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# The Role of Mites in Bark and Ambrosia Beetle-Fungal Interactions

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Additional information is available at the end of the chapter

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## Abstract

Insects share complex interactions with mites and fungi that range from obligate mutualisms to antagonistic relationships. These multitrophic interactions often result in changes to the host environment and population dynamics of the insect. Here, we review Scolytidae and Platypodidae beetles (bark beetles and ambrosia beetles, Coleoptera: Curculionidae) and their micro-organismal interactions with mites and fungi. Many bark beetles and ambrosia beetles are closely associated with mutualistic fungi used as a food source. These fungi are carried by the beetles in specialized pockets called “mycangia.” In addition to beetle-specific fungi, secondary fungi are often vectored by mite populations phoretic on the beetles. These secondary introductions create a complex fungal micro-biome within the host tree of the associated Scolytid beetles, with a myriad of consequences to beetle success and tree mortality. In this chapter, we provide a detailed review of specific beetle-fungal and mite-fungal associations, mutualistic and antagonistic effects of these fungal relations, and ecological and evolutionary consequences of beetle-fungal-mite relationships within the host complex.

**Keywords:** *Scolytinae*, phoresy, symbiosis, *Acari*, fungi, mycangia

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## 1. Introduction

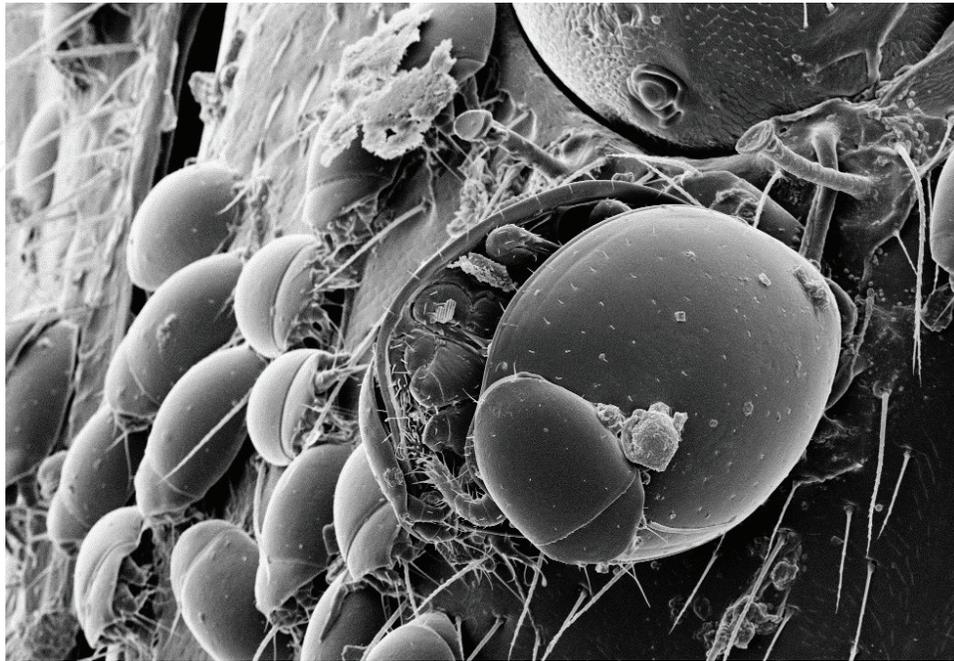
A wide diversity of symbionts has contributed to the success of bark and ambrosia beetles (Curculionidae: Scolytinae) [1]. All ambrosia beetles and most bark beetles have mutualistic fungi that serve as a nutrition source for young and adult beetles. However, some fungal (and other) symbiotic associations may be detrimental to beetles. Other beetle symbionts include mites that are frequently found traveling on adult beetles and live under the bark of beetle-infested trees [2]. Similar to fungi, the impacts of mites on beetles vary widely. Mites too can be beneficial or detrimental to beetles. Some mite species can contribute to the fungal diversity in

beetle galleries by transporting spores within and between trees [3, 4] impacting the behavior, development, and population dynamics of beetles [5, 6]. Such complex systems are evolutionary unique and can be considered principal factors in the success of Scolytid beetles.

Ambrosia beetles possess symbiotic mutualistic relationships with fungi (*Ambrosiella* and *Raffaelea* spp.) [7–9]. Ambrosia beetles excavate tunnels within the wood of host trees, termed “galleries,” within which female beetles oviposit eggs. The symbiotic fungi are carried by the female ambrosia beetle in a specialized pocket, termed “mycangium.” The fungal inoculate is deposited along the walls of the gallery where it grows and serves as food for larval broods and adult beetles [10, 11]. Fungi allow ambrosia beetles to exploit the wood that would have otherwise been a nutritionally poor resource, as well as exploit living trees. In California and Israel, an invasive ambrosia beetle poses a serious threat to avocado plantations via the introduction of a *Fusarium* fungus species causing dieback, wilting, and ultimately host tree mortality [12]. Similarly, adult leaf-cutter ants (Attini: *Atta* or *Acromyremex*) use leaves to foster the cultivation of fungi inside their colonies, which they in turn use as a food source [13], resulting in large-scale defoliation of nearby trees [14]. Contradictory, fungi can serve an antagonistic function in insect development or survival. *Cordyceps* is an obligate, directly transmitted fungus that requires specific insects for reproduction [15], parasitizes tropical ants (among many other insects), and results in colony collapse and mortality by taking control of the host ants behavior [16]. Other fungal pathogens can result in the direct mortality of insects. For instance, blue-staining fungi, such as *Ophiostoma minus*, can cause the mortality of southern pine beetle larval broods by out-competing the beetle mycangial fungi [5]. *Beauveria bassiana* is a common insect pathogenic fungi that kills insects in a variety of habitats and has been demonstrated as an effective mortality agent against bark and ambrosia beetles such as the almond bark beetle, *Scolytus amygdali* [17], responsible for the destruction of almond plantations.

