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Review

The sudden emergence of pathogenicity in insect–fungus symbioses threatens naive forest ecosystems

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Invasive symbioses between wood-boring insects and fungi are emerging as a new and currently uncontrollable threat to forest ecosystems, as well as fruit and timber industries throughout the world. The bark and ambrosia beetles (Curculionidae: Scolytinae and Platypodinae) constitute the large majority of these pests, and are accompanied by a diverse community of fungal symbionts. Increasingly, some invasive symbioses are shifting from non-pathogenic saprotrophy in native ranges to a prolific tree-killing in invaded ranges, and are causing significant damage. In this paper, we review the current understanding of invasive insect–fungus symbioses. We then ask why some symbioses that evolved as non-pathogenic saprotrophs, turn into major tree-killers in non-native regions. We argue that a purely pathology-centred view of the guild is not sufficient for explaining the lethal encounters between exotic symbionts and naive trees. Instead, we propose several testable hypotheses that, if correct, lead to the conclusion that the sudden emergence of pathogenicity is a new evolutionary phenomenon with global biogeographical dynamics. To date, evidence suggests that virulence of the symbioses in invaded ranges is often triggered when several factors coincide: (i) invasion into territories with naive trees, (ii) the ability of the fungus to either overcome resistance of the naive host or trigger a suicidal over-reaction, and (iii) an 'olfactory mismatch' in the insect whereby a subset of live trees is perceived as dead and suitable for colonization. We suggest that individual cases of tree mortality caused by invasive insect–fungus symbionts should no longer be studied separately, but in a global, biogeographically and phylogenetically explicit comparative framework.

Keywords: ambrosia symbiosis; emerging pathogens; host–pathogen coevolution

1. INTRODUCTION

The current global biotic homogenization has disproportionately benefited one unexpected life form—the symbiotic association of wood-boring insects and fungi. In the last few decades, dozens of symbioses involving insects and fungi have been introduced into non-native ranges worldwide [1,2]. Many of them have become invasive, and caused great ecological damage (loss of tree species from much of their historic range) and economic costs (hundreds of millions of dollars, [3]). The damage from these symbioses is primarily due to an apparent shift in their life history. Over a dozen introduced fungus–insect couples have become invasive by shifting from colonizing dead and dying trees to attacking living trees. This new niche allowed them to rapidly expand their geographical ranges. As they do, they threaten tree crops such as avocado [4], walnut [5,6], mango [7], pine [8], poplar (for bioenergy) [9], and nursery trees in general [10,11]. Here, we review what is known about these invasive insect–fungal symbioses, and offer testable hypotheses that might account for the life-history shifts associated with their invasions.

2. BACKGROUND: INSECT–FUNGUS SYMBIOSES

One of the most successful symbioses among eukaryotes is that between wood-colonizing insects and wood-inhabiting fungi ([12], see the electronic supplementary material). This relationship arose independently in wood wasps, lymexilid beetles, passalid beetles, and many times in the diverse clade of minute weevils known collectively as bark and ambrosia beetles (Curculionidae: Scolytinae and Platypodinae). We focus here on these beetles both because of their diversity (more than 7500 species), and because of their ecological impact. The association of bark and ambrosia beetles with fungi began as early as 60 Myr ago in multiple independent lineages [13], and led to a variety of symbioses, involving fungus farming [14], tree tissue pre-digestion by fungi [15], and fungal phoresy in which fungal species simply rely on beetles for transport [16]. Ecologically, these relationships are fascinating, but they also have a more sobering side. Such symbioses account for the majority of the world's most recent invasive tree pests.

(a) *Origins*

Since the Carboniferous, much of the Earth's plant biomass and nutrients has been tied up in wood, whether phloem, xylem or bark. Insects have evolved strategies to access this food resource, but in response, trees have

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evolved strategies to defend themselves, primarily by producing specialized chemicals, resins and latexes [17]. As a result, very few lineages of insects are able to colonize living trees. Instead, the majority of species that feed on tree bark, phloem or xylem, do so after a tree's death. Yet, even a dead tree can be a hostile environment to those who might eat it. Many defensive allelochemicals and resins in bark and phloem are fairly stable, and xylem is composed mostly of digestion-resistant polymers [18]. Repeatedly, symbioses between wood-boring insects and fungi have evolved [19] primarily as a means of dealing simultaneously with the residual defenses in dead trees and concentrating diffused nutrients.

