

Pathogens on the Move: A 100-Year Global Experiment with Planted Eucalypts

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Co-evolved plant pathogens play an important role in shaping natural ecosystems. However, plants used in agriculture and forestry have been distributed globally, and their associated pathogens have moved with them. Eucalypts constitute the largest component of global hardwood plantations, and they are increasingly plagued by numerous pathogens, all of which are inconsequential in the native forests. Eucalypts provide a particularly interesting model to study tree diseases because plantations have been established in countries where these trees are exotic but also in Australia adjacent to native eucalypt forests. These situations present opportunities for pathogen movement between the two systems. We present seven different scenarios considering pathogen movement, important disease epidemics, and biosecurity risks, illustrated with examples of well-known eucalypt pathogens and research largely from our laboratories. The overview shows that vigilant biosecurity is required to protect the biodiversity of native forests and the sustainability of eucalypt plantations.

Keywords: biosecurity, leaf pathogens, population genetics, Teratosphaeriaceae, Cryphonectriaceae, plants for planting, cryptic species, quarantine

Eucalyptus spp. native to Australia, were introduced to the rest of the world soon after European colonization and were widespread by the end of the nineteenth century (Doughty 2000). These trees were initially planted as curiosities, but many species naturalized and have become a part of the landscape in many regions of the world, to the extent that they are considered invasive in some situations (Richardson 1998, Turnbull 2000). Their ability to grow in many different, and in some cases harsh, environments and to flourish when supplied with adequate nutrients and water has made them useful for shade, pulpwood, timber, and fuel wood production, as well as for stabilizing degraded lands (King 1943, Doughty 2000, Turnbull 2000).

The first commercial exotic eucalypt plantations appeared early in the twentieth century. However, it is only in the last 30–40 years that there has been a rapid expansion of the areas under afforestation, particularly in the tropics and the Southern Hemisphere (Iglesias-Trabado and Wilstermann 2008). In 1990, there were 8 million hectares (ha) of exotic eucalypt plantations (Turnbull 2000), with the area increasing to around 20 million ha by 2008 (Iglesias-Trabado and Wilstermann 2008). Extensive trials in different regions have led to the development of hybrid species and clonal forestry using superior genotypes. Today, molecular genetic tools such as marker-aided selection (Grattapaglia et al. 2012), facilitated by the recently published *E. grandis*

genome (Myburg et al. 2014), are increasingly being used in tree-breeding programs. The future of plantations will be enhanced and directed by science.

Eucalypt plantations, both within their native range and as exotics, provide a unique model to investigate processes such as natural pathogen movement and gene flow, selection pressure, host shifts, human-mediated pathogen introductions, and globally pressing issues such as forest biosecurity. *Pinus radiata* has also been extensively planted as an exotic in the Southern Hemisphere; however, its original source was from only a few small populations in California (Moran et al. 1988), and it has been planted extensively as an exotic in the Southern Hemisphere in regions without related native conifers (Burgess and Wingfield 2001). Consequently, the opportunities for pathogen host shifts are much more limited. In this review, we compare and contrast the roles of native and introduced pathogens in native eucalypt forests and exotic plantations. In order to simplify and discriminate between these closely related but very different situations, we use the terminology presented in box 1.

Natural ecosystems are in balance with their native pathogens. In this regard, there is a constant “arms race,” with mutations leading to increased virulence in a pathogen matched by similar changes in the resistance of the host plant (Burdon et al. 2013). In natural ecosystems, the flora is mixed in composition and age; pathogens adapted to a

Box 1. Terminology used to delineate endemic from introduced scenarios.

Native forests: eucalypt forests within their native range (in Australia)

Native plantations: plantations of eucalypts within their native range

Native pathogens: pathogens endemic to native eucalypt forests

Exotic plantations: plantations of eucalypts outside their native range

Endemic forests: forests in countries where eucalypts are exotic

Endemic pathogens: pathogens endemic to a country where eucalypts are exotics

Introduced pathogens: pathogens that have been moved between countries

particular host or life stage are limited in impact by the availability of suitable resources. Human activities have disturbed this natural relationship between trees and their natural enemies. By exposing exotic eucalypts (and, in fact, any exotic tree species) to endemic pathogens, we have, to some extent, artificially driven the evolution of these pathogens.

Diseases can develop in newly established exotic plantations only when suitably adapted pathogens are also introduced or where endemic pathogens move onto the newly exposed host (host shift; Slippers et al. 2005). Classic examples of both these scenarios can be found in exotic eucalypt plantations, and these are explored in more detail below. Eucalypt plantations have also been established in Australia, and these are typically adjacent to native forests containing eucalypts, although not necessarily of the same species. Within Australia, there is also the example of the Western Australian (WA) plantation industry, which was established with *E. globulus*, a species native to southeastern Australia; effectively, these are also exotic plantations.

Most of the examples used in this review emerged from many years of collaborative investigations on the population genetics of important eucalypt pathogens between our research teams in Australia and South Africa while also benefitting from projects with colleagues globally. We consider seven scenarios: (1) native pathogens in native forests, (2) introduced pathogens in native forests, (3) introduced pathogens in exotic plantations, (4) host shifts where endemic pathogens have adapted to infect exotic plantation trees, (5) native pathogens in native plantations in Australia, (6) introduced pathogens of exotic plantation trees moving into endemic forests outside Australia, and (7) introduced pathogens in native eucalypt plantations (figure 1).

