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Novel associations between pathogens, insects and tree species threaten world forests[†]

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Abstract

It is well recognised that pests and pathogens are increasingly threatening both natural woody ecosystems and plantation forestry world-wide. This threat is largely connected to the increasing movement of people and products globally, with concomitant introductions of pests and pathogens into new environments. Typically, these invasive alien organisms are accidentally transferred from areas where they are native to the same or closely related tree hosts, to elsewhere in the world. For tree pathogens, there are many well known examples such as those for the causal agents of Dutch elm disease, chestnut blight, white pine blister rust and pine wilt caused by the pine wood nematode. Equally well known examples for insect pests are the gypsy moth, the Asian longhorn beetle, various conifer infesting bark beetles and the emerald ash borer. In addition to these pests and diseases, the introduction of which should be easier to predict given knowledge of patterns of introduction, there is growing evidence that novel host, pest and pathogen interactions are evolving. In this situation, host shifts are apparently occurring where pests and pathogens are able to infest or infect trees that would previously have been considered as non-hosts. There are also intriguing, yet very worrying, new associations emerging between insects and pathogens that are able to cause substantially greater damage to the host trees than has been known for these organisms in the past. In general, these novel associations are poorly understood and due to their unpredictable nature, they seriously complicate quarantine efforts. There is clearly an urgent need to gain knowledge regarding patterns and processes underlying the emergence of host shifts as well as novel pest and pathogen interactions. Research regarding novel associations and host shifts, which might in the past have been considered esoteric, should clearly gain vigorous support in order to reduce an emerging new threat to global forests and forestry.

Keywords: forest pathology; forest entomology; biosecurity; symbiosis.

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Introduction

Tree diseases are widely accepted as representing a substantial threat to forests and forestry world-wide. It is, therefore, surprising to recall that the field of forest pathology is relatively young, with the first text book treating the topic little over 100 years old (Hartig, 1874). Tree diseases were effectively only recognised as a scourge to forests when chestnut blight caused by *Cryphonectria parasitica* (Murrill) M.E. Barr first began to spread in the United States after its first appearance in that country in 1904 (Sinclair & Lyon, 2005; Anagnostakis, 1987). Subsequently, new introductions of alien and invasive tree pathogens into natural forest ecosystems have continued to appear world-wide (Weste & Marks, 1987; Anagnostakis, 2001; Brasier, 2000a; Parker & Gilbert, 2004; Wingfield et al., 2001).

The driving force behind the growing numbers of newly introduced tree pests and pathogens lies in the increasing movement of people and products. Recognition of this fact has resulted in growing attention to pathways of entry of alien invasive pests and pathogens (Brockerhoff et al., 2006a; Desprez-Loustau et al., 2007; Brasier, 2008; Wilson et al., 2009). Wood products and wood packaging material have been recognised as a major source of pests and pathogens and substantial attention has been given to managing this threat in recent years (Brockerhoff et al., 2006b; Haack, 2006; McCullough et al., 2006). The development of sudden oak death caused by *Phytophthora ramorum* Werres, De Cock & Man in ‘t Veld in California (Rizzo et al., 2002, 2005) has strongly emphasised the importance of the nursery trade in the movement of pathogens globally (Rizzo et al., 2005; Ivors et al., 2006). While growing attention is being given to these pathways of movement, the magnitude of the problem is immense. Its management is equally complex and, despite enormous effort, it is likely to remain a substantial challenge for the foreseeable future.

It is worrying that new introductions of tree pathogens appear to be increasing in number despite knowledge of the problem and the many efforts to reduce accidental introductions. Many times, there appears to be a substantial lag-phase before new tree pathogens are discovered and one has to wonder how many new and threatening tree diseases are “incubating” unnoticed in woody ecosystems. In this regard, and ironically, forest pathology and forest entomology are disciplines that have not been strongly supported in recent times. While these concerns are expressed in developing countries, there are many parts of the world, where funding priorities are on issues far removed from tree health, and unexplained tree death is neither noticed nor noted. Yet, foci of developing new tree diseases seriously threaten forests and forestry globally, irrespective of whether they are in the developed or the developing world. Indeed, developing world countries have economies based on trade in natural resources and shipping is often substantially less controlled than is the case in the developed world.