(b) *From phloem-feeders to fungus farmers*

The ancestral diet of bark and ambrosia beetles was freshly dead phloem [20], and their most common fungal associates were weakly pathogenic fungi [21]. The association between phloem-feeding beetles and fungi has repeatedly evolved into a variety of other relationships. Perhaps the most common case is fungal phoresy, in which fungi that confer little or no benefit to the beetle are carried by it from one dead tree to another [16]. In several bark beetle lineages [22], the association evolved into a more mutualistic relationship, wherein the fungi are inoculated by adult beetles to a newly colonized tree where they are consumed by their larvae. In many of the textbook examples of phloem-colonizing bark beetles (i.e. the Southern Pine Beetle), the beetle larvae feed less on the actual phloem, and more on specialized fungal symbionts. Many of these bark beetles have even evolved mycangia to ensure reliable fungus transmission [23].

The most elaborate of beetle–fungus interactions is true fungus farming, often called ambrosia symbiosis. Like other forms of beetle–fungus symbiosis, this relationship evolved repeatedly—'ambrosia beetle' is an ecological classification, not a phylogenetic group. Ambrosia fungi extract nutrients from xylem or, less frequently, from phloem around the beetle tunnel, and serve as the sole food source for both the adult beetles and their larvae. Each new beetle generation then carries fungal spores from the natal gallery into the next tree where a new fungus garden is established. The ambrosia farming mutualism evolved in at least 13 clades of beetles and 11 clades of fungi, with no known evolutionary reversals [13,14,21,24,25]. The broad diversity in beetle–fungus symbioses has been traditionally underappreciated. In many beetle clades, one finds individual species that blur the line between what were traditionally called bark and ambrosia beetles. The dichotomy of bark versus ambrosia beetles is partly artificial, concealing the many origins of fungus farming in both ecological groups. (In comparison, farming of fungi has evolved just once in ants, and once in termites [26].)

Fungi serve as what is often termed an 'external stomach' for the insects in that they allow extraction of nutrients from large volume of host tissue. Farming fungi inside xylem also frees the insects from directly combating some of the defenses present uniquely in phloem. Such defenses are often specific to particular tree species or lineages and require phloem feeders to become specialized. Avoiding such defenses allowed beetle–fungus symbioses that feed on xylem to have among the broadest host spectrums known among insects [27,28].

In summary, a range of beetle–fungus relationships exist within the bark and ambrosia beetles and most of these relationships have evolved more than once. Such variation is both more complex and interesting than the traditional bark beetle/ambrosia beetle dichotomy often emphasized in forest entomology. Breaking down this unnecessary dichotomy has relevance here, since the sudden emergence of pathogenicity has occurred in several independent clades of both ecological groups.

(c) *Defining fungal symbionts*

While the preference of any particular insect species for colonization of phloem or xylem is relatively constrained, the roles of the fungal symbionts themselves are more complex. First, most beetle species (and probably tree-feeding insects in general) associated with fungi have more than one fungal partner, whether in a given tree, among trees, among populations or through time. Nearly all in-depth explorations of beetle–fungus symbioses report multiple fungi associated with individual beetle species [14,26–30]. Such diversity stands in contrast to the historical view of beetle–fungus symbioses as one-on-one mutualism. It is possible and indeed likely that the ecological role and life history of beetle–fungus symbioses depends on precisely which fungal partners are involved [31]. Even the effect of a given fungal taxon on a host tree may vary with the ecological context, whether the stage of gallery development, the freshness of the host, or the presence of other organisms [19,32]. For example, some symbiotic *Fusarium* or *Raffaelea* species seem capable of both feeding the insect and defeating host tissue, depending on whether they are inoculated into a live or a dead tree [4,33,34]. Similarly the genus *Geosmithia*, which until recently was a rarely studied fungi with unknown source populations, has recently been shown to include many bark and ambrosia beetle associates [26], including nutritional ambrosia symbionts [35] and possibly tree pathogens [6].

In short, regardless of whether an insect is a fungus farmer or a phloem feeder, it appears to have the potential to vector both fungal crops as well as tree pathogens, and in fact, may do both at the same time. The ecological flexibility of the symbioses is interesting in its own right, but becomes troubling for trees in foreign ecosystems, where the new encounters sometimes result in novel, and unprecedentedly fatal consequences.

