Studies of ambrosia beetles (Coleoptera: Curculionidae) in their native ranges help predict invasion impact

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Abstract

Ambrosia beetles frequently invade non-native regions but are typically of no concern because most species live in dead trees and culture non-pathogenic symbiotic fungal gardens. Recently, however, several ambrosia beetle–fungus complexes have invaded non-native regions and killed large numbers of host trees. Such tree-killing invasions have occurred unexpectedly, and the mechanism of the ecological switch from dead trees to live trees has been left unexplained, or termed an "evolutionary mismatch." We demonstrate that the mismatch hypothesis is not supported in the redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae), because this beetle is able to colonize live trees also in its native range and its symbiotic fungus acts as a pathogen in some native hosts. We further synthesized findings from recent literature and unpublished observations on several other invasive fungus-associated beetles such as *Euwallacea fornicatus* (Eggers) (Coleoptera: Curculionidae), *Platypus quercivorus* Murayama (Coleoptera: Curculionidae), and *Pityophthorus juglandis* Blackman (Coleoptera: Curculionidae) to present an alternative to the "evolutionary mismatch" hypothesis. The revised hypothesis is that the majority of destructive ambrosia beetle species that have invaded new regions are already capable of colonizing living tree tissues in their native habitats. Furthermore, associated fungi are typically mildly to strongly pathogenic to native host tree species. A predisposition to colonize living tree tissues occurs in very few ambrosia beetle species, but these species predictably act as pests in invaded regions. Thus, simple screening of ambrosia beetle–fungus pairs for this particular ecological trait—colonization of live tree tissues—in their native habitats could help discriminate future tree-killing invasive pests from the majority of species that likely remain harmless.

Key Words: fungus farming; Scolytinae; invasive; pathogen

Resumen

Los escarabajos descortezadores frecuentemente invaden las regiones no nativas, pero normalmente no son motivo de preocupación porque la mayoría de las especies viven en árboles muertos y cultivan hongos simbióticos no patógenos. Recientemente, sin embargo, varios complejos escarabajo descortezador-hongo han invadido regiones no nativas y han matado un gran número de árboles hospederos. Tales invasiones que matan árboles han ocurrido inesperadamente, y el mecanismo del cambio ecológico de árboles muertos a los árboles vivos se ha dejado inexplicado, o denominado un "desajuste evolutivo". Demostramos que la hipótesis de desajuste no es apoyada en el escarabajo descortezador de aquacatillo, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae), porque este escarabajo es capaz de colonizar árboles vivos también en su área de distribución nativa y su hongo simbiótico actúa como patógeno en algunos hospederos nativos. Además, se sintetizaron los hallazgos de la literatura reciente y observaciones no publicadas sobre varios otros escarabajos invasores asociados a hongos como *Euwallacea fornicatus* (Eggers) (Coleoptera: Curculionidae), *Platypus quercivorus* Murayama (Coleoptera: Curculionidae) y *Pityophthorus juglandis* Blackman (Coleoptera: Curculionidae) para presentar una alternativa a la hipótesis del "desajuste evolutivo". La hipótesis revisada es que la mayoría de las especies de escarabajos descortezadores destructivos que han invadido nuevas regiones ya son capaces de colonizar tejidos de árboles vivos en sus hábitats nativos. Además, los hongos asociados son típicamente leve a fuertemente patogénicos para especies de árboles hospederos nativos. Existe una predisposición a colonizar los tejidos de los árboles vivos en muy pocas especies de escarabajos descortezadores, pero estas especies actúan como plagas en regiones invadidas. Por lo tanto, la simple selección de pares de escarabajos descortezadores-hongo para esta caracteristica ecológica particular — colonización de tejidos de árboles vivos —en sus hábitats nativos podría ayudar a discriminar plagas invasoras que matan árboles de la mayoría de especies que probablemente permanecerán no dañinas en el futuro.

Palabras Clave: cultivo de hongos; Scolytinae; invasor; patógeno

Most ambrosia beetles are harmless, economically unimportant wood-boring beetles; however, the group also includes some of the most invasive and destructive tree pests. For example, the redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae), carries a pathogenic ambrosia fungus, *Raffaelea lauricola* T. C. Harr., Fraedrich & Aghayeva (Ophiostomataceae), that has nearly eradicated plants in the family Lauraceae from southeastern North America (Hughes et al. 2015) and is impacting the avocado industry in Florida (Shearman et al. 2015). Similarly, in California and Israel, an undescribed relative of *Euwallacea fornicatus* (Eggers) (Coleoptera: Curculionidae) is killing residential trees and threatening avocado groves (Mendel et al. 2012). Recent ambrosia beetle and fungus outbreaks in Japan and South Korea have killed thousands of oak trees (Kubono & Ito 2002; Kim et al. 2009).