Mites (Subphylum: Chelicerata, Class: Arachnida, Subclass: Acari) share a common, but important relationship termed “phoresy” with insects and other organisms [18]. Phoresy refers to an interspecific relationship between two species where one acts as a host and the other acts as a “phoront,” attaching itself to the host for the purpose of dispersal or migration. Consequently, Farish [19] explicitly defines “phoresy” as follows: a phenomenon in which one animal actively seeks out and attaches to the outer surface of another animal for a limited time during which the attached animal (the “phoretic” animal or “phoront”) ceases both feeding and ontogenesis, presumably resulting in dispersal from areas unsuited for further development, either of the individual or its progeny. This sort of commensalism is common in species that live in rapidly changing environments, and/or in species that have limited mobility [20]. Mites are small-minute organisms ranging from 50  $\mu\text{m}$  to 3 mm in body length [21, 22] and thus have limited dispersal ability, other than being blown by the wind or carried by other animals or objects. They generally feed on other small arthropods or larvae and eggs of other arthropods, nematodes, fungi, bacteria, or dead organic matter [21]. Due to their small size and limited mobility, mites are likely to be phoretic on insects that are able to transport them quickly and efficiently, i.e., flying insects such as bees (Hymenoptera), beetles (Coleoptera), and flies (Diptera). For instance, mites associated with ants tend to prefer alate queens (i.e., flying queens) over workers or any other type of ant [23], presumably because they are able to travel longer distances over a short span of time and can be introduced into future ant nests. Mites are usually found attached to setae (i.e., external hairs), to grooves in

the tarsi, under the wings, under the elytra (hardened exoskeleton of beetles), or attached to any part of an insect's body that provides a firm holdfast (**Figure 1**).



**Figure 1.** Scanning electron image of phoretic mites on *Dryocoetes confusus* (Coleoptera: Scolytidae). Picture taken at Northern Arizona University by R. Hofstetter; Nov. 2006. Image is 500× magnification.

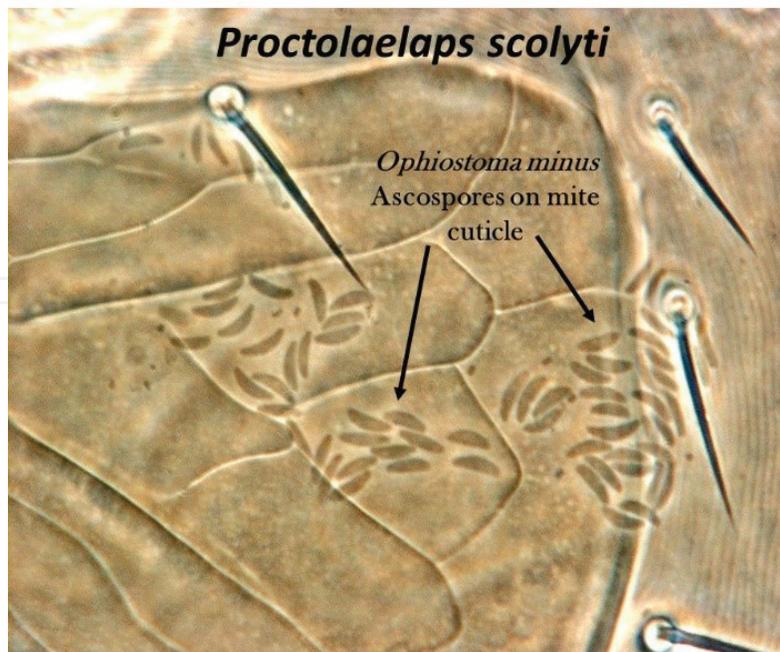
Phoretic mites may have either advantageous, disadvantageous, or no effect on their insect host. During the act of phoresy itself, even though mites cease to feed, their mere presence may be antagonistic/parasitic as insects can be weighed down by the presence of numerous mites (e.g., southern pine beetles being weighed down by masses of Uropodine mites [24]) slowing down flight speed and increasing energy expenditure (**Figure 2**). The risk of antagonistic effects increase when mites are deposited at the insect's final destination. For example, varroa mites (*Varroa destructor*) associated with honeybees (Hymenoptera: Apidae) are known to carry the deformed wing virus (Iflaviridae); this causes new bees to emerge with crumpled dysfunctional wings rendering them useless to the colony, resulting in eventual colony collapse disorder [6]. Adult bees with varroa mites have also been shown to have significantly less protein, lipid, carbohydrate, and water content [25]. Other destructive mites are known to feed on insect larvae and eggs. For example, mites of the genus *Iponemus* are predatory on beetle eggs and larvae [26]. Other mites, such as *Tarsonemus ips* vector fungi useful for the development of southern pine beetle (Coleoptera: Curculionidae, Scolytinae) larvae (i.e., associated mycangial fungi) [22, 27]. Much like beetles, mites in turn act as vectors of microbes (fungi, bacteria, and viruses), which may present either a beneficial or a detrimental consequence for the insect and/or host plant(s). For example, the mite *Siteropsis reniformis* is associated with carrying the lint rot fungus, *Nigrospora*, which results in the rotting and death of cotton bolls in California [28]. Some *Tarsonemus* mite species associated with bark beetles (such as the southern pine beetle) carry the blue-stain fungus *O. minus*, which causes infection of phloem, host tree death, and ultimately beetle mortality (**Figures 3 and 4**) [2, 5, 29].



**Figure 2.** Phoretic *Trichuoropoda* sp. mites on the western pine beetle, *Dendroctonus brevicomis*. Picture taken by R. Hofstetter, Dec. 2016. Flagstaff, AZ, USA.