3. INTRODUCED FUNGUS FARMERS AND PHLOEM-FEEDERS, BY THE NUMBERS

The wood-boring fungus–insect symbioses might have remained an interesting but inconsequential evolutionary oddity if not for the human transport of such species around the world. Insect–fungus symbioses, particularly those of bark and ambrosia beetles, are being introduced faster than any other group of introduced forest pests [2]. Exotic scolytine beetles alone are the single most common group of insects intercepted at US ports-of-entry (58% of all individuals [36]). If ports-of-entry randomly sampled the 4.9 million (or more; [37]) insect species on Earth, scolytine beetles would constitute less than 0.2 per cent of individuals. Instead, they account for more than half of the interceptions. Of the roughly 5400 species of named scolytines in the world, at least

53 exotic species —1 per cent of the world's diversity—are currently established in North American forests, and the accumulation of new introductions during recent decades has been exponential [2,36]. The literature on insect introductions has begun to reflect this trend: 50 per cent of all journal articles on introduced bark and ambrosia beetles have been published since 2008 (ISI Web of Knowledge, Thomson Reuters).

Symbioses involving beetles of the tribe Xyleborini have the greatest introduction success and rapidly increasing economic impact. Evidence from island populations of the beetles show that the haplo-diploidy of the beetles, almost clonal reproduction, and nearly unlimited host range helps xyleborines readily establish populations in new regions [38]. Theoretically, a xyleborine population could be established via a single, unfertilized female. When these introduced symbioses are successful, they can be incredibly successful. According to the US federal programme Early Detection and Rapid Response [39], the three most commonly trapped woodborers in the USA are introduced Xyleborini, representing 35 per cent of the catch (*Xyleborinus saxeseni*, *Xylosandrus germanus*, and *Xylosandrus crassiusculus*). Even allowing for potential biases of trapping methods, these results seem to lead to the inescapable conclusion that these beetles are becoming very, very common.

4. FROM A NATURAL CURIOSITY TO A MAJOR INVADER

As recently as 20 years ago, insect–fungus associations were considered a harmless curiosity associated with dead timber [40]. This notion has recently changed, specifically in the subset of those species that have been introduced to non-native regions and become invasive. One of the first examples of a tree-killing invasive insect–fungus symbioses was that of the elm bark beetle *Scolytus multistriatus* and its associated fungi *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*. These ensuing Dutch elm disease nearly eradicated elms in North America and Europe, respectively [41]. Initially, the epidemic was considered an exception, since bark beetles on broadleaf trees were generally not known to attack their hosts alive [42]. However, as the rate of bark and ambrosia beetle introductions into non-native regions has increased, so too has the frequency of cases in which these symbioses have begun to kill live trees. Below are several examples:

- one of the most bewildering current cases is the invasion of the redbay ambrosia beetle *Xyleborus glabratus* with its associated *Raffaelea* spp. in North American forests (figure 1). This East Asian beetle, rarely collected in its native range, was first noticed killing Lauraceous trees in Georgia in 2005 [43]. At that time, its fungal associates were not even named. Since then, the beetle–fungus symbiosis has spread along the southern Atlantic coast of North America, where it has been eradicating mature redbay, an understory dominant. Like redbay, avocado is also a member of the family Lauraceae, and is extremely susceptible to the pathogen. Spread of this symbiosis to the avocado-growing regions of the USA and Mexico, or to laurel-dominated Western coast, would have serious economic consequences, with estimated potential losses up to $356 million [3];
- one of the most recently reported tree-killing ambrosia beetles is *Megaplatypus mutatus* with its fungal partner *Raffaelea santoroi*. Native to the Neotropics, this symbiosis recently spread to subtropical and temperate regions of South America and Europe where it is becoming an important agent of mortality in poplar plantations associated with the bioenergy industry [9];
- some insect–fungus pairs with pathogenic attributes are at least half native. *Platypus quercivorus* was first noticed in Japan in the 1920s, but appears to be a native part of the local fauna [44]. The beetle did not have any serious effect on live plants, until a mass dieback of oaks in the 1980s was noticed [45]. Since the 1980s, this symbiosis has destroyed roughly 1000 ha of oak forest each year [46]. While the beetle appears to be native, the fungal symbiont, *Raffaelea quercivora*, may not be. The geographical origin of this fungus is unknown, but that it might be non-native to Japan is suggested by the uniformity of several DNA markers across the region [47];
- phloem-feeding bark beetles are sometimes associated with nutritional fungi, but even more often they vector weakly pathogenic fungi. It is debated whether or not the beetles benefit from the association, or if the fungi only take advantage of the transport to the next diseased tree without providing any contribution [16]. However, in non-native regions with naive hosts, even a weak association can benefit both partners and spread rapidly, with significant ecological