Scenario 1: Native pathogens in native eucalypt forests

Most Australian forests naturally support multiple species of eucalypts. These are generally the dominant tree species, although in the temperate rainforests of Tasmania and the tropical rainforest in the north of the country, they are interspersed with trees from numerous other genera and families. Unless these forests have regenerated following a major catastrophic event, such as an intense bushfire or clear-fell logging, they comprise uneven age classes as well

as mixed species. These trees are not highly susceptible to any particular pathogen throughout their lifecycle. The genetic differences and age (physiological) structure existing within native forests create the temporal and spatial variability that greatly reduces the potential impact of endemic pathogens.

In more dense forests, regeneration can occur only after gap creation because of a lack of light reaching the forest floor. In eucalypt forests, fire and drought are the main drivers of gap creation, although in undisturbed forests, older trees accumulate rot pathogens that eventually lead to tree death and the creation of small gaps. Much of the Australian vegetation is adapted to fire, and the regeneration layer quickly responds postfire, eventually resulting in communities of similar structure and diversity (Gill 1975). Alternatively, drought can have long-term impacts on forest structure (Matusick et al. 2016), leading to a change in species composition and diversity.

Fungal pathogens within a healthy ecosystem play an integral role in eliminating weak and unfit individuals (Castello et al. 1995). Especially important in this role are the numerous, often endophytic, latent pathogens, such as the members of the Botryosphaeriaceae for which disease expression is often associated with host stress (figure 2g; Slippers and Wingfield 2007). Pathogens are also thought to moderate species occurrence and distribution, especially in the regeneration layer (Bever et al. 2012, Laliberté et al. 2015).

Forestry management can result in disease outbreaks. For instance, although fungi causing leaf diseases and stem cankers, such as those in the genera *Teratosphaeria*, *Mycosphaerella*, *Holocryphia*, and *Neofusicoccum*, are commonly found in native eucalypt forests, there are no reported cases of these fungi causing significant disease problems in undisturbed forests (Park et al. 2000). However, in heavily logged regrowth forests, disturbance has resulted in localized outbreaks of native pathogens (Park et al. 2000). Similarly, in selectively logged native forests, *Armillaria* root rot is the most important pathogen. Its spread is associated with infected stumps remaining after an area has been logged. In these situations, it causes typical dieback symptoms, reduced growth, and sometimes tree death (Brown 2000).

