The Role of Mites in Insect-Fungus Associations

R.W. Hofstetter[1] and J.C. Moser[2,*]

[1] College of Engineering, Forestry, and Natural Sciences, Northern Arizona University, Flagstaff, Arizona 86011; email: Rich.Hofstetter@nau.edu

[2] USDA-Forest Service, Pineville, Louisiana 71360; email: johnmoser@fs.fed.us

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*Corresponding author

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Abstract

The interactions among insects, mites, and fungi are diverse and complex but poorly understood in most cases. Associations among insects, mites, and fungi span an almost incomprehensible array of ecological interactions and evolutionary histories. Insects and mites often share habitats and resources and thus interact within communities. Many mites and insects rely on fungi for nutrients, and fungi benefit from them with regard to spore dispersal, habitat provision, or nutrient resources. Mites have important impacts on community dynamics, ecosystem processes, and biodiversity within many insect-fungus systems. Given that mites are understudied but highly abundant, they likely have bigger, more important, and more widespread impacts on communities than previously recognized. We describe mutualistic and antagonistic effects of mites on insect-fungus associations, explore the processes that underpin ecological and evolutionary patterns of these multipartite communities, review well-researched examples of the effects of mites on insect-fungus associations, and discuss approaches for studying mites within insect-fungus communities.

INTRODUCTION

Mites play a variety of influential roles in insect-fungus associations. Mite-insect-fungus relationships occur in a wide continuum of forms, from parasitic to mutualistic, as well as from diffuse to highly coevolved associations between species. These interactions are often complex, context dependent, and widespread across insect and fungal communities. Mites can be a driving force of either diversification or stability in different insect-fungus associations, or even in the same insect-fungus association at different times and in different contexts. Mites can mediate intra- and interspecific competition and predation and facilitate the associations of fungi with insects. Examples of insect-fungus communities influenced by mites include, but are not limited to, those of leafcutter ants, gall-forming insects, bark beetles, wood borers, cockroaches, grain insects, carrion beetles, bees, wasps, dung beetles, coprophagous flies, and insects that feed on mushrooms, fruit, and other crops (83, 121, 142).

In this review, we only discuss interactions that encompass all three taxa: mites, insects, and fungi. We do not cover interactions that only include two of them (i.e., mite-fungus, insect-mite, or insect-fungus interactions). There have been many reviews of the direct effects of mites on insects (unrelated to fungal interactions) (58, 111, 125, 129, 142); of the ecology of insect-fungus interactions (47, 106, 140); and of the role mites play in fungal communities, such as arbuscular mycorrhizal (78, 119, 127), plant pathogen (88, 89, 111), and soil microbial systems (110, 119), and in commercial mushroom production (3, 109). They are not discussed here. We describe mutualistic and antagonistic effects of mites on insect-fungus associations, explore the processes that underpin ecological and evolutionary patterns of these multipartite communities, review a sample of the best-understood and well-researched examples of the effects of mites on insect-fungus associations, and describe approaches for studying mites within insect-fungus communities. There is a great need to investigate experimentally the fitness advantages to each of the players, to identify the mode of transmission and behavioral repertoires of mites that affect insect-fungus associations, and to examine phylogenetic or ecological constraints that may affect these systems.

EVOLUTIONARY INFLUENCE OF MITES ON INSECT-FUNGUS ASSOCIATIONS

Mites have the potential to alter interactions between insects and fungi and thus influence the structure, diversity, and robustness of communities. The ecological selection pressures that drive mite evolution are major contributors to the emergent structure and function of the community. The selection pressures that favor certain mite-fungus associations are not always compatible with insect-fungus associations within communities. Antagonistic, commensalistic, and mutualistic behaviors of mites have evolved as adaptations of mites within insect or fungal communities. Mites exploit or compete with conspecifics and heterospecifics for resources, leading to a complex array of interactions and associations. Individual species evolve in the context of a community, often resulting in coevolution (22, 67, 137). The evolution of mite-insect-fungus communities is dynamic in that fungi and arthropods can have different mechanisms that drive evolution. For instance, the frequency of recombination and the phylogenetic breadth of fungi among which genetic materials can be exchanged are different from those of arthropods. Intragenomic processes in fungi such as recombination are likely to have the greatest influence on short-term changes in a community, leading to population adaptation to changing conditions or new metabolic opportunities. Additional complexities arise owing to the significant difference in developmental rates and generation times between mites and insects (142).

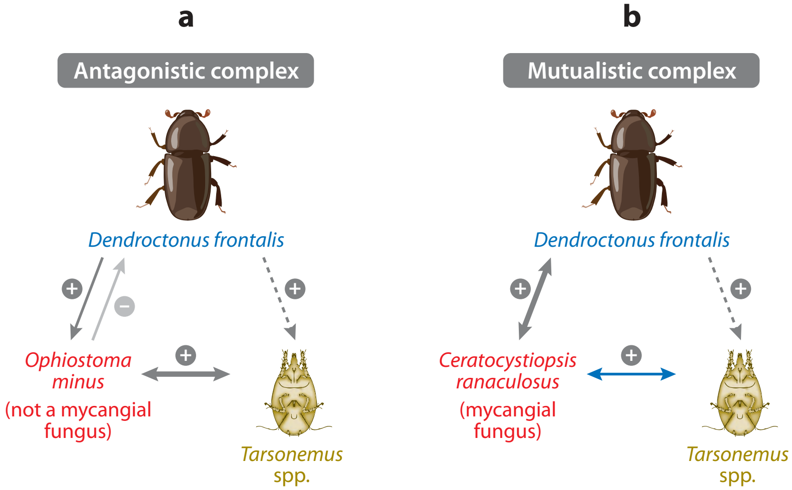

Figure 1

Models of interactions between the southern pine beetle, *Dendroctonus frontalis* (a bark beetle), phoretic mites of the genus *Tarsonemus*, and fungi. The fungal interaction includes either (*a*) the bluestain fungus *Ophiostoma 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 (adapted with permission from References 53 and 54).