Figure 1. Mass mortality of redbay (*Persea borbonia*) in Georgia, USA, caused by the invasive ambrosia beetle *Xyleborus glabratus* and its symbiotic fungus *Raffaelea lauricola*. Reproduced with permission from © Jason Smith, University of Florida.

Figure 2. Globally invasive ambrosia beetle *Xylosandrus crassiusculus* with eggs inside a garden of its symbiont fungus, *Ambrosiella xylebori* (gray-coloured surface). Reproduced with permission from © J. Hulcr.

consequences. A worrisome recent example is the rapid spread of *Hypocryphalus mangiferae* and a complex of *Ceratocystis* species through mango-growing areas in South America and the Middle East, causing mango sudden death syndrome [7]. In Oman alone, the disease has already killed over 200 000 mango trees [48];

— in short, an increasing number of beetle–fungus symbioses has shifted from colonizing dead trees to attacking live trees in their introduced ranges. The list is long and in addition to the examples we have already mentioned also includes other less well studied symbioses: *Xylosandrus germanus* with *Ambrosiella hartigii* [11,49] and *Xylosandrus crassiusculus* with *Ambrosiella xylebori* and *Fusarium* sp. (figure 2; J. Hulcr 2010, unpublished), both originally from Asia, are attacking nursery trees throughout the Eastern USA; *Pityophthorus juglandis* is spreading thousand cankers disease to walnuts across the USA (possibly caused by *Geosmithia morbida*) [6]; *Euplatypus parallelus*, putatively associated with *Fusarium* sp., is attacking *Pterocarpus* plantations in Thailand [34]; the Korean oak wilt is caused by *Platypus koryoensis* and *Raffaelea quercus-mongolicae* [50]; the Asian *Euwallacea fornicatus* with unknown symbionts is occasionally attacking live trees in California and Florida [1] and recently was found killing avocados in Israel (Z. Mendel & S. Freeman 2011, personal communication), among other examples.

Considering the escalating frequency of introductions of insect–fungus symbioses and the increasing impact of a subset of these symbioses on forest ecosystems and tree-growing industries, we suggest that this invasion syndrome is no longer a series of exceptions. Instead, it is a new global phenomenon, and one that does not always obey the established rules of invasions.

5. UNUSUAL INVASIONS

Most insect–fungus consortia established in non-native regions do not turn into tree killers; instead they remain inconspicuous members of an increasingly homogenized global fauna. In an increasing number of cases, however, introductions are associated with a shift from harmless saprotrophy (feeding/farming on dead trees) to attacking and killing live trees, typically within a phylogenetically narrow subset of tree species. The narrow range of live hosts is unusual particularly for ambrosia beetles, since, in their native environment, ambrosia beetles typically colonize freshly dead trees of a broad range of plant lineages [51,52]. Colonization of live trees is rare or non-existent under natural circumstances for both ecological groups [53]. Similarly, fungal symbionts (*Raffaelea*, *Ambrosiella*, *Amylostereum*, *Geosmithia*, etc.) rarely behave as phytopathogens. There is no indication that these fungal species have evolved strategies to combat defense mechanisms of living trees.

The shift in behaviour of insect–fungus symbioses in introduced ranges is a pivotal piece in the emergence of invasions of insect–fungus symbioses, but has gone relatively unexplored. We propose that the shift is not a consequence of a change in the insect behaviour, or a novel host association, though these may occur. It may instead be a new expression of 'old' behaviours in a new ecological context, in other words an evolutionary mismatch [54].

6. HYPOTHETICAL FRAMEWORK FOR UNDERSTANDING PATHOGENICITY OF THE WOODBORER–FUNGUS SYMBIONTS

We suggest that tree-killing in introduced bark and ambrosia beetles and perhaps insect–fungus symbioses more generally is not a manifestation of a highly evolved ecological strategy, but instead the outcome of several coincident phenomena.