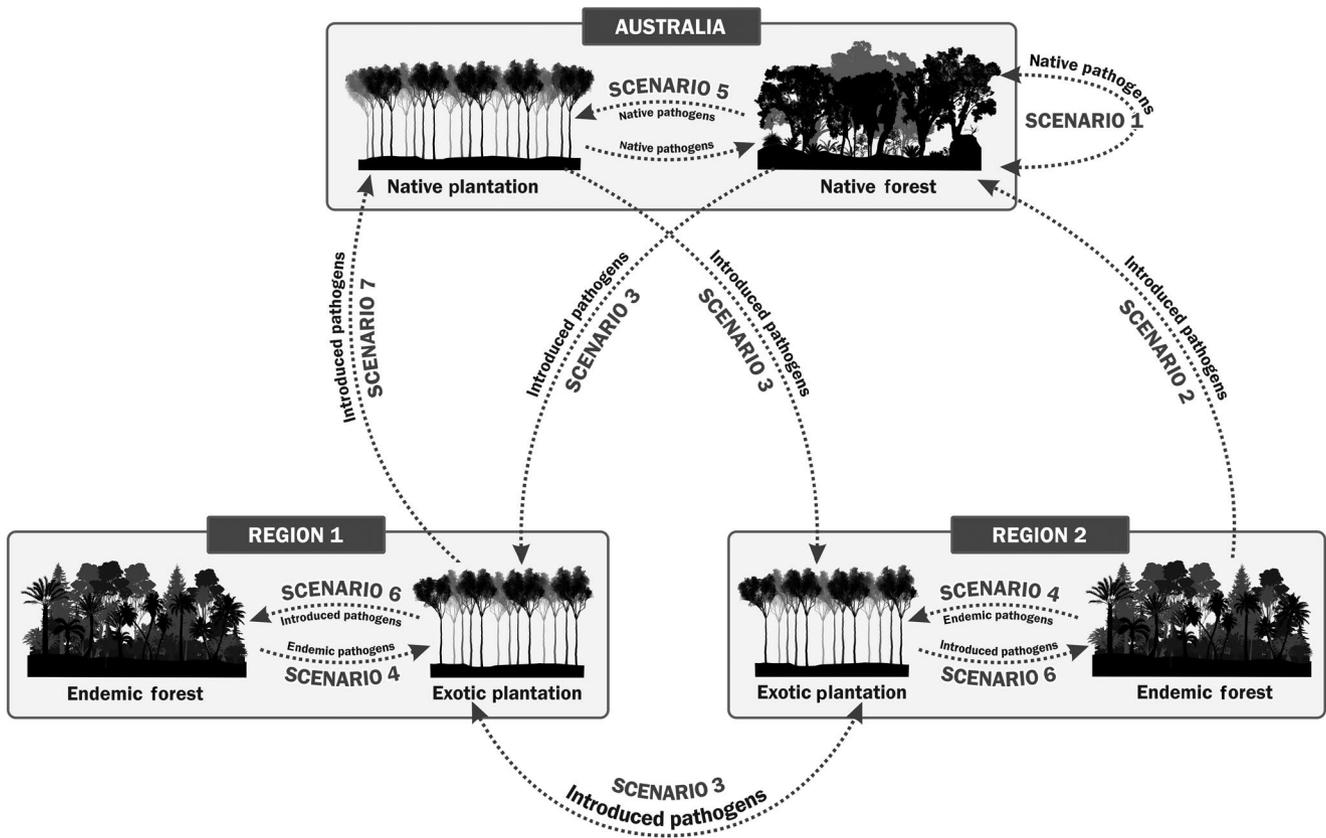


Figure 1. Seven scenarios detailing the potential and known interactions between native forests and eucalypt plantations within their native range and planted as exotics. Region 1 and 2 represent generalized countries or regions where eucalypts have been planted as exotics.

Scenario 2: Introduced pathogens in native eucalypt forests

Worldwide, there are numerous examples of destructive disease epidemics resulting from the introduction of aggressive pathogens to new environments where the host trees have little or no resistance. Well-known examples, as have been reviewed by Loo (2009), include chestnut blight caused by *Cryphonectria parasitica*, Dutch elm disease caused by *Ophiostoma ulmi* and *O. novo-ulmi* in Europe and North America, and sudden oak death in North America caused by *Phytophthora ramorum*. In Australia, the single most devastating introduced pathogen is *Phytophthora cinnamomi*, which kills not only some eucalypts but also numerous mid- and understory species in many plant families. The biology and impact of this pathogen in Australia have been the topic of numerous reviews (e.g., Weste 1986) and are consequently not considered here. All these invasive tree pathogens have had irreversible ecological impacts (Shearer et al. 2007, Loo 2009).

The most serious pathogen introduced into Australia in recent years is the rust *Puccinia psidii*. This pathogen has been referred to by several common names such as guava rust, eucalypt rust, or myrtle rust, depending on the host adaptation of various genotypes of the same species (Glen

et al. 2007). *Puccinia psidii* was first detected in Australia in 2010 and has subsequently spread along the eastern sea-board of the country (Carnegie et al. 2016). Although many *Eucalyptus* spp. have been shown in pathogenicity trials to be susceptible to the single genotype of the rust occurring in Australia, damage in the native ecosystem, while widespread, has been confined to other genera in the Myrtales (Giblin and Carnegie 2014). As an even-aged monoculture, native eucalypt plantations could provide the selection pressure required for this strain to shift onto eucalypts and potentially become more pathogenic.

Scenario 3: Introduced pathogens in exotic plantations

Early exotic eucalypt plantations were relatively free of diseases. This has been referred to as a “honeymoon period.” These disease-free situations have lasted for variable time periods, depending on the volume of trade in living plants and seed and on the speed at which their co-evolved endemic pathogens were introduced from Australia (Crous 1998, Taole et al. 2015). Concomitant with increasing areas of plantation development and larger areas of plantations being established off site, there has been an increase in the number of diseases associated with these plantations



Figure 2. Symptoms of diseases on eucalypts. (a) Defoliation of *Eucalyptus grandis* x *E. camaldulensis* hybrid trees caused by *Teratosphaeria viscidus*. (b) *Teratosphaeria destructans* infection on *E. urophylla* leaves showing profuse production of spores on the abaxial leaf laminae. (c) *Teratosphaeria nubilosa* leaf disease on *Eucalyptus globulus*. (d) Defoliation in the lower canopy of trees caused by *T. nubilosa* in *E. globulus* plantations; the unaffected trees on the right side of the image were sprayed with fungicide to control disease (Photo G. Hardy). (e–f) Lesions on the stem of *E. urophylla* caused by *Teratosphaeria zuluensis*. In the early stages of infection, lesions are discrete (e), and they later coalesce (f) to form large diffuse cankers (g). Large bark canker with discolored cambium exposed on *E. pellita* caused by a *Lasiodiplodia* sp. (h–i). Yellow pustules of the myrtle rust *Puccinia psidii* on (h) fruits of *Psidium guajava* and (i) young leaves of *E. grandis* (j–l). The stem of *E. grandis* tree with (j) a large canker caused by *Chrysosporthe cubensis* that can result in (k) girdled stems and epicormic shoots developing below the cankers. (l) A cross-section of the base of a canker caused by *C. cubensis* on an *E. grandis* tree.

(Wingfield 1999, Wingfield et al. 2001, 2015, Burgess and Wingfield 2002).

The majority of introduced pathogens of exotic eucalypts are leaf pathogens. These have most likely been introduced

with germplasm, either with seed or chaff commonly found together with seed, or as the endophytes of vegetative material (Burley 1987, Jimu et al. 2015) that has been distributed to meet the demands of the forestry companies for superior

genetic planting stock. Soil has rarely been transported with plants; consequently, there have been no reported root diseases, other than oomycetes, caused by introduced pathogens in exotic eucalypt plantations. Oomycetes such as *P. cinnamomi* were already present as invasive introduced pathogens prior to the establishment of eucalypt plantations (Burgess et al. 2016).

