Bark Beetle Management, Ecology, and Climate Change

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Effects of rising temperatures on ectosymbiotic communities associated with bark and ambrosia beetles

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1 Introduction

The order Curculionidae contains thousands of species of beetles that colonize tree tissues (Bright, 1993; Marvaldi, Sequeira, O'Brien, & Farrell, 2002; Vega & Hofstetter, 2015). Bark beetles are an ecological classification of beetles in the subfamily Scolytinae (Alonzo-Zarazaga, & Lyal, 2009; Bright, 2014; Wood, 1982; Wood & Bright, 1992) that almost invariably live in the phloem-cambium layer of trees (Vega & Hofstetter, 2015). Ambrosia beetles (Scolytinae and Platypodinae) (Hulcr, Atkinson, Cognato, Jordal, & McKenna, 2015; Jordal, Sequeira, & Cognato, 2011; Kirkendall, Biedermann, & Jordal, 2015), on the other hand, most often live within tree xylem (Batra, 1963; Weber & McPherson, 1983; Wood, 1982) but may colonize other tree parts such as seeds or phloem, feeding primarily on fungi they introduce into tree tissues (Batra, 1966; Beaver, Wilding, Collins, Hammond, & Webber, 1989; Knížek & Beaver, 2007; Raffa, Gregoire, & Lindgren, 2015). By colonizing tree tissues, bark and ambrosia beetles create habitats that enable many other species to persist and exist within an otherwise well-defended, inhospitable environment (Batra, 1963; Harrington, 2005; Hofstetter, Dinkins-Bookwalter, Davis, & Klepzig, 2015; Six, 2003, 2013). These beetles also utilize external and semiinternal structures (called mycangia or mycetangia; Six, 2003; Vega & Biedermann, 2020) and related structures that enable protection and transport of their associates, be they fungi, bacteria, or nematodes (Binns, 1982; Farish & Axtell, 1971; Hofstetter & Moser, 2014; Hulcr et al., 2012; Skelton et al., 2019). Beetles may have structures, called nematangia, that carry nematodes (Cardoza, Klepzig, & Raffa, 2006). Larger species such as mites attach to setae or the surface of the exoskeleton of adult beetles to enable transport in and out of habitats (Poinar, Curcic, & Cokendolpher, 1998) while others use glue-like materials (forming a stalk-like structure) to stick to beetle

surfaces (Hofstetter et al., 2015). Finally, many endosymbiotic organisms such as bacteria are transported within the gut of beetles and some live externally within tree tissues once introduced (Adams et al., 2013; Boone et al., 2013; Bridges, 1981, 1987; Durand et al., 2015; Haanstad & Norris, 1985; Kirschner, 2001).

In this chapter, we focus on the phoretic ectosymbiotic community associated with bark and ambrosia beetles. Phoresy refers to the use of one animal for transport by another, without specification of harm or benefit to the transporting animal (Athias-Binche, 1991; Klepzig et al., 2001; Klepzig & Hofstetter, 2011; Six & Klepzig, 2004). When ambrosia beetles and bark beetles colonize a fresh resource patch such as a tree, they carry with them an entire multispecies community of phoretic associates, which we will call ectosymbionts, that disembark or are rubbed off in beetle tunnels to pursue a free-living existence. This chapter does not address interactions among other organisms that are not typically phoretic on bark and ambrosia beetles (e.g., arthropod predators, parasitoids and competitors, reviewed in Nikitskii, 1980; Wegensteiner, Wermelinger, & Herrmann, 2015), and will also not address organisms that are strictly endosymbionts and parasites of beetles (reviewed by Bushing, 1965; Massey, 1974; Wegensteiner, 2007). For simplicity, we will primarily use the term "bark beetle" or "beetle" throughout the text, although many of the descriptions, hypotheses, life histories, and climatic effects are relevant to ambrosia beetles as well. Otherwise, when appropriate for clarity, we will refer specifically to ambrosia beetles.

The ectosymbiotic community associated with bark beetles is kingdom-diverse and speciose but tends to consist of the same general taxa: fungi, bacteria, viruses, nematodes, and mites (reviewed by Callaham & Shifrine, 1960; Hofstetter et al., 2015; Klepzig & Six 2004; Six, 2003, 2013) that are capable of living within tree tissues. Larger species such as pseudoscorpions (Arachnida: Order Pseudoscorpiones) may also be phoretic on beetles and play a role in bark beetle ecology (Poinar et al., 1998). Species that comprise the ecto-symbiotic community interact with their beetle hosts in a variety of ways ranging from mutualistic, commensal, antagonistic, among others (Hofstetter, Cronin, Klepzig, Moser, & Ayres, 2006; Klepzig et al., 2001). These interactions are rarely simple or clearly understood and are rather context-dependent, shifting with changing environments (Hofstetter & Moser, 2014; Klepzig & Six 2004; Six, 2003, 2013). Ectosymbiotic members also interact with the host tree, arthropod natural enemies, and competitors of their bark beetle hosts within trees (Fig. 1). For instance, natural enemies may be attracted by volatiles emitted by fungi and bacteria that may assist them in locating potential prey within trees (Adams & Six, 2008; Boone, Six, & Raffa, 2008; Davis, Crippen, Hofstetter, & Tomberlin, 2013; Sullivan & Berisford, 2004).