With the exception of root diseases such as those caused by species of *Armillaria* and *Heterobasidion annosum* (Fr.) Bref., the best understood and studied tree diseases are those caused by pathogens that have been introduced into new environments. Typically, these pathogens are relatively host specific yet are unknown in their areas of origin where they occur on trees related to those that are devastated in the introduced environment. Well-known examples are those of chestnut blight (mentioned above), Dutch elm disease caused by *Ophiostoma ulmi* (Buisman) Nannf. and *Ophiostoma novo-ulmi* Brasier (Brasier, 2000a), white pine blister rust caused by *Cronartium ribicola* A. Dietr. (Maloy, 1997) and the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle (Dwinell, 1997; Mota & Vieira, 2004). In the introduced environment, the related host trees have speciated in the absence of these pathogens and lack resistance to the pathogens and the results are often devastating (Parker & Gilbert, 2004). Tree pathogens with a broad host range that have been introduced into new environments, such as *Phytophthora* spp. (Weste & Marks, 1987; Linde et al., 1999; Cahill et al., 2008) are able to damage a much wider suite of trees, although typically some species are more seriously affected than others. Thus, damage due to *Phytophthora ramorum* has been most serious on tan oak (*Lithocarpus densiflous* (Oerst.) Reholer) in California and *P. cinnamomi* Rands has been especially damaging on various species of Proteaceae in Australia (Cahill et al., 2008) and South Africa (Von Broembsen & Brits, 1985; Linde et al., 1999).

The fact that tree pathogens can be introduced and cause serious disease problems in new forest environments are well understood. Where non-native trees have been used to establish plantations for wood and pulp production, commercial success has been underpinned by rapid growth, not challenged by pests and diseases. This exceptional growth, akin to that found in weeds is generally attributed to “enemy escape” (Keane & Crawley, 2002; Verhoeven et al., 2009). Consequently, the accidental introduction of pests and pathogens is recognised as one of the greatest threats to plantation sustainability (Wingfield et al., 2006, 2008; Desprez-Loustau et al., 2007; Holmes et al., 2009). Perhaps less well recognised is the damage that native pathogens can impart on non-native trees grown in plantations. Indeed, some of the most serious disease problems in plantations of *Eucalyptus* and *Acacia* in the tropics and southern hemisphere are caused by native pathogens that have adapted to be able to infect non-native hosts (Slippers et al., 2005; Wingfield, 2003). Such novel pathogen/tree associations are seriously underestimated in the threat that they pose to forestry world-wide. Likewise, novel associations are emerging between insects

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and forest trees and intriguingly between insects and tree pathogens. These and other categories of new association are poorly understood and hardly recognised in terms of their global relevance.

The objective of this review is to consider some examples of novel associations between forest insect pests and pathogens and trees. Given that many of these are poorly documented and understood, an attempt is made to identify underlying trends in terms of the threats of these novel associations to worldwide forests and forestry. Furthermore, suggestions are made to promote an improved understanding of the underlying threats associated with novel pest and pathogen associations.

Novel Pathogen/Tree Associations

Novel associations are common and well known for some categories of tree hosts and pathogens (Anagnostakis, 2001; Parker & Gilbert, 2004; Burdon et al., 2006). These occur among those pathogens with wide host ranges such as are found in some species of *Phytophthora* (Weste & Marks, 1987; Lucas et al., 1991; Cahill et al., 2008), *Armillaria* (Fox, 2000), *Cylindrocladium* (Crous, 2002) and others (Sinclair & Lyon, 2005). Where these pathogens are present as natives and where susceptible trees have been planted in these environments, disease problems are hardly surprising. Likewise, where these pathogens have been introduced into new environments and where susceptible trees are present, it is not surprising that serious disease problems have emerged. The novel tree/pathogen associations of concern in this review are those that might not have been predicted. Here, the underlying process is one of an unexpected host shift (Slippers et al., 2005). This section provides a few such examples. For the purpose of this review, unexpected host shifts are considered to have occurred where the new hosts are in genera different to those on which the pathogens occur in their areas of origin.