ECOLOGICAL INFLUENCE OF MITES ON INSECT-FUNGUS ASSOCIATIONS

Although there are only about 45,000 described species of mites, mites are hyperdiverse (or megadiverse; 141), with current estimates ranging from 500,000 to 1 million species (48). Mites are commonly associated with fungi as well as lichen, bacteria, and other microbes (e.g., 141). Mites can promote insect-mutualistic fungi by increasing fungal transmission, reproduction, and survival (e.g., 92, 102, 124); by reducing antagonistic fungi via feeding or decreased transmission (e.g., 112); or by increasing microbes that reduce insect pathogenic fungi. Alternatively, mites can negatively affect insect-mutualistic fungi or disrupt insect-fungus associations through processes such as exploitative/interference competition, predation, or encouragement of antagonistic fungi (53). These processes influence ecological and evolutionary patterns in these communities. For example, mites can increase fungal species that are poor mutualists of their insect hosts, thus altering or destabilizing the fungal association of that insect (**Figure 1**).

MITE DISPERSAL

To be influential in insect-fungus associations, mites must reach the location of the association. Mites must either be blown by wind or hitchhike on animals to reach distant habitats (6). A mite that is passively blown by wind is called anemochoric (40, 89, 97, 136); a mite carried by another animal is called phoretic [termed phoresy by Lesne in 1896 (93); reviewed in 7, 58]. Phoresy is also known as phoresis, phorecy, and phoresia (115). Phoresy by terrestrial mites typically occurs via insects (8, 15, 62, 129) and has likely occurred for millions of years (5). Some mites even use other phoretic mites for dispersal, a method called hyperphoresy (9).

There can be pronounced dimorphism between the phoretic state, sometimes called either the phoretomorph (101) or abnormal (58), and the nonphoretic state, sometimes called normal. Mites in these different states within a single species can differ from each other in behavior, physiology, and morphology (142). The interaction between the host or carrier and the phoront (phoretic guest or passenger) is temporary. Mites in the phoretic stage must possess the sensory capabilities for identifying and locating potential insect hosts, and once potential hosts are found, they must have the mechanical ability to climb on and attach to the host insect (57). The sensory capabilities of mites are virtually unknown.

In evolutionary terms, phoresy can be viewed as a transitional or temporal stage in the life history of a species, between a parasitic and mutualistic state of the phoront to its transporting host (10, 24, 58). Phoretic dispersal and behavior in arachnids, including mites, has been well reviewed (136). The fact that most mite species are restricted to particular insect species or genera implies that adaptations for coexistence with insects require some degree of specificity by mites. Alternatively, many mites have lost the ability to be phoretic and typically disperse by walking or by passive movement by wind, water, or plant material (40). Nonphoretic mites are typically restricted to marine and tidal habitats, soil and litter habitats, or plant material (111). Phoresy by mites on insects can evolve and influence multitrophic relationships between organisms (9).

EVOLUTION OF SPOROTHECAE IN MITES

Some mite species have evolved special structures called sporothecae (79) to hold and carry fungal spores. Sporothecae have been recorded in species within the heterostigmatic mite families Siteroptiidae (e.g., 84, 135), Trochometridiidae (88), Tarsonemidae (94, 98), and Scutacaridae (35, 36, 65). Different types of sporothecae (e.g., a pouch on the hysterosoma just behind the fourth pair of legs in *Siteroptes* mites or tergite C on lateral sides of *Tarsonemus* mites; **Figure 2**) demonstrate their analogous character, as they have evolved independently at least four times (88, 98).

CASE STUDIES

Mite-Fungus Associations with Bark Beetles

Standing dead wood and live trees attacked by insects and pathogens are home to a variety of mites that invade alone or in association with wood-inhabiting insects (e.g., >96 mite species associated with the southern pine beetle, *Dendroctonus frontalis* Zimmermann) (56, 105). These mite communities consist of fungivores, herbivores, scavengers, and predators and can have important effects on the evolution and ecology of wood-infesting insects and their associated microbes. For instance, some species of mites are capable of altering the frequency of bark beetle mutualistic fungi (55) or the abundance of antagonistic fungi, which can drastically affect bark beetle behavior and population growth (53, 55, 92) (**Figure 3**).

The fungi most commonly associated with bark beetles are ophiostomatoid fungi, which include the genera *Ceratocystis* Ellis & Halst., *Ceratocystiopsis* H.P. Upadhyay & W.B. Kendr., *Cornuvesica* C.D. Viljoen, M.J. Wingf. & K. Jacobs, *Gondwanamyces* G.J. Marais & M.J. Wingf., *Grosmannia* Goid., and *Ophiostoma* Syd. & P. Syd. (74), and related anamorph genera such as *Geosmithia* Pitt (66) and *Leptographium* spp. (64). Ophiostomatoid fungi are important because they are often associated with tree diseases, and many of these fungi cause blue stain on tree xylem and lumber (144). Yeasts belonging to the genera *Candida*, *Pichia*, *Saccharomyces*, and *Cryptococcus* are common as well (23, 49, 146). Basidiomycetes occasionally occur with bark beetles (146) and belong to the genera *Entomocorticium* (77), *Gloeocystidium* (133), and *Heterobasidion* (75).