**Figure 3.** *Tarsonemus ips* mite with *O. minus* ascospores (dark banana shape spores). Mite was collected from the southern pine beetle, *Dendroctonus frontalis* in Alabama 2001 by R. Hofstetter.



**Figure 4.** *Proctolaelaps scolyti* mite with *O. minus* ascospores (dark banana shape spores). Mite was collected from the southern pine beetle, *D. frontalis* by John Moser.

## 2. Bark and ambrosia beetle-fungal interactions

Ambrosia beetles and bark beetles (Coleoptera: Curculionidae, Scolytinae) are known to share intimate relationships with fungi. The subfamily Scolytinae consists of bark beetles (~7000 species), ambrosia beetles (~3400 species), and other various seed and pith-feeding beetles [8, 30]. A prominent characteristic of Scolytinae is a widespread association with fungal species, particularly the bark beetles and ambrosia beetles. These fungal associations are mutualistic or commensal (i.e., benefiting the fungi via dispersal by beetles) with beetles and are primarily Ascomycetes in the genera *Ophiostoma*, *Fusaria*, *Grosmannia*, *Ceratocystiopsis*, and *Ceratocystis* [7, 31, 32]. Scolytinae are thought to have evolved in the late Jurassic—early Cretaceous period with these fungi, historically switching back and forth from angiosperm hosts to coniferous hosts [8]. The development of mutualisms with fungi helps explain diversification of Scolytinae to inhabit coniferous habitats and exploit a limiting resource such as living tree tissues by growing supplementary fungi within it.

### 2.1. Bark beetle-fungal associations

Bark beetles can be distinguished from ambrosia beetles and other Scolytinae by the fact that they exclusively invade the bark and phloem of trees, and not the woody tissue. Fungi associated with bark beetles are carried/introduced to the host in one of two ways—mycangially or nonmycangially—which indicate the specificity of the relationship between the fungus and the beetle. Some bark beetles such as the southern pine beetle (*Dendroctonus frontalis*) and the mountain pine beetle (*Dendroctonus ponderosae*) possess specialized structures called “mycangia” or “mycetangia,” meaning “fungal vessel.” Mycangia are strictly defined as specialized

invagination of the integument lined with secretory glands used for the transport of fungi [33]. However, the term “mycangia” is often loosely used to describe invaginations that carry fungal spores [7]. These mycangial fungi (grown as a yeast-like structure or spores within the mycangia) are introduced by the beetle into the tree phloem where it eventually provides food for the developing offspring. The growth of fungi within the mycangia is supported by the glandular secretions of the mycangia [34]. Nine bark beetle species are known to have well-defined mycangia [32] (**Table 1**). There are several different kinds of mycangial fungal species: bionectrotrophic blue-staining ascomycetes, saprophytic ascomycetes, or saprophytic basidiomycetes [35]. For example, the southern pine beetle is associated with two types of mycangial fungi: *Ceratocystiosis ranaculosus* (ascomycete) and *Entomocorticium* sp. A (basidiomycete) [4, 36], and the mountain pine beetle is associated with three Ophiostomatoid mycangial fungi—*Ophiostoma montium* [37], *Grosmania clavigera*, and *Leptographium longiclavatum* [38, 39] but are also known to harbor *Ceratocystiopsis* and *Entomocorticium* [40]. However, only one fungal species exists within an individual beetle’s mycangium and is inherited from the original parental pair [2, 41]. Other bark beetles such as (most) *Ips* spp. transport fungal spores without using a mycangia; i.e., spores are present in grooves or pits found on the beetle’s exoskeleton. For example, *Ips typographus*, the spruce beetle, which is responsible for extensive

Bark Beetle	Tribe	Principal plant hosts	Mycangial type	Ascomycete associates	Basidiomycete associates
<i>Dendroctonus frontalis</i>	Tomicini	<i>Pinus</i> spp.	Prothoracic, glandular	<i>Ceratocystis ranaculosus</i>	<i>Entomocorticium</i> sp. A
<i>D. brevicomis</i>	Tomicini	<i>P. ponderosae</i> , <i>P. coulteri</i>	Prothoracic, glandular	<i>C. brevicomis</i>	<i>Entomocorticium</i> sp. B
<i>D. approximatus</i>	Tomicini	<i>Pinus</i> spp.	Prothoracic, glandular	Unknown	<i>Phlebiopsis gigantea</i>
<i>D. adjunctus</i>	Tomicini	<i>Pinus</i> spp.	Prothoracic, glandular	<i>Leptographium pyrinum</i>	Unknown
<i>D. ponderosae</i>	Tomicini	<i>Pinus</i> spp.	Maxillary	<i>Ophiostoma clavigerum</i> , <i>O. Montium</i>	<i>Entomocorticium dendroctoni</i> , <i>E. sp. D,E,F,G,H,P. gigantea</i>
<i>D. jeffreyi</i>	Tomicini	<i>P. jeffreyi</i>	Maxillary	<i>O. clavigerum</i>	<i>Entomocorticium</i> sp. E
<i>Tomicus minor</i>	Tomicini	<i>Pinus</i> spp.	Unknown	<i>O. canum</i> , <i>Ambrosiella tingens</i>	Unknown
<i>Ips acuminatus</i>	Ipini	<i>Pinus</i> spp.	Mandibular	<i>O. clavatum</i> , <i>A. macrospora</i>	Unknown
<i>I. avulsus</i>	Ipini	<i>Pinus</i> spp.	Unknown	<i>O. ips</i>	<i>Entomocorticium</i> sp. 1
<i>Pityoborus comatus</i>	Corthylini	<i>Pinus</i> spp.	Prothoracic, pubescent	Unknown	<i>Entomocorticium</i> sp. C.