In forest pathology, one of the most intriguing diseases caused by a pathogen that has clearly undergone a host shift is that of guava rust. This disease is caused by *Puccinia psidii* G. Winter that is native to south and central America on native Myrtaceae (Coutinho et al., 1998; Glen et al., 2007; Old et al., 2003). The pathogen was first recognised as having undergone a host shift when it infected non-native myrtaceous trees such as clove (*Syzygium aromaticum* (L.) Merr. & L.M. Perry) and *Eucalyptus* in Brazil. Some tree species are highly susceptible to guavas rust and the disease is considered as one of the greatest threats to woody ecosystems in Australia, Africa and Asia where various species of native Myrtaceae are known to be highly susceptible to the disease (Rayachhetry et al., 2001; Glen et al., 2007). It is especially worrying that *P. psidii* has recently appeared in Hawaii where it infects native *Meterosideros* spp. (Uchida et al., 2006).

An interesting suite of examples of an unexpected shift of hosts and thus a new association between host and pathogen is found amongst species of *Chrysoporthe*. This is a relatively newly established genus to accommodate species previously treated as *Cryphonectria cubensis* (Bruner) Hodges (Gryzenhout et al., 2004, 2009). The fungus now known as *Chrysoporthe cubensis* (Bruner) Gryzenh. & M.J. Wingf. has been found on numerous species of native Melastomataceae in South and Central America and South East Asia. These fungi have clearly undergone a host shift to infect non-native *Eucalyptus* spp. that have been established in those regions in intensively managed plantations (Wingfield, 2003). Likewise, in Africa, the closely related fungus *Chrysoporthe austroafricana* Gryzenh. & M.J. Wingf. (previously known as *C. cubensis*) in the area (Gryzenhout et al., 2006) is apparently native on native species of *Syzygium* (Heath et al., 2006) and has undergone a host shift to infect plantation-grown *Eucalyptus* and *Tibouchina* spp. (Melastomataceae) growing as ornamentals. All of the native hosts of *Chrysoporthe* spp. that have adapted to infect *Eucalyptus* reside in the Myrtales, a large order of plant families that includes the Myrtaceae and the Melastomataceae (Figures 1 and 2). These “new” pathogens certainly pose a threat to some species of *Eucalyptus* and possibly other woody Myrtales in their native ranges.

The two examples highlighted in this section are surprising because the new hosts are apparently only distantly related to the hosts of the pathogens in their areas of origin. It might be argued that many invasive alien tree pathogens (the Dutch elm disease fungi, chestnut blight pathogen, pine wood nematode, etc.) have undergone host expansions in infecting species different to those on which the pathogens occur naturally. However, with some pathogens such as those discussed here, shifts appear to have occurred between hosts much less closely related. This must change the approach that we take to evaluating risks and questions relating to host range for what might previously have been considered relatively host specific pathogens deserve further study.

Little is known regarding hybridisation amongst tree pathogens, but there is growing evidence that this process is probably more common than has previously been appreciated (Brasier, 2000b, 2001). Hybridisation can also be a driving force underpinning shifts to new hosts by tree pathogens. Thus, the hybridisation of host specific poplar rusts *Melampsora medusae* Thüm. and *M. occidentalis* H.S. Jacks., later described as *Melampsora ×columbiana* G. Newc. (Newcombe et al., 2000) led to a rust pathogen able to infect hybrids of these two poplar species. This hybridisation represents a clear example of a host shift, albeit one that might have been predicted. Likewise,

FIGURE 1: Native *Melastoma* sp. growing in close association with non-native *Eucalyptus* trees in a plantation;
FIGURE 2: Basal canker on a *Eucalyptus* tree caused by *Chrysoporthe cubensis* originating on native Melastomataceae in Colombia;
FIGURES 3-5: Damage to pine shoot caused by the bark beetle *Tomicus piniperda*; and
FIGURES 6-8: Damage on a *E. nitens* stem caused by gregarious larvae of the cossid moth *Coryphodema tristis*.

there is evidence of hybridisation in *Phytophthora* spp. that has given rise to important root pathogens of *Alnus* spp. in Europe (Brasier et al., 1999, 2004, Ioos et al., 2006). Although these examples are few in number, they suggest that hybridisation between tree pathogens in the future could be an important source of new and serious tree diseases.