The most commonly occurring leaf and shoot pathogens of eucalypts are members of the Mycosphaerellaceae and Teratosphaeriaceae. These fungi cause diseases known collectively as Mycosphaerella leaf diseases (MLD) and Teratosphaeria leaf diseases (TLD; Hunter et al. 2011). More than 150 species have been associated with MLD and TLD (see Hunter et al. 2011 for an extensive review). Interestingly, the majority of these species were first described from countries outside Australia, although with time and effort, many have now been found in Australia. Researchers interested in these diseases believe that the species responsible originate in Australia because they have co-evolved with their hosts.

Most species causing MLD and TLD are minor pathogens. In many cases, multiple species can be recovered from a single lesion including lesions caused by insects and they could be saprophytes existing as endophytes for long periods of their life cycles (Maxwell et al. 2003). However, of all the known species, there is one group of closely related species responsible for all the major disease problems (figure 2a–d). These include *T. nubilosa* and *T. cryptica* on *E. nitens* and *E. globulus* planted in temperate climatic zones (Mohammed et al. 2003, Hunter et al. 2009, Pinkard et al. 2010) and *T. destructans*, *T. pseudoecalypti*, *T. suttonii*, and *T. viscidus* on *E. grandis*, *E. camaldulensis*, and *E. urophylla*, as well as their hybrids in the tropics and subtropics (Andjic et al. 2007, 2010a, 2011, Taole et al. 2012). *Teratosphaeria nubilosa* and *T. suttonii* have a global distribution where they have caused various levels of damage. *Teratosphaeria cryptica* and *T. eucalypti* are known only in Australia and New Zealand (Dick and Gadgil 2009), and *T. viscidus* is known only in Australia (Andjic et al. 2010a). Until recently, *T. pseudoecalypti* was known only in Australia (Andjic et al. 2010a), but it has now emerged as the cause of a serious disease in South America (Ramos and Perez 2015). *Teratosphaeria destructans* was first found in Indonesia and for many years was known only in Asia (Wingfield et al. 1996, Andjic et al. 2011). However, it has recently been recorded in South Africa (Greyling et al. 2016). A report of this species in the north of Australia (Burgess et al. 2007) has recently been attributed to a new closely related species (see box 2). During the course of the past 10 years, many *Teratosphaeria* species have been subjected to genetic analyses, including populations collected from both within their native range in Australia and from exotic plantations.

Within its native range in Australia, *T. nubilosa* can be clearly separated into three genetically isolated groups, which do not hybridize, even when they are co-located (Pérez et al. 2012). Group A is native to northern New South Wales—colonizing native *E. dunnii* and introduced *E.*

globulus. Group B is widely distributed in both Tasmania and Victoria, and its exact origin could not be determined. Group C is native to Victoria—colonizing native and commercially propagated *E. globulus*. Group B has been introduced into New Zealand and WA, where the low observed allele and genotypic diversity reflects that of a founder population (Pérez et al. 2012). Conversely, representatives of group C have been introduced to most *E. globulus* plantations worldwide, with confirmed presence in South Africa, Ethiopia, Kenya, Tanzania, Spain, Portugal, Brazil, and Uruguay (Hunter et al. 2008, 2011, Pérez et al. 2012). With the exception of those in South Africa, all of the introduced populations have very few multilocus haplotypes (MLH). The type isolate of *T. nubilosa* resides in group C, and as a consequence of this study, group B isolates have been described as a new species known as *T. pseudonubilosa* (Pérez et al. 2014). Although *T. nubilosa* is already widespread globally, care must be taken not to also introduce *T. pseudonubilosa* into new environments.

Similar to the situation with *T. nubilosa*, *T. suttonii* is native to eastern Australia and has been spread globally with the expansion of the eucalypt plantation industry. It has a broad host range and is not considered a major pathogen, but it can cause leaf blight in young seedlings under conducive environmental conditions (Taole et al. 2012). Native populations of *T. suttonii* in eastern Australia show strong population structure and limited gene flow. In contrast, introduced populations from South Africa, Vietnam, China, Indonesia, Florida, and Uruguay all bear the signature of repeated introductions either directly from Australia or from intermediary countries (Taole et al. 2015). Historical gene flow was from Australia, and although self-recruitment was dominant in all populations, there was evidence for contemporary gene flow, with South Africa being the most common source and Uruguay the most common sink population (Taole et al. 2015).

The impact of *T. cryptica* is often in Australian plantations and is similar to that of *T. nubilosa*. However, unlike *T. nubilosa*, which has a very restricted host range, *T. cryptica* has a very broad host range (Crous 1998). It is also widespread, although not as a major pathogen, in native forests. *Teratosphaeria cryptica* causes different symptoms on different hosts but almost always results in a characteristic crinkling of the leaves. The pathogen has been collected along the entire eastern seaboard of Australia and Tasmania and is considered as native to the whole region. Curiously, although *T. nubilosa* has been spread around the world, the only region where *T. cryptica* has been recorded outside its native range is New Zealand. Within Australia, populations of *T. cryptica* show strong structure and isolation by distance. Some contemporary gene flow has been observed, and this was attributed to movement of the pathogen during the establishment of the eucalypt plantations where seedlings were transported from nurseries to different regions of Australia. In WA, *T. cryptica* is widespread and can seriously hinder the regeneration of native species such

Box 2. Plants for planting: The case of *Teratosphaeria destructans*.