**Table 1.** Information adapted from Harrington, 2005 (Insect-fungal associations: ecology and evolution, p. 264)—Nine species of bark beetles associated with well-defined mycangial, and their associated fungi.

tree damage in Europe and in Asia [42], is associated with fungal species of *Ceratocystiopsis*, *Ceratocystis*, and *Grosmania* as well as *Pyxidiophora* sp. carried externally in grooves on the surface of the exoskeleton [43]. *Ips perterbatus* (the northern spruce engraver) is associated with 13 different Ophiostomatoid fungi [44] and thus also acts as a potential vector of tree-killing Ophiostomatoid fungal pathogens. *Ips sexdentatus* (a highly prevalent species in Europe) is associated with carrying a plethora of ascospores, some among the *Ophiostoma* genus [45]. Consequently, beetles that are mycangially associated with fungi seem to possess a stronger fidelity to their allied fungi, whereas those that are not mycangially associated are less specific as they are merely vectors [8]. For example, western pine beetle (*Dendroctonus brevicomis*) is known to exhibit strong fidelity to one of two inherited mycangial fungal symbionts, *Ceratocystiopsis brevicomi* and/or *Entomocorticium* sp. B, which is suggestive of coevolution of the beetle with their associated fungi [35, 41]. Other fungi associated with the western pine beetle, such as *O. minus* or *O. ips*, are not carried in the mycangia and are antagonistic to the beetle.

## 2.2. Ambrosia beetle-fungal associations

Ambrosia beetles (Family: Curculionidae; subfamily: Scolytinae) occur worldwide and share close novel symbioses with fungi, such as *Ambrosiella* spp. and *Raffaella* spp. [7–9, 46], which rely on arthropods for efficient dispersal. Beetle-fungal symbiosis in ambrosia beetles is one of the earliest known associations of insect-fungal relationships, and this specific association is a primary reason for their success [8, 30]. Ambrosia beetles are “xylomacrophagous” (feed on fungi grown in the xylem), and their activity is easily recognized by the distinct staining of wood by the inoculation of ectosymbiotic fungi, used as the sole nutrient source by both adults and larvae [10, 11, 47, 48]. Like bark beetles, ambrosia beetles transport these fungi via specialized mycangia [49], the location of which differs between beetle species [50]. Typically (as seen in European ambrosia beetles), females tend to have more well-developed mycangia [49], i.e., large and lined with glandular dermal cells containing a waxy substance [51] than males, and are responsible for depositing the fungi along the tunnel walls [10, 50]. The waxy secretions of the female mycangium contribute to the growth of ambrosia cells [52]. Ambrosia beetles may or may not exhibit specificity to ambrosia fungi. Batra [10] suggests that ambrosia beetles rely on a primary (mycangial) and auxiliary ambrosia fungi depending on the life stage and do not exhibit mycangial specificity to ambrosia fungi. However, further study shows ambrosia beetles in the genus *Xylosandrus* (which are exotic in the United States [46]) exhibit high specificity to a given ambrosia fungus in the genus *Ambrosiella* [53]. This type of fungal specificity highlights a unique obligate symbiosis between ambrosia beetles and ambrosia fungi and suggests coevolution of the beetle with its fungal associate [8].

Ambrosia beetles are not typically associated with significantly damaging tree diseases in the way bark beetles are, as they often attack trees that are already dead or severely stressed [41, 51, 54, 55]. Coevolution theory suggests that the ambrosia beetle-fungal association is adaptable to a given host environment. However, problems arise when atypical beetle-host relationships form, i.e., exotic ambrosia beetles attack foreign hosts [50, 51, 54]. A recent concern in North America is an increase in exotic species of ambrosia beetles attacking living trees with. In most cases, these beetles are inoculating trees with non-native ambrosia fungi, for which native North American trees have little resistance [46]. For example, the redbay ambrosia

beetle (*Xyleborinus glabratus*) is an exotic beetle from southeast Asia, responsible for extensive mortality of redbay trees (*Persea borbonia*) [46, 55, 56]. These beetles are closely associated with a *Raffaella lauricola*, an asexually reproducing fungus, which grows within the xylem (wood) and causes affected branches to wilt, exhibiting a symptomatic black staining of the sapwood [55, 56]. In another example, an *Euwallacea* sp. ambrosia beetle is causing damage to more than twenty tree species in California, with particular concern to avocado [12]. The damage is caused by the spread of a novel *Fusarium* fungus causing tree wilting and dieback [12].

The full ecological potential of ambrosia beetle-fungal relationships for exotic invasives is still unknown [55]. There is little available detail on phoretic mite populations of ambrosia beetles as there is for bark beetles. Therefore, we are unaware of specific mite-fungal interactions for a given species of ambrosia beetle. There is a potential for similar complex mite-fungal interactions in ambrosia beetles as there are in bark beetles, particularly in situations with multiple beetle species attacking one host tree(s).

### 2.3. Factors affecting beetle-fungal associations

Both mutualistic and antagonistic fungal associations are context-dependent and highly affected on a combination of biotic and abiotic factors such as temperature, moisture, host tree defenses, presence of other microbes (i.e., bacteria, yeast, etc.), and other arthropods. Depending upon the beetle complex in question, such context-dependent conditions suggest that some fungi benefit from multipartite relationships in bark beetles more than others, and that the beetle's ecological niche is determined by the external factors that govern it [57, 58].