Novel Fungus/Insect Associations

Novel associations between tree pathogens and insects are relatively well known in forest pathology. Perhaps the best example relates to Dutch elm disease where the pathogen *O. ulmi*, likely of Himalayan origin, established a novel association with the European and North American scolytine bark beetles *Scolytus scolytus* F. and S. *multistriatus* Marsham (Webber, 1990). In a similar fashion, the pine wood nematode *Bursaphelenchus xylophilus* was accidentally introduced into Japan, most likely on infested pine timber from North America. In Japan, it developed an association with a new vector *Monochamus alternatus* Hope (Wingfield, 1987; Mamiya, 2004). *Bursaphelenchus xylophilus* has more recently established an association with *M. galloprovincialis* (Olivier) (Mota et al., 1999; Sousa et al., 2001; Naves et al., 2007) in Europe where it is causing serious damage to *Pinus pinaster* Aiton in Portugal.

The abovementioned novel associations are for insects that are most likely very closely related to those that carry the pathogens in their areas of origin. There is, however, emerging evidence that, when introduced into new environments, bark beetles are acquiring fungi with which they are not associated in their areas of origin. For example, surveys of the fungi associated with the European bark beetle *Tomicus piniperda* L. (Figures 4-6), where it has been introduced into North America, have shown that it has introduced *Leptographium wingfieldii* M. Morelet into North America with it (Jacobs et al., 2004). More intriguingly, other bark beetles, native to North America such as *Dendroctonus valens* LeConte, in infested trees were also found to be carrying *L. wingfieldii*. These native North America insects have, thus, acquired a new fungal associate that is relatively virulent in its area of origin. The implications of this new association remain unknown but they clearly deserve attention.

Another intriguing example of a new association between a scolytine bark beetle and fungi is found for *Dendroctonus valens* in China. This insect, native to North America has been accidentally introduced into China where it has caused serious damage to *Pinus tabuliformis* Carrière (Yan et al., 2005). Surveys of the fungi associated with *D. valens* in China have shown that it carries a suite of fungi including some (*Leptographium procerum* (W.B. Kendr.) M.J. Wingf.) that are associated with it in its area of origin (Lu et al., 2008). In addition, there are other fungi, such as *L. sinoprocerum* Quan Lu, Decock, Maraite, that are associated with *D. valens* in China and these are probably native to that country (Lu et al., 2008). The introduced insect has thus assumed a novel suite of fungal associates and it is possible that this might, at least in part, explain why a relatively non-aggressive insect pest in North America has become a serious and damaging pest in China.

Novel Insect/Tree Associations

Like fungi, many forest insect pests are polyphagous with wide host ranges. There are thus, many examples of native insects infesting introduced trees, including those used for plantation development (Lanfranco and Dungey, 2001; Gebeyehu et al., 2005; Verhoeven et al., 2009). Polyphagous insect pests have also been accidentally introduced into new environments, resulting in severe damage. Perhaps the best known of these is the gypsy moth (*Lymantria dispar* L) that was accidentally introduced into North America more than a 100 years ago (Davidson et al., 1999; Liebhold et al., 2000) and has caused severe damage to native North American forests. Also like fungi, more specific forest insect pests have been introduced into new environments where they damage related, yet not necessarily the same tree species. Examples of these pests are far too numerous to mention, but they include a wide variety of different orders of insects.

An intriguing example of an unexpected host shift for a forest insect pest is found in the case of the cossid moth *Coryphodema tristis* Drury infesting *Eucalyptus nitens* (Deane et Maiden) Maiden (Figures 6-8) in South Africa (Gebeyehu et al., 2005). This insect is apparently native to South Africa and it is a pest of various introduced fruit crops such as grapes and quince. However, its appearance on *E. nitens* has been surprising and difficult to explain. This is because the insect has not been found on any other *Eucalyptus* spp., despite the fact that other relatively closely related species of *Eucalyptus* occur close to the areas of infestation. A similar example is found in Chile where the native cossid *Chilecomadia valdiviana* Philippi that feeds on *Salix chilensis* Molina has adapted to infest *E. nitens*, but not other closely related species of *Eucalyptus* (Lanfranco & Dungey, 2001).