Overwhelming evidence for the movement of pests and diseases between continents and countries illustrates the basic failure of quarantine measures. This is either due to lack of resources or poorly regulated pathways (Liebhold et al. 2012). The first reports of a new pathogen in one region are commonly followed in rapid succession by reports for the same pathogen in other regions. This suggests that the forestry companies are unwittingly moving these pathogens with germplasm. The destructive shoot and leaf blight pathogen *T. destructans* provides an apt example. The pathogen was first found (and described) in Indonesia in 1995 (Wingfield et al. 1996), and it subsequently appeared in Thailand, Vietnam, and all eucalypt-growing provinces of China (Andjic et al. 2011) over a relatively short period of time. Its recent appearance in South Africa (Greyling et al. 2016) represents the first report outside of Asia and implies that it is likely to continue to move globally. Microsatellite analysis revealed only six multilocus haplotypes among isolates from Indonesia, but extraordinarily, only one haplotype is present in all other regions. This spread of a single clone of *T. destructans* throughout Asia provides good evidence of the human-mediated movement of the pathogen (Andjic et al. 2011).

as *E. marginata* and *E. gomphocephala*. However, the genetic diversity in WA is relatively low, and we believe it has been introduced to this region.

For all *Teratosphaeria* leaf pathogens of eucalypts so far examined (and where the origin is known to be Australia), populations are characterized by structure, population differentiation, and isolation by distance within the native range of the pathogen in Australia. The diversity of the introduced populations of these pathogens varies and includes examples of very low allele and genotypic diversity to those with high levels of diversity. This appears to be linked to the maturity or age of the plantation industry in the respective locations (Taole et al. 2015). For example, populations in South Africa and New Zealand generally have high diversity suggesting numerous introductions over the 100 years of the industry. This is in contrast to the lower levels of diversity in countries having relatively young industries such as Uruguay, with an approximately 15-year-old industry. The regular reports of these pathogens in new regions are evidence of the lack of regulation in the trade of seed and other germplasm.

Scenario 4: Endemic pathogens infecting exotic plantation trees (host shifts)

The 20 million ha of genetically uniform exotic eucalypt plantations have exerted considerable selection pressure on endemic pathogens to “jump” hosts and infect eucalypts (Wingfield et al. 2015). Exotic eucalypts are commonly planted in close proximity to endemic and related plant species such as those in other families, genera of the Myrtales. These plantations are also often established on land recently cleared of endemic vegetation but where the understory still persists, providing numerous niches for pathogens. There are now growing numbers of well-studied host shifts from endemic Myrtales to exotic eucalypts (Wingfield et al. 2010). In most of these cases, the diversity and distribution, as well as the purported origins, of the pathogens have been verified using molecular genetic tools such as microsatellite markers.

The most striking example of a pathogen host shift to eucalypts is the rust fungus *Puccinia psidii* (figure 2h–i; Glen et al. 2007). The rust has a broad host range and is found on numerous species of endemic Myrtales in South and Central America (Giblin and Carnegie 2014), although the original

endemic host of the genotype that underwent a host shift to eucalypts in South America is yet to be identified (Graça et al. 2013). In general, the young leaves and buds of host plants are most susceptible to infection, resulting in stunted multi-stemmed trees and, in extreme cases, death. Following the first records of *P. psidii* in Brazil, this pathogen has been recorded in Florida, Hawaii, Japan (Glen et al. 2007), and, more recently, Australia (Carnegie et al. 2010), China (Zhuang and Wei 2011), South Africa (Roux et al. 2013), and Indonesia (McTaggart et al. 2016). The same dominant “invasive” genotype, as determined by microsatellite markers, is found in Australia, Hawaii, and Indonesia, but this is not the same as the genotype affecting eucalypts in Brazil (Machado et al. 2015, McTaggart et al. 2016) or South Africa (Roux et al. 2016). The movement globally of a single dominant genotype is likely due to the so-called bridgehead effect (Garnas et al. 2012, Wingfield et al. 2015), in which successive introductions of a pathogen lead to inoculum build-up and an increased likelihood of subsequent introductions. There must be many native genotypes of *P. psidii* in South America, and although intensive sampling might reveal the origin of the current invasive genotypes, this does not detract from the most important issue, which is that other genotypes of the pathogen are also likely to spread globally.

The Cryphonectriaceae represent another group of highly virulent pathogens of eucalypts that have evidently emerged through host shifts. Cryphonectria canker, caused by the pathogen then known as *Cryphonectria cubensis* (now *Chrysosporthe cubensis*), was one of the first serious diseases to have emerged as a serious threat to intensively propagated eucalypts outside their native range (figure 2j–k). This problem first emerged in Brazil, giving rise to the rapid emergence of vegetative propagation of eucalypt hybrids resistant to this disease (Wingfield 2003). Studies on these fungi during the course of the past 30 years reveal the Cryphonectriaceae causing eucalypt canker diseases reside in a phylogenetic clade distinct from the notorious canker pathogen of chestnuts, *Cryphonectria parasitica* (Gryzenhout et al. 2004). The most aggressive of these now reside in the genus *Chrysosporthe* and include *C. cubensis*, *C. deuterocubensis*, *C. austroafrica*, and *C. doradensis* (Gryzenhout et al. 2004, van der Merwe et al. 2010). All of

these fungi are endemic on the Myrtales in the areas where they are found, and they have evidentially undergone host shifts from these endemic plants to infect exotic eucalypts in plantations. Interestingly, *C. deuterocubensis* has been recovered in Australia (reported as *C. cubensis*), isolated from both exotic *Tibouchina heteromalla* in Cairns Botanical Gardens in tropical Queensland (Pegg et al. 2010) and from *E. marginata* roots in WA (Davison and Coats 1991). However, to date, there are no reports of the canker disease on eucalypts in Australia.