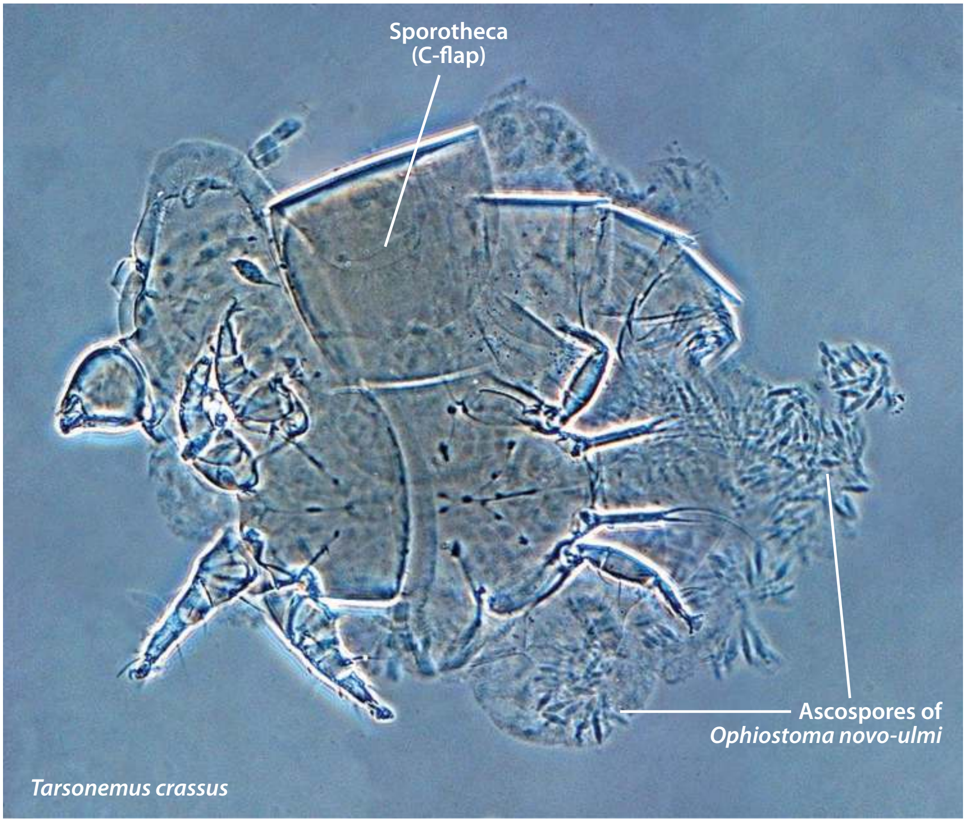

Figure 2

Tarsonemus crassus female carrying ascospores of *Ophiostoma novo-ulmi* in two paired structures under tergite C, termed sporothecae or C-flaps, that are similar in function to a pocket. Spores may be stuffed in these pockets. Image courtesy of J.C. Moser.

Fungi and bark beetles have evolved morphological and behavioral adaptations to maintain the symbiosis. Several bark beetle species have specialized structures called mycangia or mycetangia (13, 41) that transport, protect, and/or preserve fungi or fungal spores (130). Likewise, phoretic mites play an important role in the transmission of ophiostomatoid fungi (19, 53, 77, 92), and many of the mites associated with these fungi have their own special structures (sporothecae) to transport fungal spores (98).

Much of our general understanding of mites associated with bark beetles comes from research on the community associated with *Dendroctonus frontalis*. Many species of mites live within *D. frontalis*–infested trees (105), and perhaps half of them are phoretic on *D. frontalis* adults (87, 105). Several mite species interact with fungi associated with *D. frontalis* (19, 54, 71, 72, 98). The presence of a bluestain fungus, *Ophiostoma minus* (Hedgcock) H. & P. Sydow, in phloem negatively affects *D. frontalis* larval growth and survival (18, 21, 43, 92), and the abundance of *Tarsonemus* mites positively influences *O. minus* abundance within trees (53, 91). Thus, *Tarsonemus* mites appear to be a meaningful driver in *D. frontalis* population dynamics by influencing *O. minus* abundance in infested trees (53, 55, 91).

Mycangia: structures on the body of an animal that transports fungi

Tarsonemus mites (*T. ips* Lindquist, *T. krantzii* Smiley and Moser, and *T. fusarii* Cooreman) associated with *D. frontalis* possess sporothecae (19, 94, 105, 131) (**Figure 2**). In *T. ips* and *T. krantzii*,