Conclusions

There are many examples of novel associations between trees and the pests and pathogens that damage them in non-native environments. However, in most of these cases, the new hosts for the pathogens and pests are trees closely related to those on which the damaging agents occur as natives. Most commonly, the novel hosts reside in the same genus of tree. There appear to be emerging examples of host shifts that are less easy to predict, however. This is because they occur between pathogens and pests and hosts that are relatively distantly related to those that are found in the native environment. These host shifts complicate predictions that might be made to guide quarantine procedures aimed at reducing the likelihood of accidental introductions into new environments. This fact adds weight to calls to regulate pathways to reduce the overall risk of pests and pathogens entering new environments, rather than targeting only specific species through quarantine.

Amongst the most common insects accidentally introduced into new environments are xylophagous bark beetles and wood borers. Many of these insects live in a symbiosis with fungi or nematodes, which, in some cases, are serious tree pathogens in their own right. Some of these pathogens, such as those causing Dutch elm disease and pine wilt, have been moved to new environments in timber. Once there, they have developed associations with native insects closely related to those that carry them in their areas of origin. However, there are emerging examples of introduced xylophagous insects acquiring new microbial associates, which are more pathogenic than those with which they co-exist in their native environments. The implications of these new associations have yet to emerge, but they have the potential to transform our understanding of the biology of pests and pathogens.

The cultivation of non-native trees for fruit, wood and paper products is a well-established practice dating back many centuries. Yet commercial forestry is now emerging as a possible catalyst for the possible evolution of important new pests and pathogens. Where native and relatively host specific pathogens develop the capacity to infect non-native trees, these essentially become a threat to the same trees or their relatives in their areas of origin, or elsewhere in the world.

One of the greatest challenges to understanding trends relating to the global movement of pests and pathogens relates to the difficulties associated with identifying them. Although not exclusively so, this problem is greater for pathogens such as fungi that have fewer morphologically distinguishing characters than insects. The fact that it took more than ten years of relatively intensive research to recognise that *C. austroafricana* was different to *C. cubensis*, illustrates this point well (Wingfield, 2003). Certainly without modern DNA-based diagnostic techniques, this discovery would not have been possible. In this regard, DNA-based techniques have revolutionised diagnostics and they are increasingly revealing new and unexpected patterns relating to pests, pathogens their hosts and their global distribution.

There is growing evidence that hybrids represent an important category of tree pathogens. Given the very large number of fungi and other micro-organisms that have been transported around the world, it is likely that there are many more hybrid organisms in the forestry environment than we are able to recognise presently. Others will surely also emerge from the many new associations of microbes and trees that have emerged from the activities of humans. The impact of anthropogenic activities has only just begun to emerge.

It is perhaps not surprising that the exposure of trees to new pests and pathogens could lead to globally threatening novel pests and pathogens. This has been a concept well recognised in medicine with many serious diseases emerging from the close association between humans and animals (Woolhouse et al., 2005). The human immunodeficiency virus (HIV) and the associated acquired immune deficiency syndrome (AIDS) that it causes, and the more recent emergence of severe acute respiratory syndrome (SARS) provide vivid examples. We might then predict that many new and important tree pests and pathogens will arise in the future due to the many complex mixtures of trees that are being planted in foreign environments.

New pest epidemics and diseases are emerging in forests and forestry world-wide. Many are associated with novel associations between insects, microbes and trees and many would not easily have been predicted prior to their emergence. Scientists and policy makers face an enormous challenge to reduce the level of damage that could occur in forests world-wide. Likewise politicians have the responsibility to provide adequate funding to protect the world's forests, the biodiversity and the industries that are associated with them. With adequate vision, one can hope to be optimistic about the future of forests and forestry. Otherwise, the prediction of the medical doctor and sage Albert Schweitzer that "Man has lost the capacity to foresee and to forestall. He will end by destroying the earth" could be more true than most of us would wish to believe.

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