Much like the case for eucalypt canker pathogens in the Cryphonectriaceae, the stem canker pathogens *Teratosphaeria zuluensis* and *T. gauchensis* represent another example of a pathogen appearing in exotic eucalypt plantations at several locations more or less simultaneously (figure 2e–g). These fungi cause severe cankers on the young green stem tissues of many eucalypts (Wingfield et al. 1997) and were originally thought to represent a single species. Phylogenetic and microsatellite-based population genetics studies have shown them as distinct taxa with distinct global distributions (Cortinas et al. 2006b). *Teratosphaeria zuluensis* is found in Asia (Cortinas et al. 2006a, Chen et al. 2011a), *T. gauchensis* in South America (Cortinas et al. 2011) and Europe (Silva et al. 2015), and both species in Africa (Cortinas et al. 2010, Jimu et al. 2016a, 2016b). Intriguingly, neither species has been found in Australia. However, a very closely related species, *T. foliensis*, was described from leaves in Queensland (Andjic et al. 2010b). The presence of a species with a common ancestor in Australia and their host specificity toward eucalypts suggest that both *T. zuluensis* and *T. gauchensis* are native to Australia and will eventually be found there. If this did happen, then these species would no longer represent a host shift but rather introduced pathogens originating in Australia (scenario 3).

In addition, to these dramatic examples of host shifts, numerous generalist pathogens can use exotic eucalypts as a carbon source (Park et al. 2000). Necrotrophic leaf pathogens with global distributions, such as *Alternaria* spp., can even cause defoliation in stressed trees, especially if humidity is high (Park et al. 2000). The movement of endemic pathogens onto exotic trees is more evident if the exotic tree species is phylogenetically related to the endemic plant communities (Vacher et al. 2010). Therefore, when eucalypts are exotic in regions with native Myrtales, it is likely that over time, many endemic pathogens will adapt to this new host.

Scenario 5: Native pathogens in native plantations in Australia

In Australia, plantations and native forests are in close proximity, and there is no barrier to pathogen gene flow in either direction (Burgess et al. 2006). This proximity, coupled with even-aged monocultures, provides a selection pressure similar to that which drives host shifts of endemic pathogens toward exotic plantation trees (scenario 4). In the case of eastern Australian native eucalypt plantations, there have been periodic reports of native pathogen outbreaks

and of plantation collapses. Where inappropriate eucalypt species have been planted and/or where selected sites are ill suited to these species, the plantations have failed to develop beyond the juvenile stage and have commonly collapsed (Carnegie 2007a, 2007b, Whyte et al. 2016). Such situations occur as a consequence of constant defoliation due to pests, pathogens, or abiotic stress, because of which, with time, leaves become increasingly smaller to a point at which trees become depleted of resources and die (Mitchell et al. 2015, Whyte et al. 2016). Plantations of the eastern Australian species *E. globulus* in WA provide an intriguing situation explored further in box 3.

The eucalypt plantations in different climatic zones of Australia have experienced different problems. For example, in the temperate climate of Tasmania, plantations of the native *E. globulus* were replaced with *E. nitens* because constant TLD resulted in trees remaining in the juvenile leaf stage (Mohammed et al. 2003). Similarly, in the Green Triangle Plantation Estate (bordering Victoria and South Australia), TLD is seasonally severe in some regions (Carnegie et al. 1994, Barber et al. 2008). In New South Wales, off-site plantings of various *Eucalyptus* spp. have been totally decimated by a suite of native pathogens, most notably *T. suttonii* (Carnegie 2007a, 2007b). The plantations in southern and central Queensland were established in the early 2000s with predominantly *E. grandis*, *E. dununii*, and *E. camaldulensis*. This establishment coincided with a decade of drought (1995–2007) and low growth rates (Whyte et al. 2016). However, as the drought eased in 2007 and then ended in 2009, TLD became very common. In this region, existing taxa trials and newly established trials were rated for their tolerance to TLD, and in 2009, it appeared as if some hybrids, especially those with *E. pellita*, were tolerant. But within a year, even the hybrids collapsed because of the accumulation of native pathogens causing TLD, and it was necessary for the plantation industry to abandon these plantings (Andjic et al. 2010a). A suite of *Teratosphaeria* spp., including *T. suttonii*, *T. viscidus*, and what was thought to be *T. eucalypti*, caused the disease. Previously, *T. eucalypti* had been associated with only irregular, patchy disease outbreaks in Australia and New Zealand (Andjic et al. 2010a). After a detailed morphological and phylogenetic study, the pathogen in temperate regions was shown to be *T. eucalypti*, whereas in the subtropics of Queensland, a new cryptic species, *T. pseudoecalypti*, drove the disease epidemic (Andjic et al. 2010a). The only effective management of these and other native pathogens in Australia is to ensure appropriate silviculture, to establish taxa and provenance trials to select for disease tolerance, or to plant “nonnative” natives or hybrids.

Scenario 6: Introduced pathogens on exotic eucalypts moving into endemic forests

Once an introduced pathogen is established in a plantation of exotic trees, it can move freely into adjacent endemic forest where it can become naturalized or even invasive.