(a) *Live hosts smell dead*

Why do woodborers attack living trees in non-native regions? Here we propose three potential explanations. First however, it may be useful to clarify the general mechanisms of host choice by wood-boring insects.

The majority of wood-boring insects that have been well studied are attracted to odour profiles indicative of freshly dead trees, specifically volatiles associated with tree metabolic stress, tree tissue decay, or occupation by other insects, fungi and/or bacteria [55,56]. Related host species are likely to have similar odour profiles, but this is not always the case [57]. An insect's search for dead trees proceeds in steps. First, an insect must detect a suitable tree at a long range. Next, an insect typically uses a different set of cues to locate suitable trees at short distances. Subsequently, gustatory attractants may be used in the final choice of whether or not to bore into a tree [58,59]. In short, an individual insect is not choosing a 'tree' as humans see it. Instead, it continuously assesses clouds of volatiles, and directs its flight to follow the concentration gradient of those volatiles, to which it has evolved an attraction.

A1. One possible explanation for the shift from dead to live trees is 'olfactory mismatch'. In native ecosystems, wood-boring beetles have search patterns 'tuned' to compounds indicating recently dead wood. The new regions invaded by these beetles may include trees that emit such compounds when alive. In a subset of cases, these trees may also happen to be susceptible to the fungus infection. Two observations are consistent with this hypothesis. First, the living trees attacked in the invaded regions tend to be from a phylogenetically narrow (and perhaps similar-smelling) subset of the broad range of dead hosts colonized in their original regions. Perhaps the insects do not switch to different volatile cues in the non-native range, but instead remain attracted to similar chemical cues and fail to recognize that some of their hosts are still alive [10]. Observations from the invasive redbay ambrosia beetle, *X. glabratus*, are consistent with this hypothesis. When the first redbay beetle lands on a healthy tree, it starts to bore its entrance hole, at which point the deadly *Raffaelea* fungus is inoculated into the tissues, grows systemically, and kills the tree. Surprisingly, these pioneer beetles often abandon the tree very early during gallery construction [4]. It is possible that their olfactory senses indicate that the tree is dead, but their gustatory senses reveal that it is actually alive, and not yet suitable for colonization. Only the beetles that arrive at the same tree after the fungus has established are able to colonize the tissues disarmed by the fungal pathogen [4]. The olfactory mismatch hypothesis provides a testable prediction: volatiles from the attractive living trees should overlap with that of attractive dead trees, while at least some of these compounds should be missing in the majority of other living trees (both different species and non-attractive conspecifics).

A2. A second possibility, the ‘permissive choice hypothesis’, is that beetles may vary genetically in their choice of cues used to detect hosts, and are subject to rapid selection for preferring live tree-associated odours, where naive trees are available. Many species of bark and ambrosia beetles are attracted to volatile mixtures indicating tree stress or the process of dying, in order to enter tissues that are already free of defense, and still free of competition. However, this period is signalled by unreliable mixtures of volatiles, and estimating it is partly a matter of hedging bets. Perhaps that is what maintains the heritable variation in olfactory preferences that bark beetles are known for [60–62]. Indeed, several ambrosia beetle species do occasionally attack live trees even in their native habitats, but only a fraction of the population displays such behaviour [10,63]. In the native range of beetles, selection should strongly favour beetles attracted only to dead trees since live trees are appropriately defended. In invaded ranges, however, selection may favour genes associated with being attracted to or even preferring live trees. The ‘permissive choice hypothesis’ suggests two testable assumptions: a signature of genetic divergence between populations of invasive beetles specialized on live and on dead trees, and a heritable difference in substrate choice in native and non-native beetle populations.

(**b**) ***Only naive trees die***

A second major question is why live trees attacked by the beetles and their symbionts die. The virulence that we see in the ‘new pests’ has in no case been documented to be their typical ecological strategy in their native forests [42,52].

B1. Fungal symbionts that kill trees in non-native regions fall into two categories, which may differ in their dynamics: mild pathogens specialized on weakened or freshly dead tree tissues, and ambrosia fungi that are normally entirely non-pathogenic.