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The ~3,500 species of ambrosia beetles include members of at least 11 independent clades of minute wood-boring weevils (the majority of them in the subfamily Scolytinae) that have obligatory associations with ambrosia fungi. The majority of these beetles seek dead or dying trees and excavate tunnels in the xylem, where they inoculate symbiotic fungi. Obtaining nutrients from the deteriorating tree tissues, the fungi are established in a "garden" to be eaten by the beetles and their progeny.

A small percentage of ambrosia beetle species introduced into non-native habitats cause significant damage to live trees whereas most species continue to occupy their original ecological niche, dead wood. Therefore, the few ambrosia beetle invasions that have caused major damage to economically important trees are regarded as surprises (Ploetz et al. 2013). Most cases of newly established ambrosia beetles are still assumed to be non-damaging because researchers lack understanding of which traits may predispose some species to become tree-killing invasive pests.

Unfortunately, invasive ambrosia beetles have been studied primarily in their introduced ranges. A lack of native-range studies is not unique to ambrosia beetles; most invasive species are studied only where they cause damage (Hierro et al. 2005; Prior et al. 2015), yet documenting species ecology and interactions in native ranges can clarify the traits that increase species' invasion potential (Sakai et al. 2001; Hierro et al. 2005; Prior et al. 2015). Identifying traits associated with invasiveness has been a long-standing goal in invasion biology (Kolar & Lodge 2001). Identifying the traits associated with invasiveness and pathogenicity in a species' native environment is especially important so that the potential for confounding the effects of evolutionary mismatches in novel environments can be taken into account (Sakai et al. 2001).

Recent observations of ambrosia beetles in their native ranges suggest that most invasive ambrosia beetles that cause damage share one trait: the capacity to colonize living tree tissues. In contrast, the majority of ambrosia species that are economically inconsequential in invaded habitats appear restricted to dead trees in native regions. To test the above hypothesis, we pursued new observations on the native ecology of the most destructive invasive ambrosia beetle, *X. glabratus*, and compared our case with several other cases of invasive ambrosia beetles where information has become available about their life histories and ecological interactions in their native ranges. Taken together, these cases suggest that the ability to colonize living tree tissues occurs in very few ambrosia beetle species, and those species predictably act as pests in invaded regions. Thus, by testing more widely for a preexistent capacity to colonize living tree tissue, a more refined subset of potentially pestiferous species is more likely to be determined.

Materials and Methods

We observed the ecology of *X. glabratus* in its native range in Taiwan, specifically in the Huisun forest reserve of the National Chung Hsing University (NCHU). For 10 d, ambrosia beetles from any tree material in the vicinity of the station including from stressed but living trees, recently dead trees, and trees in decline were collected and identified in the field by using a handheld 20× magnifier. Ambrosia fungi from the galleries of *X. glabratus* were collected and identified. Three separate beetle galleries from surveyed trees (*Machilus zuihoensis* Hayata; Lauraceae) that displayed wilting of foliage were dissected. In the NCHU mycology laboratory, the fungi were extracted from the galleries in a laminar flow hood by using a sterile scalpel and were plated on *Ophiostoma*-selective cycloheximide-streptomycin malt agar (Harrington et al. 2011). We also plated wood from adjacent branches displaying wilted foliage and black staining in the cambial layers. The fungi consistently isolated from both galleries and symptomatic branches were initially identified based on morphology, and the identification was confirmed by comparison of their large subunit ribosomal DNA sequences to that of other *Raffaelea* species downloaded from National Center for Biotechnology Information GenBank (EU123077, EU177443, EU984299, EU984284). Data on other species treated here are from literature or from personal communications as referenced in the text.

Results

In Taiwan, we repeatedly observed *X. glabratus* colonizing living tissues of *M. zuihoensis* that exhibited localized, possibly transient, damage. Although we were able to collect beetles from one degraded log, *X. glabratus* is reliably collected in the field by searching for lauraceous hosts that are not in decay but are injured or have recently died. Such colonization of injured trees was also previously observed in Taiwan on another lauraceous host, *Cinnamomum osmophloeum* Kanehira (J. Peña, University of Florida, personal communication). Even small injuries such as those from a squirrel removing bark can support a localized beetle colony (Fig. 1), which then results in fungus establishment, adjacent tissue necrosis, and foliar wilt (Fig. 2). On branches bearing wilted leaves, internal symptoms of the colonization consist of dark streaks of vascular discoloration originating from the beetle galleries and extending vertically in the branches. These symptoms in Asian hosts are consistent with those seen in North American Lauraceae in decline due to laurel wilt disease. *Raffaelea lauricola* was the dominant isolate in all sampled tree tissues. We conclude that in North American hosts *R. lauricola* does not trigger disease as a result of an "evolutionary mismatch" (Hulcr & Dunn 2011). More simply, the interactions between the beetle, the fungus, and lauraceous hosts already occur in the native ranges on the native tree hosts.