Box 3. Exotic “native” plantations with native “introduced” pathogens: The West Australian bluegum industry.

Disease risk in plantations is increased largely because of the reduced genetic variation, the age, and the often-nonideal site conditions (Potts and Pederick 2000). Native eucalypt plantations in eastern Australia have succumbed to numerous native pathogens. However, Australia is a large continent effectively divided by the central desert. Western Australia (WA) has been geographically isolated from eastern Australia for 40,000 years (Boland et al. 1984). This isolation should have enabled the establishment of a disease-free plantation industry in WA using an eastern states species, *E. globulus*, particularly when supported by the application of interstate quarantine. This should have avoided introducing numerous pathogens common in the eastern *E. globulus* plantations. However, this has not been the case. In 1994, *T. cryptica* was the only serious pathogen in the *E. globulus* plantations in WA (Carnegie et al. 1997). However, by 2003, 10 species of pathogens had been recognized (Maxwell et al. 2003), and this number increased to 13 in 2008 (Jackson et al. 2008) and to 21 in 2014. During this time, there was a rapid expansion in the plantation industry from only a few hundred hectares (ha) in the mid-1980s to over 300,000 ha today (ABARES 2012). Some of these pathogens may already have been present in WA, and the plantation estate acted as a sentinel, drawing them out of the native forests. However, all the microsatellite studies to date on *T. nubilosa*, *T. suttonii*, and *T. cryptica* have provided clear evidence that the pathogen populations in WA plantations bear the signature of a founder effect: they have few multilocus haplotypes (MLH) and limited diversity. *Teratosphaeria nubilosa* populations from WA consist of just a few MLH that can be linked to one region in Victoria (Pérez et al. 2012), whereas *T. suttonii* has three MLH linked to southern QLD (Taole et al. 2015). *Teratosphaeria cryptica* has been present in WA for longer than the other species, and it has a wider host range. However, the MLH from native forests belongs to a different structure group from those rare isolates found in *E. globulus* plantations in WA.

The plantation forestry industry in WA is young, and there have been forest health researchers working alongside this industry since its establishment. Consequently, it has been possible to follow the emergence of *Mycosphaerella* leaf diseases (MLD) and *Teratosphaeria* leaf diseases (TLD), as well as the pathogens associated with these diseases. Their emergence coincided with an unprecedented requirement for nursery stock for planting due to the rapid expansion of the industry in the early 2000s. Many of the seedlings were purchased in eastern Australia and transported to WA. The seedlings were checked and sprayed before transport, but the inability to detect sublethal infections, or infectious propagules trapped in the potting mixture, was the most probable cause of new species introductions (see box 2).

However, there have been very few studies on this topic. One example has been reported from Uruguay, where the known eucalypt endophyte *Neofusicoccum eucalyptorum*, native to Australia, was isolated from both exotic eucalypts and endemic Myrtales (Pérez et al. 2009, 2010). Similarly, *Neofusicoccum australe*, a common endophyte from WA (Burgess et al. 2005, Taylor et al. 2009), has been recovered from endemic *Syzygium* trees in South Africa (Pavlic et al. 2007). The consequences of these introductions remain unclear but they deserve to be monitored and studied.

Scenario 7: Introduced pathogens in native plantations

Although native plantations in Australia have been seriously damaged by native pathogens, there is no evidence of new introduced eucalypt pathogens (those arising on exotic plantations) on plantations in Australia. These pathogens have been moved around the world in the exotic setting; however, the strict quarantine regulations in Australia have so far been effective in preventing the introduction of these pathogens. An exception arose in 2010 when, as we documented above, *P. psidii* appeared in Australia. However, although the introduced strain has been shown to infect eucalypts in pathogenicity trials (Morin et al. 2012, Carnegie et al. 2016), there are no reported infections in plantations or native forests. Nevertheless, its introduction and establishment over a wide area in a short space of time show that the pathways

for introduction are open regardless of strict quarantine measures.

Future prospects

Future prospects for establishing and maintaining healthy plantations require an understanding of the transmission pathways of pathogens, enhanced quarantine and biosecurity measures, and the use of early warning systems such as monitoring sentinel plantings. Healthy forests—and, to a great extent, individual tree species within these forests—are rarely severely affected by fungal pathogens. Conversely, plantations can act as “magnets” for pathogens. The honeymoon period, a time when plantations could be grown relatively free of pests and pathogens, is clearly over. Previously, this disease-free period lasted several decades, but since the turn of the century, this period has become increasingly shorter because new plantation industries establishing in new countries are quickly infected. This implies that the pathogens are being moved with the germplasm used to establish these plantations, and this theory is supported by molecular evidence (Wingfield et al. 2013, Jimu et al. 2015). Ironically, it is the people whose interest it is to produce healthy trees (forestry companies) who are strongly influencing the distribution of pests and pathogens.

Plants for planting is seen as the major pathway for pathogen dissemination (Liebhold et al. 2012, Migliorini et al. 2015). Because many plant pathogens have endophytic

Box 4. Eucalypt canker and leaf pathogens in contrast.