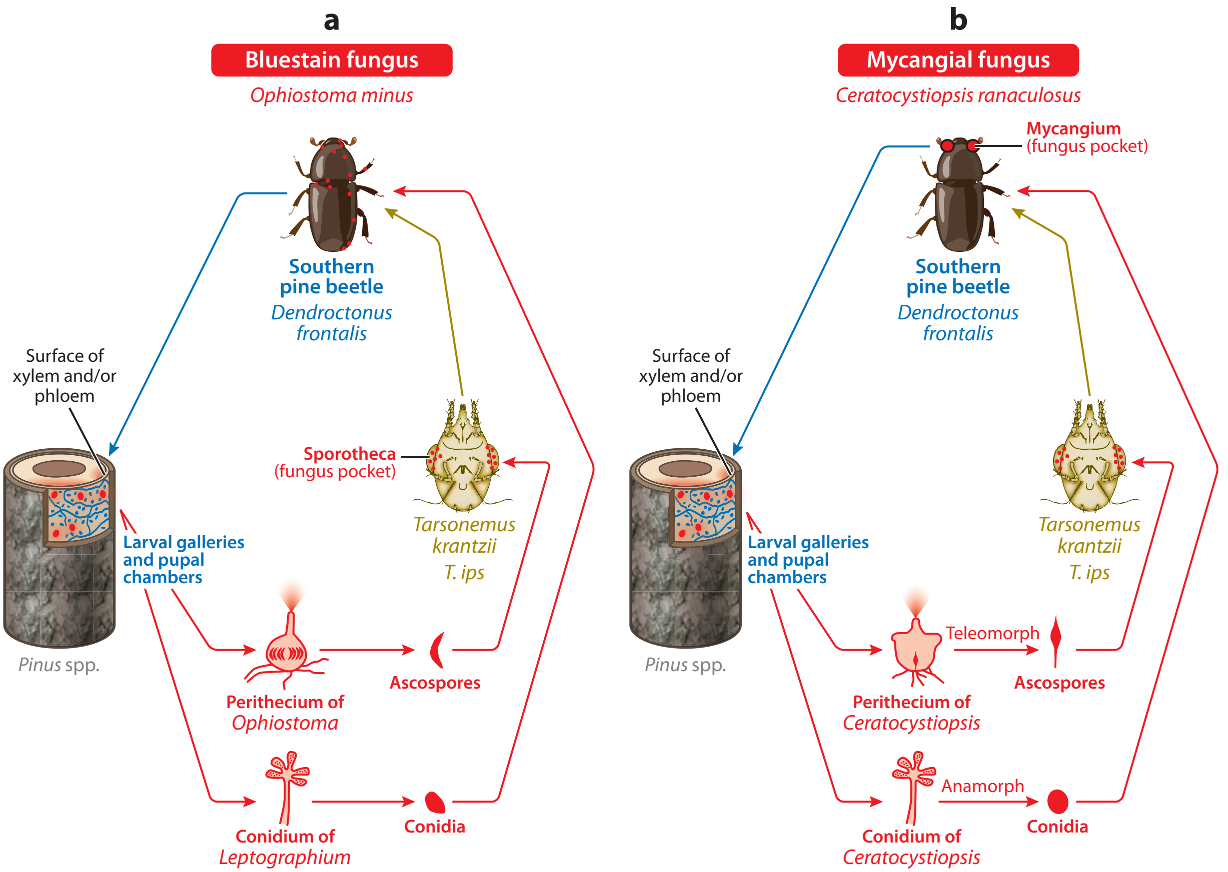

Figure 3

Interactions between the southern pine beetle (*Dendroctonus frontalis*), fungi, and mites. Graphical model of the transport and introduction of (*a*) the bluestain fungus *Ophiostoma minus* (and *Leptographium*) or (*b*) the mycangial fungus *Ceratocystiopsis ranaculosus* into trees by *D. frontalis* and the phoretic mites *Tarsonemus krantzii* and *Tarsonemus ips*. *O. minus* is harmful to *D. frontalis*, and *C. ranaculosus* is beneficial and considered a mutualist. In both situations the mite is capable of transporting the sexual and asexual spores of the fungi.

these sporothecae frequently contain ascospores of *O. minus* or *Ceratocystiopsis ranaculosus* Bridges and Perry (19, 98, 104). *C. ranaculosus* and *Entomocorticium* sp. A Hsiau and Harrington are mycangial fungal mutualists of the southern pine beetle. Although *Entomocorticium* sp. A is the more beneficial of the two mycangial fungi for *D. frontalis* and may be a key to the success of *D. frontalis* larvae (43), neither species of *Tarsonemus* mites has been found to transport *Entomocorticium* sp. A. Thus, in this interaction, the mites play the role of facilitators of a symbiotic relationship between *C. ranaculosus* and *D. frontalis*. By transporting certain fungi to serve as substrate for their own reproduction and development, *Tarsonemus* mites indirectly influence the dynamics of the interactions between their bark beetle hosts, the fungi with which they interact, and the tree host that contains them all. Several mite genera other than *Tarsonemus* that are associated with *Dendroctonus* beetles may be partially or wholly mycetophagous (feeding on fungi); these include *Elattoma*, *Heterotarsonemus*, *Histiogaster*, *Parawinterschmidtia*, *Schwiebia*, *Trichouropoda*, and *Tyrophagus* (73, 105).

Although no relationship has been found between mites associated with *D. frontalis* and *Entomocorticium* sp. A, a relationship that is similarly complex, though perhaps less highly evolved,

Figure 4

Physogastric females of the mite *Elattoma bennetti* feeding on symbiotic fungi of the bark beetle *Ips avulsus* within the beetle galleries and pupal chambers.

is found between another species of *Entomocorticium* fungus associated with the bark beetle *Ips avulsus* (Eichhoff). As the larvae of *I. avulsus* develop and eventually pupate, growth of a white, heavily sporulating fungus becomes obvious. The fungal growth is so abundant that newly formed pupae are covered with spores (44). Newly emergent beetles graze on the fungal growth on the pupae (150). Although *I. avulsus* possesses a gallery system, behavior, and biology similar to that of *D. frontalis*, no mycangium has been discovered in *I. avulsus* (44, 45). Gouger (44) hypothesized that the mutualist *Entomocorticium* sp. is instead transmitted phoretically by propagules adhering to the beetle exoskeleton or by the passage of propagules through the intestinal tract. Interestingly, the mite *Elattoma bennetti* (Cross & Moser) feeds on the *Entomocorticium* lining the galleries of *I. avulsus*. As the female mites feed, they become physogastric (massively swollen) and thus more noticeable within the galleries (**Figure 4**). The female *E. bennetti* mites continue to feed and swell, nourishing developing larval mites within their abdomens. The developing larval mites mate while still inside the parent female, who, after prolonged feeding and swelling, ruptures to give birth to reproductively mature adult mites. These mites are then ready to be carried phoretically by emerging *I. avulsus* that disperse. As in the *D. frontalis* system, there is a high degree of dependence by a phoretic mite on the symbiotic fungus of its bark beetle host. The degree to which the mite affects the beetle-fungus relationship is unclear, although the possibility certainly exists for the mite to vector the fungus (77). The life cycles of all three taxonomically distinct groups are tightly interwoven and interdependent. The genus *Elattoma* comprises many mite species (69), but only the biology of *E. bennetti* has been well studied in bark beetle systems.