Several other examples of tree-killing ambrosia beetle–fungus complexes suggest that the capacity could be predicted from an understanding of ecological traits and interactions in the species' native ranges. In the next paragraphs, we present data from literature and personal communication.

Euwallacea fornicatus is a clade of cryptic beetle species associated with several ambrosial *Fusarium* species (Nectriaceae). Historically reported as a pest of tea in its native range in Asia, *E. fornicatus* has received recent international attention after its introduction into Israel and California, where the symbiotic complex damages urban and fruit trees, particularly avocados. Similar to that of *X. glabratus*, the tree-killing behavior exhibited by *E. fornicatus* was not predicted and was considered a surprise (Mendel et al. 2012; Eskalen et al. 2013). However, with the accumulation of new observations from the native region, it appears that the outbreak could have been predicted. In their native region, certain genotypes of *E. fornicatus* (currently termed the tea shot hole borer; Eskalen et al. 2013) are well-known pests on live tea bushes. Recently, populations (i.e., unidentified genotypes) of the *E. fornicatus* complex attacking live trees in their native regions have been reported. In China, these populations attack maples planted in a city (Li et al. 2014); in Vietnam, most damage is on plantations of *Acacia mangium* Willdenow (Fabaceae) (R. Rabaglia, United States Department of Agriculture Forest Service, personal communication); and in Thailand, damage has been identified in durian orchards (W. Sittichaya, Prince of Songkla University, personal communication). The beetle–fungus couple exhibits the same interactions with trees in Asia as it does in Israel and in the United States: slow accumulation of and eventual mass colonization by the beetles in susceptible trees facilitated by the mild pathogenicity of the fungus. The invasion of *E.*

Figs. 1 and 2. *Machilus* (Lauraceae) trees in Huisun Forest, Taiwan, colonized by *Xyleborus glabratus* and *Raffaelea lauricola*. **1.** Wood pieces excised from an injured but living tree. Staining is a reliable sign of *R. lauricola* establishment. **2.** Injured trees showing symptoms of laurel wilt. Photographs by A. Black.

fornicatus in California and Israel would not have been a surprise if the beetle interactions with hosts had been documented in its native range in Asia.

Platypus quercivorus Murayama (Coleoptera: Curculionidae) and its fungal mutualist *Raffaelea quercivora* Kubono & Shin. Ito (Ophiostomataceae) have been destroying oak forests across Japan at the rate of approximately 2,000 ha/yr. It is unclear whether the beetle is truly native to Japan, but it is clear that its range has expanded dramatically as a result of epidemics occurring roughly since the beginning of the 21st century (Shoda-Kagaya et al. 2010). Consistent with our hypothesis, the beetle has been infesting living trees since the early 20th century (Saito 1959), but such infestations have rarely been reported and never in western literature until the recent major outbreaks.

The genus *Xylosandrus* contains multiple species that are globally invasive and frequently damaging in nurseries and orchards, most notably *Xylosandrus crassiusculus* Wood (Coleoptera: Curculionidae), *Xylosandrus germanus* Hoffman (Coleoptera: Curculionidae), and *Xylosandrus compactus* Wood & Bright (Coleoptera: Curculionidae). All three have been reported as occasional pests of live trees and shrubs in their native southern and eastern Asia (Kaneko et al. 1965; Nobuchi 1981; Lin et al. 1994).

Several other ambrosia beetle species had been recorded as capable of colonizing live trees before they became invasive. The fungal symbionts of some of these beetles were also reported as weak pathogens. Examples include *Megaplatypus mutatus* Bright & Skidmore (Coleoptera: Curculionidae) with *Raffaelea santoroi* Guerrero (Ophiostomataceae) (Alfaro et al. 2007) and *Euwallacea interjectus* Wood & Bright (Coleoptera: Curculionidae) with *Fusarium* sp. (Kajii et al. 2013).

The hypothesis that ambrosia beetles engaging with live hosts often cause damage in non-native regions may be extended to invasive bark beetles (Curculionidae: phloeophagous Scolytinae), specifically to cases where the bark beetle species is associated with a fungus. The walnut twig beetle, *Pityophthorus juglandis* Blackman (Coleoptera: Curculionidae), appears to have been introduced from its native populations in southern Arizona and Mexico into several regions across North America. Across the non-native regions, the beetle became a vector of what appears to be a native but originally rare fungus *Geosmithia morbida* Kolarik, Freeland, Utley, & Tisserat (Hypocreales) (Zerillo et al. 2014) and killed many individuals of a non-native host species, the black walnut (Tisserat et al. 2009). This invasion was a surprise because most other *Pityophthorus* species are known to colonize dead tissues, and it was assumed that this previously unstudied bark beetle likewise caused no damage. However, a recent closer inspection of the ecology of this beetle in its native range revealed that it is a specialist on stressed and shaded-out living twigs, and thus is unusual among *Pityophthorus* species (Tisserat et al. 2011).