Host tree type and conditions (moisture, phytochemical composition/concentrations, etc.) have a significant influence on bark beetle-fungal associations. For instance, changes in the chemistry and nutritional content of the host tree have the ability to alter the distribution and relative prevalence of fungal associates within the tree [8, 59–62]. A conifer tree's primary defenses are resins and other induced secondary chemical compounds, which vary between tree species [57, 60, 63, 64]. In their study of the effect of tree defenses against fungi associated with the southern pine beetle, Hofstetter et al. [65] found that in general the phytochemistry of *Pinus* tree species negatively impacted the growth-rate of *O. minus* fungi vectored by beetles (and their accompanying mites) but (bar a few exceptions) did not hinder growth of the mycangial fungi. This indicates that the fungal microbiome of some bark beetles is dependent upon the geographically dominant host tree species and can accordingly benefit or pose a threat to beetle population dynamics [57]. Other host tree factors like moisture content can determine the success of a fungal inoculant as well (i.e., a moisture-rich tree typically serves as a better fungal host than a dry tree [33]). Ayres et al. also found that presence of basic elements such as high nitrogen concentration is dependent on the presence or absence of mycangial fungal associations [66].

Variations in temperature are one of the most vital factors affecting the relative abundance and diversity of fungal species, in turn affecting the ecological associations of the fungus' host bark beetle [3, 67–69]. The mountain pine beetle, *D. ponderosae*, for example, is associated with *Grosmannia clavigera* and *O. montium* mycangial fungi [37, 38]. The two fungi possess differential optimal temperatures with *G. clavigera* ceasing to grow past 25°C and *O. montium* dominating between 25 and 32°C [67]. Thus, the fungal association of *D. ponderosae* bark beetles is predictable

over changes in season; i.e., the beetle will vector *G. clavigera* in cooler climates and *O. montium* in hotter climates. This in turn allows the beetle to occupy a wide geographical range (from southwestern North America into Canada) due to its ability to exploit not one, but two symbiotic resources that span a wide range of host environments. Hofstetter et al. [3] found that the growth rate of the symbiotic fungi (*O. minus*, *C. ranaculosus*, and *Entomocorticium* sp. A) of the southern pine beetle, *D. frontalis*, differs within a range of temperatures [3]. While the growth rate of *E. sp. A.* increased steeply between 8 and 22°C before reaching a stable constant, the growth rates of *O. minus* and *C. ranaculosus* were much less up to 22°C and increased in growth rate past 22°C. The growth of the two mycangial fungi associated with the western pine beetle, *D. brevicomis* (*C. brevicomi* and *Entomocorticium* sp. B) is also similarly affected by temperature and can vary between beetle populations [35]. *C. brevicomi* tends to thrive better than *E. sp. B.* at cooler and hotter temperatures, but fair similarly in intermediate temperatures. This differential growth may thus potentially reduce competition between the two fungal symbionts and vary seasonally with the beetle's movement [69]. Such differential growth can also determine which associative symbionts are lost with climate change [35].

For bark beetles associated with multiple mycangial symbionts, the prevalence of a specific mycangial fungal associate depends upon the beetle's environmental temperature and consequently determines the beetle's ability to survive in a given geographic location. Often, the presence of multiple beetle-associated fungi results in competition between the different fungal species with one species dominating the other. Changes in external factors (such as host tree chemistry and temperature) can determine the competitive advantage of a resource between multiple fungal symbionts, and also determine the success of antagonistic tree-killing pathogens such as species of blue-stain (*O. minus*, *O. picae*, *O. penicillatum*, etc.). As blue-stain fungi thrive at higher temperature ranges (recall, *O. minus* growth rate increases past 22°C), the prevalence of blue-stain will depend on climate change and its consequential temperature conditions [70]). A thorough understanding of biotic and abiotic factors affecting pathogenic and mycangial fungi can thus allow us to predict which species of fungi will potentially establish itself within a major bark beetle's niche, and what effects it may have on host tree conditions and mortality. Thus, differential responses of mutualistic fungi to temperature could reduce competition between fungal symbionts by allowing each to dominate at different times as temperatures vary seasonally, annually, or geographically [69]. These differences are also likely to determine the future symbiotic complex of beetle populations as warming increases. However, mites have the potential to disrupt, alter, or magnify beetle-fungal symbiotic complexes.

### 3. Mite-fungal-beetle interactions

Mites are a prominent phoront of bark beetles and some ambrosia beetles [2, 58]. Mites (Arachnida: Acari) are subdivided into two main super orders: Parasitiformes and Acariformes [71]. The Parasitiformes are further divided into four orders—Ixodidae, Holothyrida, Opilioacaridae, and Mesostigmata, and the Acariformes are divided into two orders—Sarcoptiformes and Trombidiformes [22]. Mites phoretic on bark beetles are predominantly species of the order Mesostigmata and Trombidiformes [62, 72, 73] and range from 80 µm (e.g., *Iponemus* sp.) to 5 mm (*Mexecheles* sp.) in body length [22]. Mites are very efficient

