time, become less suitable for the pathogen and a decrease in damage will be observed (Burgess et al. 2017). It is also likely, however, that climate change will lead to an increase in the latitudes and altitudes at which *P. cinnamomi* can establish and survive, with impacts in regions where this pathogen has hitherto not been a problem, including Canada and Scandinavia. Although the changes in climate suitability for *P. cinnamomi* to become active may result in greater damage in northerly latitudes, it is possible that regions around the Mediterranean Sea will become less suitable for the pathogen to be active. It is known that *P. cinnamomi* survives in northerly latitudes (e.g., Chavarriaga et al. 2007), possibly in the roots of symptomless host plants (Jung et al. 2013), indicating that the organism has already spread widely in the world, being transported into forests via infections in plant nurseries (Jung et al. 2015, Benavent-Celma et al. 2022).

Dothistroma septosporum: The global distributions of *D. septosporum* and *D. pini* are well-known (Drenkhan et al. 2016), along with the environmental requirements for DNB to occur and cause epidemics. Based on the available data, a number of models have been published to predict the future spread and severity of *D. septosporum* (e.g., Watt et al. 2011, Möykkynen et al. 2017). These models are useful in determining the likely pattern of spread and regions where severity may increase in the future, along with predicting the effects of human interventions on the likely spread of the pathogens.

Using a model derived from a cell-based mechanistic approach, Möykkynen et al. (2017) simulated the spread of *D. septosporum* in Europe, assuming infected seedlings were the main sources of infective material, with further spread to trees of any age in the forest after planting; hence, the affected nurseries were assumed to be points of entry for the pathogen. Changing climate was included in the model utilizing ecoclimatic index maps for *D. septosporum*, derived from CLIMEX, using climate data from 1960 to 1990 as the baseline and future climate predicted using the IPCC (2007) scenario A1B.

This approach was supported by the proposal that the upsurge in DNB in the UK occurred following the transport of young pines between regions in the UK, resulting in the long-distance movement of more virulent strains of *D. septosporum* through the country (Mullett et al. 2017, Ennos et al. 2020).

Simulations derived from the model suggested that DNB will increase in incidence and severity in more northerly regions of Europe, whilst a decrease will occur further south, including in the Balkans peninsula. Some of the regions where disease is likely to increase include major pine-growing countries, such as Sweden and Finland. These predicted changes were related to the likely increases in rainfall and temperature during spring and summer months, generating the humidity required for spore dispersal and infection, as suggested elsewhere (Gadgil 1974, 1977, Woods et al. 2005, Dvorak et al. 2012, Welsh et al. 2014, Woods et al. 2016).

CONCLUSIONS

It is clear that, without the immediate imposition of more strict standards for the import and export of plants and plant materials on a global scale, invasions of potentially damaging alien pests and pathogens will continue. Under current global trade rules, it is difficult to impose tighter controls, due to the over-riding requirement for free trade whenever possible. Some steps in the direction of better controls have been imposed, however, such as the requirements for heat treatment of wood and timber (International Standards for Phytosanitary Measures No. 15 [ISPM 15]) to control possible transport of *B. xylophilus* and other wood-inhabiting organisms, and the far more stringent rules outlined in ISPM 36, which, partly at least, transfers responsibilities for exporting 'clean' stock to the producing nurseries and regions. Many individual states are tightening up their plant import regulations too, in order to improve biosecurity.

Overall, climate change appears to be making the issues caused by invasive pests and pathogens worse than previously anticipated, although the activity of pathogens may reduce in certain regions, due to climatic changes that alter the suitability of different ecological zones for establishment and infections to occur (Sturrock et al. 2011, Burgess et al. 2017, Tank et al. 2021).

Considerable hope, however, lies in the enormous genetic 'power' in plants: humans could, given the political will, establish selection and breeding programmes that will ultimately enable us to maintain plantings of trees with far greater tolerance of changing climate and both endemic and invasive pests and pathogens (e.g., Sniezko 2006, Budde et al. 2016). Harnessing the 'omics' revolution will enable the application of marker assisted breeding, based on a much more thorough understanding of the physiological and molecular processes in plants that result in resistance to both biotic and abiotic problems. For example, a breeding approach was applied over many years in order to develop genotypes of *Castanea* with considerable resistance to *Cryphonectria parasitica* and in the past 15 years, clones of these resistant trees have been planted in the east of North America (Clark et al. 2019): it took over 100 years to get from the first record of *C. parasitica* and sweet chestnut canker in the USA to a point where resistant trees with similar growth forms to the American sweet chestnut could be planted out. There are also clones of *Ulmus* hybrids available that show resistance to the Dutch elm disease pathogen, *O. novo-ulmi*, with little sign of the resistance breaking down, as can happen when single or oligomeric resistance is deployed (e.g. Smalley and Guries 1993, Solla et al. 2005). Of course, with state-of-the-art technologies, the time line for introducing truly resistant clones of any tree species may be reduced considerably, as indicated in recent research on ash dieback, for example (Cross et al. 2017, Sambles et al. 2017, Stocks et al. 2019, Nemesio-Gorriz et al. 2020).

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Conflicts of Interest

The authors declare no conflict of interest.

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