Discussion

Several species of ambrosia beetles and fungi are capable of colonizing living tree tissues as a normal part of their ecology. Therefore, the capability to colonize and kill living tree tissues in a non-native habitat is an adaptive trait in these several species rather than an "evolutionary mismatch" as previously proposed by Hulcr & Dunn (2011). Colonization of living tissues appears to be a result of evolutionary adaptations such as olfactory preferences in the beetle and in some cases may have been facilitated by the evolution of pathogenicity of the symbiotic fungus. The key implication is that invasions of these particular tree-killing ambrosia beetles into new regions and colonization of susceptible tree hosts are predictable and should no longer be perceived as surprises.

The key support for our hypothesis comes from new observations on *X. glabratus*, the redbay ambrosia beetle, and its symbiotic fungus, *R. lauricola*, in their region of origin. Previously, Hulcr & Dunn (2011) and other authors treated the "emergence" of tree-killing behavior in invaded habitats as "sudden" based on the assumption that this beetle species is an "ordinary" ambrosia beetle that colonizes dead tissue in its native habitat. The initial hypotheses explaining the change included altered beetle behavior and altered interactions between its symbiotic fungus and naïve host plants. Our revised hypothesis based on our new observations suggests that the beetle behavior and the fungus pathogenicity are original traits, and we assert that this is a more parsimonious hypothesis than the sudden-change hypothesis.

In some cases, scolytine beetles in their native regions attack non-native live trees. Frequent reports from tea, coffee, and acacia plantations across Asia support this statement. In those cases, the hypothesis of evolutionary mismatch still remains a valid working hypothesis because the 2 taxa had not interacted in their evolutionary past.

The ~3,500 ambrosia beetle species employ many ecological strategies ranging from living in rotten wood (Li et al. 2015) to parasitizing live tree tissues (Kirkendall 2006). For the unusual species capable of colonizing stressed but still living tree tissues, this habit may not be an obligate or even a common strategy and may be expressed only in situations where hosts are stressed. The key point is that these few species are capable of occupying this ecological niche. This is different from the majority of other ambrosia beetle species, which are not capable of colonizing living host tissue as a part of their ecological repertoire, whether in native or invaded regions.

The several case studies that we present here, including our new native range observations, highlight that species ecology needs to be studied in native environments before the taxa establish elsewhere and cause damage. Knowledge about species ecology may facilitate the ability to predict invasion and tree-killing capability thus increasing the ease of pre-invasion assessments. We suggest that in ambrosia beetles pre-invasion evaluation is feasible. The biological feature that seems most relevant to predict damaging ambrosia species is the ability to colonize tree tissues that are still fully or partially alive. Beetle faunas overseas can be readily screened for this capability as it is straightforward to experimentally injure trees and assess which species can breed in the moribund tissues.

Such screening for species with the capacity to colonize living tissues should not be equated with screening for beetles that are already high-profile pests in their native habitat. It is not the pest status in the native region that can predict pestiferous behavior in the non-native region. Instead, it is an intimate ecological relationship between the beetle and its host plant. For example, the "Prioritized offshore pests" list used by United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) is composed largely of species that have been classified as pests elsewhere. More often than not, damage to native hosts results from the beetle's adaptation to local hosts and conditions and, therefore, is not necessarily a universal predictor of invasiveness.

Additionally, we do not argue that any ambrosia beetle and fungus that cause twig death in native habitats are automatically a biosecurity threat. Instead, we suggest that these species should be the first candidates for pathogenicity testing of the fungus against important tree commodities elsewhere.

A popular approach to predicting potentially invasive species relies on gross-scale models where species–environment relationships are modeled using a few variables across species (Kamata et al. 2002; Evangelista et al. 2011; Marini et al. 2011). Such approaches are facilitated by contemporary statistics and global data availability but have yet to yield reliable predictions for particular ambrosia or bark beetle invaders. Our field observations suggest that a nimbler, group-specific focus may be more revealing than gross-scale perspective. Group-specific focus allows for the depth necessary to explore insects in their native habitats where they are often understudied and allows for the inference of unique variables that are too detailed for gross-scale modeling, but that are necessary for predicting potential invasive species and their impacts.

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