Eucalypt leaves are naturally well defended against pathogen attack by their thick, waxy cuticles and densely packed epidermal and palisade layers on both their abaxial and adaxial surfaces (Smith et al. 2007). However, leaf pathogens, such as those causing *Teratosphaeria* leaf diseases (TLD) and *Mycosphaerella* leaf diseases (MLD), generally infect juvenile leaves, often before they are fully expanded (Park and Keane 1982), before the waxy cuticle is formed, and when defenses are low. Another pathway for infection is through wounds made by chewing insects (Whyte et al. 2011).

The pathogens of eucalypt leaves have emerged over long periods of co-evolution and have developed mechanisms to overcome these leaf defenses. In exotic environments, the leaf pathogens causing MLD and TLD have been introduced with the eucalypt hosts from Australia. The only non-Australian example is *T. destructans*, which was most likely a native pathogen of *E. urophylla* in Timor. Conversely, there are several well-documented cases of canker pathogens on endemic Myrtales undergoing host shifts to infect exotic eucalypts. Important examples include the well-studied species of *Chrysosporthe* but also numerous examples of less pathogenic “latent” canker pathogens and endophytes in the *Cryphonectriaceae* (Chen et al. 2011b, Vermeulen et al. 2013) and *Botryosphaeriaceae* (Slippers et al. 2009, Pérez et al. 2010). From this emerging evidence, it would appear that the bark and stems of eucalypts are less well defended than their leaves.

or biotrophic life stages, they can easily slip through the quarantine “net” in or on asymptomatic plants or alternatively in seed or the chaff associated with seed. Even in Australia, where strong quarantine protocols act to reduce this pathway, pathogens (and pests) were introduced into new plantations in WA. In this regard, forest biosecurity is of paramount importance; it will be more so in the future. However, from all evidence over the past few years, calls to regulatory organizations to improve monitoring surveillance and quarantine have largely fallen on deaf ears.

Sentinel plants can be used to provide early warning systems against potential pathogen invasions or as traps to lure pathogens from surrounding areas. For example, trap trees can be planted in high-risk sites such as near ports or botanical gardens anywhere in the world or in specially designed trials placed in strategic locations to trap particular pathogens (Britton et al. 2010). In addition, tree species can be planted within or adjacent to natural ecosystems in an attempt to trap pathogens from their surroundings. Common gardens (taxa trials) planted in different environments act as useful sentinel plantings. For several years, we have used sentinel plantings to survey for introduced pathogens in Australia. Based on symptoms, on two occasions, it appeared we had recovered the leaf blight pathogen *T. destructans*. In the first instance, surveys of isolated taxa trials in northern Queensland recovered an organism causing *Teratosphaeria* leaf blight, but the pathogen responsible proved to be a new species, *T. viscidus* (Andjic et al. 2007). In the second instance, we reported the presence of *T. destructans* within a sentinel trial we had established on the remote Tiwi Islands in northern Australia (Burgess et al. 2007). However, subsequent studies have led us to also describe these isolates as a new species, *T. tiwiana* (Andjic et al. 2016).

Conclusions

Epidemics of native pathogens are rare in undisturbed native forests (scenario 1). Even though many native eucalypt forests have been managed for timber, the combination of

species and age class heterogeneity has restricted widespread pathogen outbreaks in these forests. Conversely, in both exotic (scenario 3) and native (scenario 5) even-aged plantations, epidemics are common, and losses can be dramatic. Interestingly, almost all serious pathogens of eucalypts were first reported in exotic plantations outside the native range of these trees. This provides strong evidence that insufficient attention was paid to quarantine when the plantation programs were established. In addition, where population genetic studies have been undertaken, it is often shocking to note the very substantial diversity of pathogens in some countries where exotic plantations have been established, including evidence of repeated introductions. Many of the more important pathogens of eucalypts, first discovered outside their native range, have eventually been found occurring naturally in Australia. Given the high level of host specificity of many of these fungi and particularly of the leaf pathogens, it is likely that most eucalypt pathogens will eventually be discovered in the native range of these trees.

Increasing numbers of host shifts of endemic pathogens onto exotic eucalypts are being discovered (scenario 4), particularly for stem pathogens (box 4). These pathogens, and especially the *Cryphonectriaceae*, are relatives of one of the most devastating tree pathogens known—that is, the chestnut blight pathogen *Cryphonectria parasitica*. In our opinion, these pathogens pose one of the greatest threats to eucalypts in their native range. Research to better understand the nature of host shifts in eucalypt pathogens has been neglected and should be substantially expanded if the risks are to be understood, let alone mitigated.

Eucalypts are hugely important components of ecosystems in areas where they are native. They are equally but differently important to plantation industries globally. It is consequently ironic that relatively little attention has been paid to the diseases (and insect pests) damaging these trees. A proactive or pre-emptive approach to protect eucalypts in the native environment and in planted forests is required, rather than reactive measures being taken after a disease

has been identified. Our call is for funding organizations, as well as plantation industries, to invest in research to expand the base of knowledge that could mitigate the long-term negative impacts of eucalypts diseases globally.

Forest biosecurity provides the only means by which pathogen movement can be restricted. Examples provided in this review include many instances of repeated breaches or failures of quarantine to restrict pathogen movement. The tools are available to deeply understand the pathways of movement of tree pathogens. There are also growing numbers of technologies, including those relating to genomes and genomics, that can be used to protect eucalypts from the ravages of disease. The missing link is adequate investment in these technologies (Wingfield et al. 2013, 2015). As we learn to understand the threats and we discover means to mitigate them, the global security of eucalypts will be increasingly assured.

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