The first group includes necrotrophic pathogens, fungi that specialize on dying trees, and which need to suppress the defense of living host tissue before they can digest it. Their metabolic arsenal includes some virulence factors, but these factors appear insufficient to overcome healthy trees in their native ranges (e.g. some *Ceratocystis* or *Fusarium* spp. [7,33]). Their association with beetles is unclear: while a few congeners of these fungi appear to be primary nutritional symbionts [33,64], in most cases their irregular presence alongside other nutritional fungi suggest low nutritional value for the beetles [65]. However, it may be that, when the weak pathogenicity of these fungi is combined with increased susceptibility of non-native hosts, it is sufficient to account for the observed tree deaths (e.g. *Hypocryphalus mangiferae* and *Ceratocystis* spp., above).

The second category includes the nutritional ambrosia fungi, namely *Raffaelea* spp. The ambrosia fungi did not evolve to be pathogenic, and the mechanisms underlying the diseases caused by these fungi are only beginning to be understood. One intriguing explanation is that tree death is not caused by virulence factors from the fungus, but by an exaggerated response of naive tree tissues to a novel threat, resulting in tree suicide [66,67]. This ‘exaggerated response’ hypothesis posits that tree hosts in the native range have evolved an appropriately mild immune response to non-pathogenic ambrosia fungi, but such fine-tuning of response has never occurred in regions lacking such fungi.

The two cases that have been studied in detail lend support to the exaggerated response hypothesis: the laurel wilt caused by *Raffaelea lauricola*, and the Japanese oak wilt caused by *Raffaelea quercivora*. Neither fungus is a typical tree pathogen. Instead, the lethal effect to trees in both cases appears to be the tree’s over-expressed expansion of walls in xylem vessels. This normally prevents a disease from spreading in a tree, except that in the cases of overreaction, tree kills itself ([67], R. C. Ploetz & J. A. Smith 2010, personal communication). The importance of selection pressure for the evolution of tree resistance to wood-boring beetles has been also recently documented in conifers and bark beetles. Conifers, which had been protected from bark beetles by cold weather, are suffering huge mortality after the beetle range expanded during warm years [68,69].

B2. Rapid increase of pathogenicity in the insect–fungus symbiosis may be triggered by two additional mechanisms that have been shown to occur in other systems. One is new associations of the insect vector with fungi that are more pathogenic than the original symbionts. It is becoming increasingly clear that many insect vectors carry more than one fungal species or strain, and these strains regularly differ in their ecological roles [25,30,32].

B3. The other possibility is a lateral transfer of genes coding for virulence factor. Ambrosia beetles are often associated with fungal species of the genus *Fusarium*, in which lateral transfer of virulence genes between closely related species appears common [17].

7. IMPLICATIONS AND HYPOTHESES

If the theoretical framework we propose here is correct, then several practical implications follow:

— the emergence of pathogenic ambrosia and bark beetle symbioses, and perhaps invasive insect–fungus symbioses more generally, is ultimately a probabilistic process, depending on the chance mismatch between insect and novel host, combined with the chance event of the host being susceptible to the fungal symbionts. The good news is that such probabilities are relatively low for any given introduction event;

— the bad news is that the world's tropical and subtropical forests harbour thousands of fungal species associated with thousands of insect species. Even if a small percentage of those have the necessary attributes for killing naive trees, it may result in large numbers of catastrophic outbreaks. Predicting which symbioses will cause these outbreaks be may be impossible;

— tree killing requires insects to choose live trees, and it requires fungi to be pathogenic. As such, the shift of native insects into tree-killing lifestyles seems likely to be rare;

— given the diversity of insect–fungus symbioses, and the high rate of their introductions, the important research question is: are there many more 'strong invaders' around the world that are yet to invade non-native regions [2,70]? Or has the recent rise of commerce already helped release the most potent ones and the rate of dangerous introductions is likely to decline in the future?

Tree-killing by introduced insect–fungus symbioses appears to be a global phenomenon with repeated features. To understand what triggers the sudden emergence of virulence, new cases should not be studied in isolation, but within an ecological and evolutionary framework. The threat appears to be growing. As it does, the need for a comparative analysis and a more coordinated approach to the wave of invasions also grows. To date, traditional forest protection approaches based on quarantine, pesticides, and pheromones have not been successful in dealing with invasive fungus-associated woodborers. As experience with other invasive pests shows, when a comprehensive research programme is not established in response to an exotic pest introduction, the permanent loss of the host tree species is a real possibility, perhaps even likely [71].

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