The fungus *Ophiostoma novo-ulmi* Brasier (Ascomycota, Ophiostomatales) is the causal agent of Dutch elm disease, a lethal vascular wilt disease of elm species (*Ulmus* spp.) in Europe, Asia, and

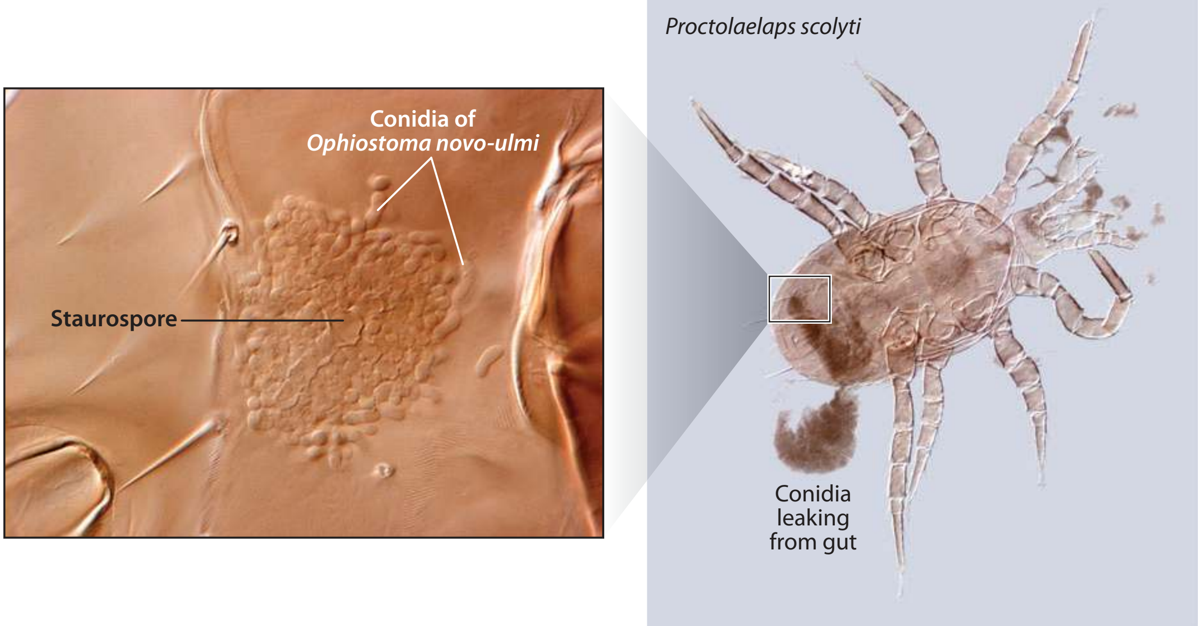

Figure 5

A *Proctolaelaps scolyti* mite, phoretic on *Scolytus* spp. bark beetles, with a bolus of Dutch elm disease fungal conidia (*Ophiostoma novo-ulmi*) leaking from its gut. Inset: A higher magnification of the conidia inside the gut. This large mite possesses mouthparts that allow it to grasp and carry thousands of spores. Photo by J.C. Moser.

North America (17). In Europe and Asia, the fungus is transmitted by native bark beetles belonging to the genus *Scolytus*, and in North America a native bark beetle *Hylurgopinus rufipes* (Eichhoff) and the introduced beetle, *Scolytus multistriatus* (Marsham), serve as vectors of the pathogen (85, 143). *Scolytus scolytus* (F.) have been found to carry as many as 10 species of mites in a population (102). Three mite species, *Proctolaelaps scolyti* Evans, *Tarsonemus crassus* (Schaarschmidt), and *Elattoma fraxini*, feed on *O. novo-ulmi* or carry its spores, thus transmitting the fungus into elm trees (102) (**Figures 5–7**). Other mites, such as *Tyrophagus putrescentiae*, consume *O. novo-ulmi* in elm bark beetle galleries (16, 32).

Webber & Gibbs (144) found evidence that *O. novo-ulmi* is detrimental to beetle larval development, similar to the effects of *O. minus* on *D. frontalis* (53). *O. novo-ulmi* may be essential for the nutrition of the mites *Proctolaelaps scolyti* and *Tarsonemus crassus*, and it may thus be beneficial for these mites to transmit the fungus on which they rely. Given that these mites transport *O. novo-ulmi*, whereas the bark beetles associated with this system may suffer harm from the fungus, the importance of mites in the epidemiology of this destructive vascular wilt disease needs to be further addressed.

Other species of *Elattoma* associated with bark beetle fungi occur in Eurasia and thus this interaction may be more widespread than has been documented (69). Similar mites have been found on *Ips typographus* (L.) and *Tetropium fuscum* (F.) on Norway spruce (*Picea abies*), *Xyleborus glabratus* Eichhoff on redbay (*Persea borbonia*), *Agrilus auroguttatus* Schaeffer on oaks (*Quercus* species), and *Phloeosinus spinosus* Hopkins on Arizona cypress (*Cupressus arizonica*) (56), all of which result in eventual tree death. Nannelli & Turchetti (108) found evidence that the mite *Scheloribates latipes* (C.L. Koch, 1844) can spread chestnut blight, *Cryphonectria parasitica*, even though no association with

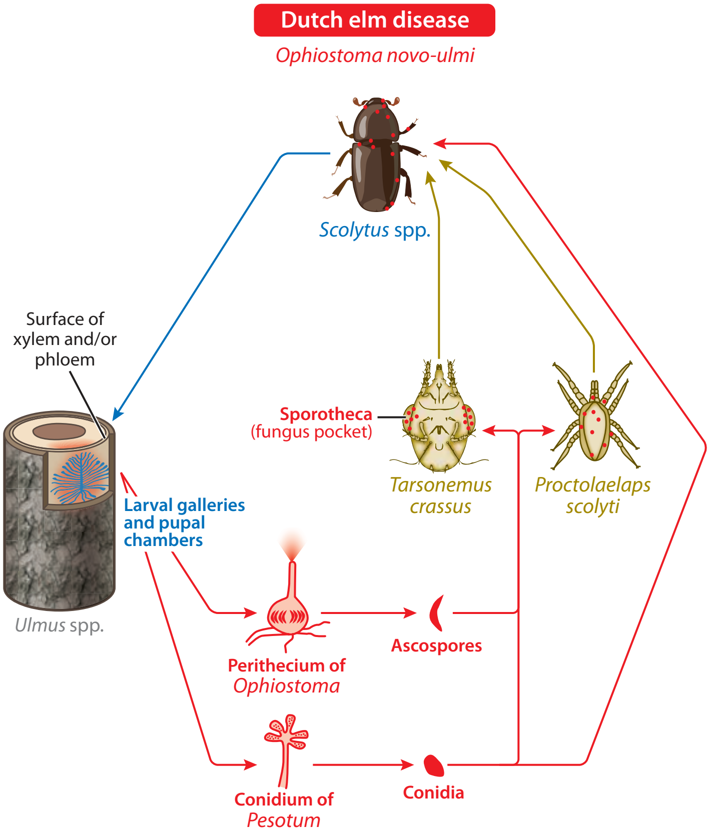

Figure 6

Graphical model of the transport and introduction of the fungus *Ophiostoma novo-ulmi* (Dutch elm disease) into trees by *Scolytus* spp. bark beetles and by the phoretic mites *Tarsonemus crassus* and *Proctolaelaps scolyti*.