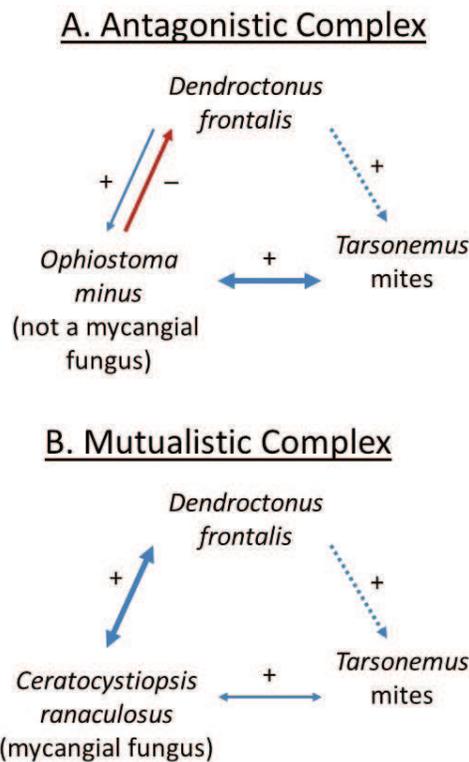
phoronts, often having specialized structures, such as suckers and tenet hairs to cling on to the host [20]. These organisms also have specialized adaptive stages/morphs for phoresy; e.g., many species (e.g., Acari: Astigmata) exhibit phoresy in the deutonymph (juvenile second-stage nymph) stage, and only one life stage is specialized to be phoretic for a given species of mite [21, 22]. Many mites phoretic on bark beetles predominantly tend to be female [26], i.e., mites exhibit sexual dimorphism where one (the female) is termed the “phoretomorph” (coined by Moser & Cross, 1975) and the other (the male) is “normal.” This phoretomorph dimorphism is seen in Pyemotidae mite species (Acarina: Tarsonemoidea) [74] and (likely) provides the opportunity for females to develop in a suitable environment for egg laying. Mites can be found attached under the elytra, at the base of the elytra, within grooves in the tarsi, on external setae, under the wings, etc. However, each mite species is specific in the location on which they attach themselves to the beetle [75], depending upon what specialized clasping adaptations it may have (based on species). Like its host insect, mites also share complex interactions with fungi; however, the details of most mite-fungal interactions are relatively unknown and understudied [58]. Mycetophagous mites (mites which feed on fungi) such as *Tarsonemus krantzi* (specifically feed on the blue-staining *O. minus* Ophiostomatid fungus) and *Histiogaster* spp. (generalist fungal feeders) carry spores on their bodies to deposit in their designated host environment (usually a medium such as the inner tissues of vascular plants/trees from which the fungi may draw nutrition). *Tarsonemus* mites possess specialized structures known as sporothecae in which they carry the fungal spores (see **Figure 3**) [62, 76]. The sporothecae are similar to the beetle’s mycangia except for the presence of gland cells. The fungi also do not multiply within the sporothecae but do so once it has been deposited in a suitable host environment [62].

The fungal symbionts of bark beetles often provide a food source for the mites, and the fungal associations of the mites provide a food source for the beetle. *Tarsonemus* mites associated with the southern pine beetle carry *C. ranaculosus* spores, which are mycangially associated with the beetle [77]. This enhances the growth of *C. ranaculosus* as a food source for both the beetle and the mite. However, between the southern pine beetle’s two mycangial fungi, *C. ranaculosus* and *Entomocorticum* sp. A., the latter is a more beneficial food source for the beetle. And the presence of *C. ranaculosus* outcompeting *Entomocorticum* sp. as the dominant fungus [77], resulting in a minor reduction of relative fitness for the beetle, but serves as a compromise for both organisms. Inadvertently, not all mite-beetle interactions result in such harmonious coexistence between the two organisms. In many cases, the presence of mites results in decreased fitness, changes in reproductive success, and even beetle mortality.

### 3.1. Role of mites in altering population dynamics of bark beetles

We know little of the potential impact of mites on beetle population dynamics. A few studies indicate that mites may influence factors affecting beetle life history such as reproductive success, development, and mortality, for example, *Iponemus confuses* L. parasitizes bark beetle eggs resulting in mortality before the occurrence of the larval stage [26]. *Resinosa* mite spp. cause mortality in *Dendroctonus pseudotsugae* eggs and early instars of larvae [36]. *Cercoleipus coelonotus* and *Dendrolaelaps quadrisetus* have been known to feed on the eggs and larvae of *I. typographus* (pine engraver) bark beetles. As mentioned earlier, *Tarsonemus* mites can cause beetle mortality by introducing blue-stain fungi that outcompete the beetle’s mutualistic mycangial fungi, causing

host tree and beetle mortality [2, 5, 29, 77]. Similarly, *Cercoleipus* mites are known to carry strains of *Ophiostoma* (specifically *Ophiostoma bruneo-cilium* and *O. montium*) that cause damage to the pine hosts of carrier bark beetles [78]. Conversely, Pfammatter and Raffa assessed the effects of phoretic mites such as *Dendrolaelaps* spp., *Iponemus* spp., *Histiogaster* spp., *Tarsonemus* spp., etc., on the reproductive success of *Ips grandicollis* bark beetles (a nonmycangial beetle) and noticed a weak positive relationship between the abundance of mites and emergence of *I. grandicollis*. This suggests that there might also be a potential mutualistic relationship between the abundance of mites and the reproductive performance of beetles. This may be due to mutual suitability of the host substrate [36], but it is still uncertain whether mites truly encourage beetle performance. Most of our understanding of mite-beetle-fungal interactions come from the widely studied southern pine beetle. *Tarsonemus* mites carrying *O. minus* spores within sporothecae deposit the fungi in the host environment of the beetle; where at first, the beetles are able to coexist and feed on this fungus; however, over time the fungus outcompetes the beetles and invades the phloem of the tree killing the beetle brood and the tree (Figure 5). The presence or absence of a particular fungal species or strain can determine the success of development emergence of beetle progeny in mountain pine beetles. Six (1998) found that mountain pine beetles associated with *O. montium* mycangial fungi had a higher production of progeny adults with earlier emergence than those associated with *O. clavigerum* fungi [79]. Adult southern pine beetle individuals that developed with the presence of mycangial fungi were also found to be larger than individuals that developed in the absence of mycangial fungi [66, 80, 81].

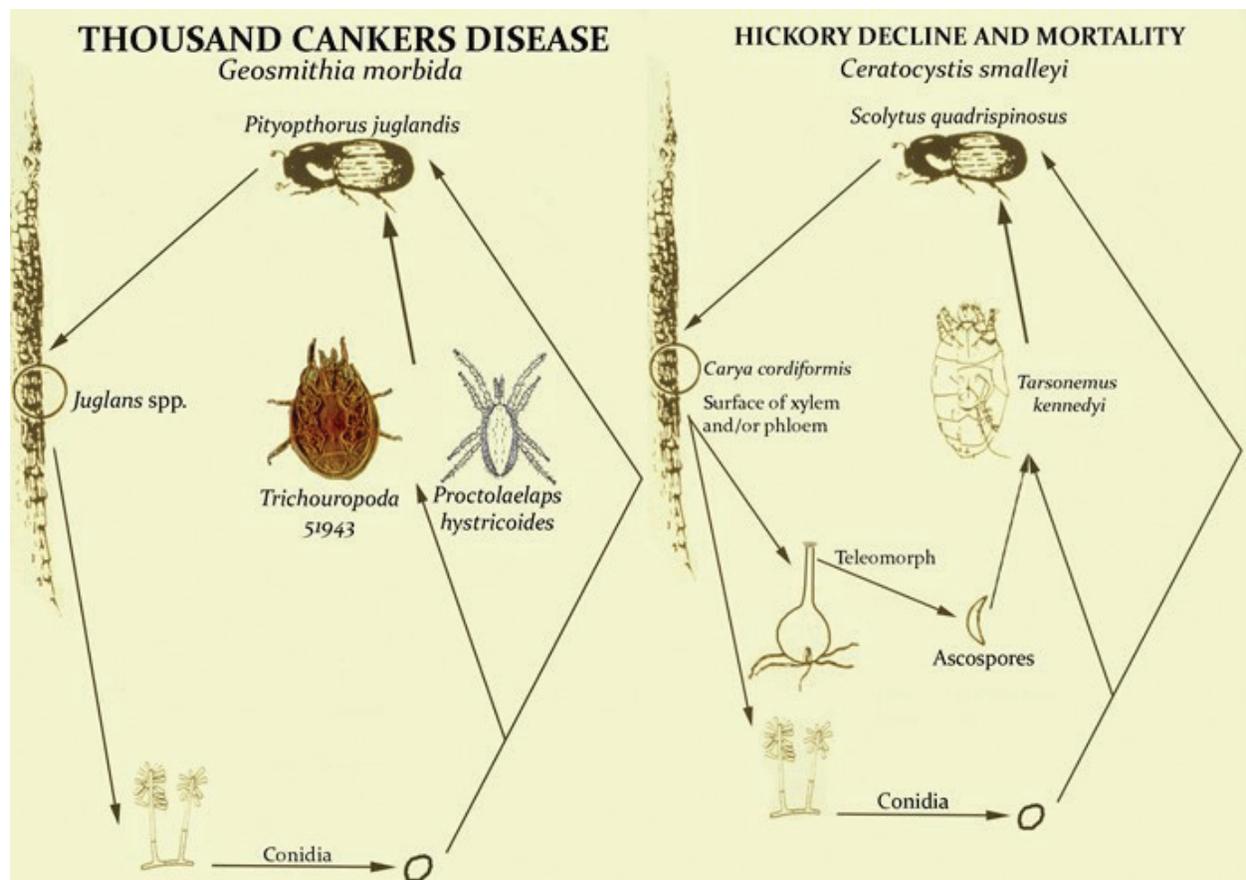


**Figure 5.** Models of interactions between the southern pine beetle, *D. frontalis*, phoretic mites of the genus *Tarsonemus*, and fungi. The fungal interaction includes either (a) the blue-stain fungus *O. minus*, which is not found associated with the bark beetle mycangium and is an antagonist of *D. frontalis*, or (b) the mycangial fungus *Ceratocystiopsis ranaculosus*, which is a mutualist of both *D. frontalis* beetles and *Tarsonemus* mites. Model A represents an indirect negative-feedback complex, and Model B represents an indirect positive-feedback complex.

The effect of mite-vectoring fungi varies between mycangial and nonmycangial bark beetles. The presence of symbiont specific mycangia (e.g., *D. frontalis*, *D. ponderosae*, and *D. brevicornis*) indicates specificity for a fungal resource and a lack of adaptability to foreign fungal competition, whereas nonmycangial beetles (such as *Ips* spp.) are simply carriers and may possess greater adaptability to a variety of potential fungal introductions. While there is no literature supporting this hypothesis, it is a topic for future study to help us understand the role of mites in beetle life history.

### 3.2. Role of mites in spreading fungal pathogens

Bark and ambrosia beetles have been pinpointed as one of the primary vectors of tree disease-causing pathogens such as *Fusarium* dieback and Dutch elm disease. In some cases, tree pathogenic fungi have been isolated from the external surface of beetles, i.e., they are not mycangial fungi. Mite-beetle interactions suggest that it is more likely that the guilty party is the mites vectored by the beetle than the beetle itself (e.g., **Figure 6**) [82, 83].



**Figure 6.** Hypothetical beetle-fungal-mite complex resulting in host tree disease or decline as seen in the Thousand Cankers Disease and Hickory Decline and Mortality. Created by J. Moser 2012.

Bark beetles are associated with an array of mites. The southern pine beetle alone is associated with 96 different species of mites [73]. The mountain pine beetle is associated with 57 different phoretic mite species [83], and the spruce beetle (*Dendroctonus rufipennis*) is associated with up to 10 different species of mites [84]. Other bark beetles such as *Ips* beetles (pine

engravers) are also associated with mite species, though the diversity is less than that of *Dendroctonus* species. *Ips grandicollis*, a bark beetle prevalent in the Great Lakes area, was found to be associated with nine different phoretic mite species [36] and *Ips pini* is associated with up to five different species of phoretic mites [85]. *I. sexdentatus* have been associated with nine different mite species, which in turn were associated with ~16 morphologically distinct fungi [45]. Not all of these bark-beetle-associated mites are carriers of fungal pathogens. However, there are specific genera of mites that are associated with the spread of fungal pathogens and whose occurrence overlaps between the different species of bark beetles.