bark beetles has been found. However, the ambrosia beetle *Xyleborus dispar* (F.), which was introduced into the United States, could transport these mites to chestnut trees (*Castanea dentata*) (145).

Mite-Fungus Associations with Ants

The mite fauna associated with social Hymenoptera is vast and includes obligate and facultative representatives of all major acarine orders except for the ticks (Ixodida). A number of mite species have been described from bees (Anthophoridae, Bombidae, Apidae, Halictidae), ants (Formicidae), and wasps (Vespidae) or their nests (39, 62, 83).

Myrmecophilous mites such as *Odontocheles attaphilus* Krantz and Moser (Macrochelidae) often display morphological and/or behavioral adaptations that may have evolved to better protect them in an ant nest habitat where nonconformity is inimical to survival (82). For example, the series of tiny teeth on the fixed cheliceral digit of *O. attaphilus* suggests a scraping function, which in turn raises the possibility that the mite feeds on fungal spores in the detritus cavities of ant nests (*Atta texana*). In fact, spores and mycelia have been recovered from the body cavities of several female mites taken from detritus cavities. However, the well-developed capitular groove of *O. attaphilus* suggests a liquid rather than a solid diet, although a mixed diet of fungi and nest microfauna

Figure 7

Ascospores of *Ophiostoma novo-ulmi* (Dutch elm disease) on the dorsal surface of the mite *Proctolaelaps scolyti* phoretic on *Scolytus* spp. bark beetles. Photo by J.C. Moser.

is a possibility. The presence of a weakly defined bidentate tooth on the female cheliceral digit suggests that phoresy could play a role in mite colonization of new nests, as a bidentate tooth is often correlated with a phoretic lifestyle in macrochelid mites (80).

O. attaphilus is one of 17 mite species found along with eight nonacarine inquilines in nests of the ant species *Atta texana* (Buckley) in Louisiana. Recorded nest habitats for these species include galleries, fungus gardens, and detritus cavities (99). Individual fungus gardens in *A. texana* nests flourish for only a month, after which they senesce and are removed to detritus cavities by ant workers. Some arthropod species are routinely found in fungus gardens or galleries, but *O. attaphilus* has been collected exclusively from detritus cavities. These cavities are difficult to pinpoint in nest excavations because a bulldozer or a backhoe is often the principal excavating tool, as *A. texana* nests may exceed a depth of 12 feet (99). Only three of the nests excavated in Louisiana since 1959 contained specimens of *O. attaphilus*, all of which were collected from detritus cavities. *O. attaphilus* has been successfully maintained in laboratory colonies for long periods on nest detritus taken from the field, though limited reproduction has been observed (99).

The mite *Histiostoma bakeri* Hughes & Jackson has been found in many habitats, including the nests of *A. texana* (59) and nests of termites such as *Coptotermes formosanus* (116). Wirth & Moser (148) noted that *H. bakeri* develops in *A. texana* detritus, which contains many species of fungi, but not in the fungus gardens. Both major and minor workers of this ant may be covered by deutonymphs of *H. bakeri*. Large numbers of the mite covering the ventral head and legs of ants disturb locomotion and orientation of those ants. Conspicuous rubbing of the hindlegs on the sides

Deutonymph: nonfeeding stage of mites; stage that molts into the adult form of the body did not remove the mites, but the mites were removed by the grooming behavior of minor workers. Most mite deutonymphs survived this cleaning procedure, and afterward climbed onto other ants. Ants with only a few deutonymphs did not elicit grooming by minor workers. The role of this mite in the ant nest is unknown, but *Histiostoma* mites are microbial feeders and could prevent bacterial infections. Workers of both *Atta sexdens* and *A. vollenweideri* (Forel) have been observed to carry *H. bakeri* (148).

Of the 29 species of mites in nests of the red imported fire ant (*Solenopsis invicta* Buren) (100), at least 11 mite species belonging to the families Pygmephoridae, Microdispidae, Neopygmephoridae, Scutacaridae, Tarsonemidae, and possibly the Uropodidae may feed on fungi within nests (28, 33, 38, 70). The spores of fungi that live inside *S. invicta* nests are potentially carried by these mites (100). *Histiostoma blomquisti* Wirth and Moser prefer female ant dealates and alates of *S. invicta* (132). Wirth & Moser (149) also noted that *S. invicta* nest queens are literally covered by deutonymphs of *H. blomquisti*, and that workers of *S. invicta* remove nest queens and alates that have many deutonymphs of *H. blomquisti*. There were significantly more deutonymphs, which is the phoretic stage, on nest queens than on alates. A few deutonymphs, tritonymphs, and females of *H. blomquisti* were found in the nest soil samples (149). However, these mites were not successfully reared on detritus or cadavers in the laboratory. *Histiostoma* spp. consume microorganisms (such as fungi and bacteria) associated with insect wounds (83, 147).

The many species of microorganisms phoretic on these mites may also be essential to the nest community and possibly affect the vigor of both the ants and the mites (100). Ascospores of an unidentified fungus were observed to propagate within females of the mites *Imperipes louisianae* and *Gaeolaelaps invictianus* Walter & Moser phoretic on *S. invicta*.

Mite-Fungus Associations with Bees

Understanding phoretic mites is important for the management of bees because of the mites' impact on bee ecology (95). Mites associated with bees are well studied (reviewed in 31, 125) due to their potential negative effects on honeybees (*Apis mellifera*) (27) and other bee systems. For example, *Varroa* mite infestation is an important vector of viruses of *A. mellifera*, causing mortality and colony collapse (61, 128). Bee colonies with *Varroa* mites also appear to have an increased incidence of chalkbrood disease caused by the fungus *Ascosphaera apis* (90). Spores of *Aspergillus* spp. (the cause of stonebrood disease) have also been found on *Varroa* mites (90). *Imparipes* mite species found in bee and sphecid wasp nests carry *Fusarium* and *Mortierella* fungal spores in a sporotheca and *Aspergillus* on their integuments. These fungal spores grow to provide essential food for the mites, particularly when a nest is newly colonized (34, 37). By transporting their own fungus, the mites maintain their independence in their environment, which allows them to change hosts across a spectrum of soil- and wood-dwelling bees and sphecids (35).

The nature of some mite-fungus interactions within bee nests are context dependent and blur the line between antagonistic and mutualistic. The mites *Trochometridium tribulatum* Cross and *Imparipes apicola* (Banks) feed on the eggs and larvae of solitary bees. However, after the bee eggs or larvae die, the mites feed on fungal mycelia growing on the carcasses (28, 30). When these mites feed on fungal mycelium within bee cells, fungal growth may decrease, benefitting the remaining bees (39). Biani et al. (14) tested the cleaning effect of *Laelaspoides* mites in nests of tropical *Megalopta* bees and found that there was a significant correlation between the presence of mites and the absence of fungi inside the brood cells, as well as between the absence of mites and increased bee mortality. Other mites, such as *Parapygmephorus costaricanus* Rack and Eickwort, *Dinogamasus*, and *Proctotydeus therapeutikos*, all of which live within bee nests, may feed on and reduce fungal presence (57, 118). Some bees possess pouch-like structures called acarinaria that allow phoretic movement by mites (113, 114). Phoretic histiostomatid mites are associated with the acarinarium (90) and are observed to feed on microorganisms harmful to bees (112). The mite *Trochometridium tribulatum*, found in the nests of ground-nesting bees, disperses via phoresy on bees from nesting aggregations. The phoretic mites carry fungal spores in a sporotheca, and upon entering a new host bee cell, a mite kills the egg and inoculates the egg with fungal spores. Mite offspring then develop on the fungi, later leaving as adults through the soil to seek new bee hosts (29, 88).

Mite-Fungus Associations with Other Insects

The previous case studies represent the best-documented cases of the roles of mites in insect-fungus relationships. There are many systems in which mites influence insect-fungus relations but they are not as well understood or as intensely studied. Some of these examples include the effects of mites associated with termite-microbe interactions (e.g., 107); fly dung communities (e.g., 134); moth-pollinator relationships (63); and beetle systems such as passalid beetles in rotting wood (86), weevils in palms (4), beetle pollinators on *Protea* plants (123), and staphylinids and tenebrionids in mushrooms (111). Oribatid mites are common fungus feeders in soil ecosystems, are important in nutrient cycling and decomposition (110), and act as vectors for carrying and transmitting molds associated with plant roots and food crops on their bodies or in their digestive tracts (1). These oribatid mites either walk or use insects as phoretic hosts to travel among and between habitats (e.g., 46). Further study is needed to determine the effects of mites on many other insect-fungus systems.

EFFECTS OF MITES ON THE GENETIC DIVERSITY OF FUNGAL PARTNERS

Mites frequently carry within their sporothecae ascospores, which are the products of sexual recombination (19, 20, 98, 103, 104). For instance, *Tarsonemus* mites associated with *D. frontalis* carry the ascospores of *O. minus* and *C. ranaculosus* (19, 52, 98, 104). *C. ranaculosus* is one of the mutualistic mycangial fungi of *D. frontalis*, which transmits it vertically from beetle parent to offspring. Interestingly, this transmission method directly propagates particular fungal strains, resulting in continued introduction of the same strain from tree to tree, across beetle generations. The nonrandom selection of fungal strains by the beetle acts like purifying selection on the fungal populations, reducing genetic diversity (130). Mites, on the other hand, feed on the reproductive structures of *C. ranaculosus* and transmit ascospores. Thus, in this case, mites promote greater genetic diversity of the beetle-mutualistic fungi.

The transmission of ascospores by mites likely occurs with other bark beetle–associated fungi such as *O. minus*, which is associated with *D. frontalis*, and *O. montium* (Rumbold) von Arx, which is associated with the mountain pine beetle (*Dendroctonus ponderosae*) (96). Owing to mite preference for particular fungi, the two mycangial fungi associated with *D. frontalis* and *D. ponderosae* likely experience different dispersal patterns and degrees of genetic variability as a result of mite and beetle dispersal patterns. Roe et al. (122) further support this hypothesis by detecting evidence for recombination in *O. montium*, whereas evidence of recombination in the other mycangial fungal species was weak. Fungal species that produce ascospores transmitted by mites have higher genotypic diversity than asexually reproducing fungal species, and are expected to have higher numbers of unique, recombinant genotypes (12). Thus, mites increase the ability of fungi to transmit new genetic combinations, allowing rapid adaptation to changing conditions such as transitions to new host trees or changing climate. Further research is needed to explore how mites influence patterns and rates of recombination of fungi associated with insects and how this affects the stability and evolution of insect-fungus mutualisms.