Dutch elm disease, a vascular wilt disease that affects elm trees, is caused by the introduction of the Ascomycete species (such as *Ophiostoma novo-ulmi* and *Ceratocystis ulmi* (Buis)) (Kinn, 1970). The spread of this deadly disease in Europe has been associated with elm bark beetles in the genus *Scolytus* [72]—*Scolytus multistriatus*, *Scolytus pygmaeus*, and *Scolytus scolytus*. However, like many other bark beetles, these elm bark beetles are associated with phoretic mite species such as *Elattoma fraxini*, *Proctolaelaps scolytii*, *Pseudotarsonemoides*, and *Tarsonemus crassus* [86]. Consequently, Moser et al. (2009) found that *P. scolytii* and *T. crassus* carried *O. novo-ulmi* spores, with *T. crassus* carrying the most number of spores, indicating that these beetles are only carriers of this disease because of its introduction by phoretic mites—the true carriers of the pathogen. Such interactions could occur in other beetle-fungal-mite complexes as well (Figure 6). Likewise, studies have shown the *O. minus*-associated southern pine beetle and the mountain pine beetle in North America [39, 87] are associated with a *Tarsonemus* mite sp. similar to the one found on elm bark beetles, *T. krantzii*, which carry the ascospores of *O. minus* [83, 88].

## 4. Conclusion

Complex interactions, particularly mutualisms like that of bark and ambrosia beetles and mycangial fungi have vast implications on the ability to exploit marginal resources and determining habitat range, which in turn affect the host tree environment, spread of fungal pathogens, changes in fungal community structure, etc. Mite-beetle-fungal interactions are likely to alter these ecological implications and effects. Phoretic mites (e.g., *Cercoleipus*, *Dendroctonus*, and *Iponemus* spp.) may reduce bark beetle success/fitness via antagonistic ecological interactions such as feeding on beetle eggs and beetle larvae [72], or feeding on other mutualist mites beneficial for the beetle. Many other mites serve as vectors of pathogenic fungi, such as *Histiostoma ovalis* (introduces *Ophiostoma bruneo-ciliatum* and *O. montium* (blue-stain fungi)) [78]. The introduction of antagonistic fungi by mites may ameliorate the effect of beetle-fungus mutualisms by outcompeting them. This has been documented in southern pine beetle populations in which associated mites carry antagonistic fungi in sporothecae and outcompete the beetle's mutualistic mycangial fungi [89]. Scolytinae have evolutionarily jumped back and forth from angiosperm to coniferous host types. The development of symbiotic associations with fungi has (potentially) assisted in the transition of using a tough resource such as pine bark [8, 32]. The evolutionary pressure exerted by a change in fungal environment introduced by mites (over time) may lead to yet another change in the fungal symbiont of emerging beetles. Mountain pine beetle (*D. ponderosae*), for example, are known to be associated with only one of three mycangial symbi-

traits passed on from parent to offspring. Increased fungal competition introduced by mites in mountain pine beetle populations could cause an adaptive shift for the most successful fungal species or strain [39]. Therefore, utilizing microorganismal interactions is a promising area for future developments of biocontrol [62], particularly natural fungal inoculation via mite phoresy.

Scolytid beetles, mites, and fungi share a unique tripartite relationship that has the potential to affect entire ecosystems. Bark beetle-fungal relations are a primary cause for pine tree mortality, and mite-induced fungal complexity may potentially alter the effects/progress of such pathogenic fungi by either enhancing or diminishing them. For example, mites associated with the southern pine beetle cause blue-stain by vectoring *C. minor* (later renamed as *O. minus*). However, reference [81] indicates that the detrimental effect of *C. minor* naturally occurring within the tree is inhibited in the phloem where it coexists with the beetle and other microorganisms and is amplified when the fungus acts alone. It is very likely (though not experimentally clarified) that this is due to competitive diversity of the fungal microbiome being enhanced by spores that are introduced by the beetle and its associated mite population. Consequently, the beetle-associated timber loss leads to the need for control/management measures. Fungal associates and fungal biocontrol methods have been explored, such as the potential use of *B. bassiana* as a natural insecticide [79, 90]. However, the role of mites has generally been overlooked in these studies and thus the full ecological potential of biologically controlling beetle outbreaks remains unknown. If mites have the potential to alter beetle-fungal associations, factors such as optimal temperature range and geographic range of specific beetle species may also change. Some fungi are adaptive to higher temperatures and some to lower thus determining the geographic expansion of the beetle associated with it. In the past decade, the mountain pine beetle has expanded in range across North America, making its way into the northern forests of British Columbia [91], resulting in tree death. Climate change is the foremost theory for this expansion, as changes in thermal regime has a direct effect on factors such as host tree vigor, resource availability, etc. [91, 92]. However, it is important for managers to understand the consequences of climate and temperature change on bark beetle resource dependence. Mycangial (or other resource-dependent) association with fungi adaptable to colder temperatures will extend beetle populations up north into regions of colder climate and vice versa. The predominance of such a fungus may be influenced by its abundant dispersal by phoretic mites that favor it as a nutritional resource.

While bark and ambrosia beetle populations are typically monitored, their mite and fungal associations are not. We believe that geographic expansion, reproductive fitness, and other factors of beetle population dynamics rely on a thorough understanding of the mite and fungal diversity associated with beetles. The mite-beetle-fungal tripartite relationship is a relatively new realm of study in the field of multipartite symbioses, with a vast scope for new discoveries that expand our knowledge and understanding of ambrosia and bark beetle ecology.

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