MITES AS TRANSPORTERS OF FUNGAL PATHOGENS OF INSECTS

There are over 700 species of entomopathogenic fungi (120) and mites transmit some of these pathogens to insects (117, 126). Entomopathogenic fungi such as *Beauveria*, *Entomophthorales*, *Hirsutella*, and *Nosema* species are common pathogens of mites (139) and insects (47), but whether they are transferred to insects by mites is not known in many cases. *Hirsutella* fungi were frequently isolated from mites associated with bark beetles under the bark of spruce (*Picea*), pine (*Pinus*), fir (*Abies*) and oak (*Quercus*) trees (138), and *H. nodulosa* fungus transmitted from tarsonemid mites infected several bark beetle larvae (11). *Beauveria bassiana*, a well-known entomopathogenic fungus, has been isolated from the mites *Tyrophagus*, *Rhizoglyphus*, and *Histiostoma* associated with onion (*Allium cepa*) plants (1). Other soil-dwelling mites potentially vector *B. bassiana* (119). The role that mites play in fungal epidemiology is unclear, and more research is needed to broaden our understanding of the transfer and spread of entomopathogenic fungi among insects and mites.

MITES AS TRANSPORTERS OF FUNGAL PATHOGENS OF PLANTS

Many mite families in different suborders interact with plant pathogenic fungi (42). Mites can facilitate fungal infection by vectoring pathogen spores or by creating wound sites in plants for fungal penetration (2, 51). Many close associations between mites and fungal plant pathogens (42, 81, 89) significantly affect plant, fruit, or flower production and survival (e.g., *Fusarium* glume spot on wheat in South Africa; 68). How mites affect the insect-fungus relations that influence plants is less clear. Many cases of introduced fungus–insect systems have become invasive by shifting from dead or dying trees to living trees, threatening tree crops such as avocado (*Persea*), walnut (*Juglans*), mango (*Mangifera*), pine (*Pinus*), and other nursery trees (60). Hulcr & Dunn (60) propose that the shift is the result of an evolutionary mismatch between fungi and host trees. We propose that the increased tree mortality or shift from dead to living trees could also be a consequence of a change in mite behavior or of novel associations by mites. There is some evidence that the presence of mites exacerbates and increases the virulence of fungi associated with herbivorous insects (e.g., elm trees, *Ophiostoma novo-ulmi*, mites, and bark beetles; **Figure 5**) (102, 103). Mites can vector fungal spores and enhance disease severity in elm trees (19, 94, 102). Mites also improve short-range dispersal by moving the spores within the plant, thereby increasing the number of infection sites (e.g., 91). An additional factor causing tree mortality in some systems is that many mites (and their insect hosts) vector more than one fungal species or strain, and these strains regularly differ in their ecological roles (50). Increases in abundance and diversity of fungal associates can lead to greater tree mortality (60).

APPROACHES FOR STUDYING MITE-FUNGUS-INSECT COMMUNITIES

Most studies of mite-fungus-insect interactions have considered them binary interactions; indeed, binary interactions are simpler to understand and are a necessary step toward understanding the full range of interspecific interactions in a community context. A holistic approach should consider these interactions (which can range from mutualism to commensalism to antagonism within a symbiont pairing) across the extent of the mite, fungus, and insect life cycles (76). There is still a great need to determine the mite and fungal compositions of many insect systems. The use of genetic methods will be extremely important for accurately identifying mite species. After identifying the species present within a community, the next challenge is to identify the effects of these species on the community.

Understanding these interactions is important for building predictive models that provide a deeper understanding of ecological community principles and dynamics from both applied and theoretical standpoints. Much of the baseline research needed to generate such models depends on determining which species are present in a community, what their functions are, and how they interact with one another. There is also a need for improved statistical approaches and tools for analyzing community structures, comparing across communities, and estimating the relative impacts of species through space and time within communities. Advances in molecular biology and computational biology are resulting in better predictive ecological models that are poised to enhance biological control in multipartite communities (60). Increased research in these systems, by using new approaches and exploring a broader range of questions, has shown the importance of associations with mites, fungi, and insects (25, 122). Bringing together molecular and ecological approaches will yield new insights. Complexities uncovered by better techniques and increased interest in this field will only show the need for interdisciplinary, collaborative, and holistic approaches (26, 76).

CONCLUSIONS

Many mite species feed and transport fungi, and use insects to access resources and for dispersal. These multitripartite associations range from mutualistic to antagonistic. Many of these mites are mycetophagous, feeding on the fungi associated with insects. Mycetophagous mites can affect the evolution and ecology of fungi and thus affect insect-fungus associations and insect population dynamics. Many mites remain undescribed or, if they are described, have unknown life histories. In addition, the nature of many insect associations with fungi, whether antagonistic or mutualistic, remains poorly understood. The role that mites play in many ecosystems is often overlooked or ignored, although there are insect systems, such as bark beetles, bees, and ants, in which mites have been long studied and their roles in the community well documented. Mites have important effects on community dynamics, ecosystem processes, and biodiversity within many insect-fungus systems. Given that mites are understudied but highly abundant, it is likely that they have bigger, more important, and widespread impacts on communities than we currently realize.

SUMMARY POINTS

1. Mites are a driving force of diversification and stability in insect-fungus associations, and they have important effects on community dynamics, ecosystem processes, and biodiversity.
2. Many mites are phoretic on insects and can transmit insect and plant pathogens. We propose that recent increases in tree mortality or shifts by insect pests from dead to living trees could be a consequence of a change in mite behavior or of novel associations by mites.
3. Mites promote greater genetic diversity of fungi associated with insects and plants and can influence the frequency of recombination, allowing for greater adaptation to new hosts, environments, and changing climate.
4. There is still a great need to determine the mite and fungal compositions of many insect systems. The use of genetic methods to identify mites will be extremely important for accurately identifying mite species. Mites are underdescribed and many species are yet to be discovered.

5. Phoresy is a principal adaptation that mites require to associate closely with insects. Reliable transport of mites on insects requires mites to possess the mechanical and sensory capabilities to identify, find, and attach to insect hosts. Mites synchronize phoretic life stages to match those of their insect hosts.
6. Among the best-understood cases of mite-fungus-insect interactions are systems of bark beetles, leafcutter ants, bees, and wasps.
7. The role of mites in many ecosystems is often overlooked or ignored, although there are systems such as those described here in which mites have been long studied and their roles in microbial ecology well documented.

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