Life cycles of ectosymbiotic species are closely aligned with those of their phoretic hosts, which maximizes the chances of their progeny attaching to beetle progeny that exit the tree. These species have specialized morphology and structures that allow for phoretic transport on beetles, and also have life history traits that allow for coexistence with each other and beetles within tree tissues (Lindquist, 2001; Moser, 1985; Walter & Proctor, 1999). Once inside the tree, most symbionts grow or move freely within the tree or among beetle
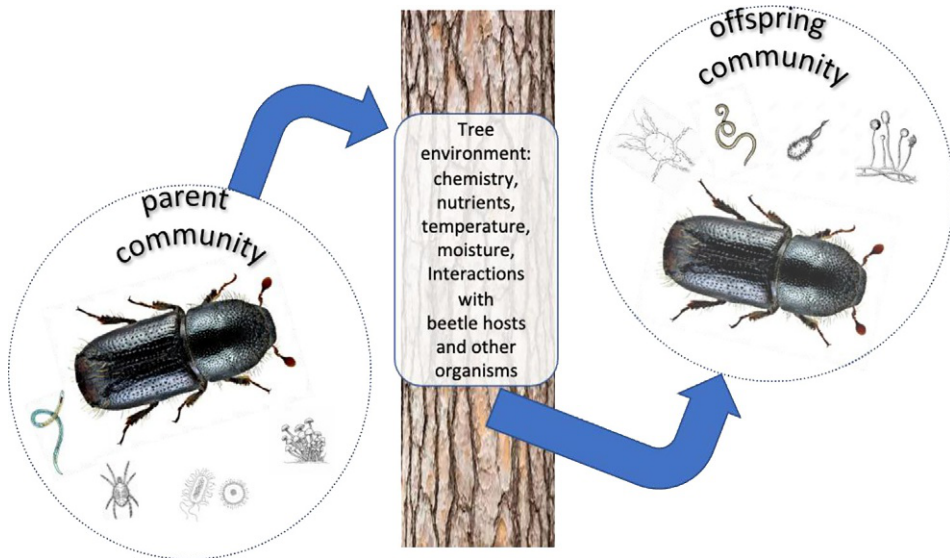
FIG. 1 Ectosymbiotic community associated with (parent) beetles colonizing a tree and the factors that affect the ectosymbiotic community associated with emerging (progeny) beetles from that tree. Here 'tree environment' includes other biotic organisms found within beetle colonized trees, such as fungi, yeasts, bacteria, algae, viruses, nematodes, mites and arthropod predators and competitors.

galleries (Błoszyk, Klimczak, & Leśniewska, 2006; Kirisits, 2004; Lindquist, 1975) where they feed, mate and produce progeny or spores. Many beetle species actively disperse and maintain specific microorganisms within galleries and deter or eliminate others (Cardoza, Klepzig, & Raffa, 2006; Cardoza, Moser, Klepzig, & Raffa, 2008; Cardoza, Vasanthakumar, Suazo, & Raffa, 2009). Dispersing adult beetles transport specific fungi, bacteria, nematodes, and mites to new habitats thus promoting the close association (Adams, Currie, Cardoza, Klepzig, & Raffa, 2009; Cardoza, Klepzig, & Raffa, 2006). Not all fungi associated with beetles are desirable as food and some beetles limit their growth through the use of antibiotic-producing oral bacteria (Cardoza, Paskewitz, & Raffa, 2006), or they may compete directly with beetle-mutualistic fungi (Klepzig & Six 2004; Wang, Lu, Cheng, Salcedo, & Sun, 2013; Wang, Salcedo, Lu, & Sun, 2012). For instance, larvae and adult southern pine beetles (*Dendroctonus frontalis* Zimmermann) will avoid tunneling in areas where an antagonistic blue-stain fungus, *Ophiostoma minus* (Hedgc.) Syd. & P. Syd. grows (Barras, 1970, 1973; Goldhammer, Stephen, & Paine, 1990; Hofstetter, Cronin, et al., 2006). Mites, nematodes, and other animals are commonly associated with bark and ambrosia beetles and use phoresy to reach tree habitats. Similar to phoretic bacteria and fungi, these animals are specialized for this lifestyle and their morphology, physiology, and life cycle are adapted to persist inside beetle-colonized tree tissues (Lindquist, 2001; Walter & Proctor, 1999).

In this chapter, following a brief recap of the role of and interactions among the ecto-symbiotic community associated with bark and ambrosia beetles, we describe the effects

of changing climate on the composition and interactions of this community. We address (1) how increases in temperature can differentially affect growth and reproduction of ectosymbiotic species, (2) how climate driven changes in tree condition increases or decreases secondary defenses, phloem nutrients, and moisture thus affecting the ectosymbionts community composition associated with beetles, and (3) how climate change affects interactions among ectosymbionts within trees.

2 Functions and interactions of ectosymbionts within beetle-infested trees

Phoretic systems associated with ephemeral food sources (e.g., carrion beetles, dung beetles, bark beetles) are typically highly dependent on their insect hosts. In most cases, these associates cause few to no negative impacts, and most phoronts (phoretic organisms) even provide benefits to their beetle hosts including enhanced fitness in, protection from, and resilience against perturbations to the system. Some phoronts associated with bark and ambrosia beetles, however, are antagonistic or exhibit predatory behaviors and include organisms such as entomopathogens and natural enemies (Wegensteiner, 2007; Wegensteiner et al., 2015). Still other phoronts may be opportunistic species that utilize tree habitats and compete or deter other species within the tree and may ultimately affect bark beetle fitness.

2.1 Ectosymbiotic fungi

Bark and ambrosia beetles most commonly associate with Ascomycete fungi and the fungal genera often separate by host tree affiliations; for example, Ophiostomatales are typically associated with conifers while Microascales are common in angiosperms (Harrington, 2005; Kirisits, 2004), with some notable exceptions such as *Ophiostoma novo-ulmi* Brasier (the causal agent of Dutch elm disease; Brasier, Kirk, Pipe, & Buck, 1998) in American elm, or *Raffaellea* species (including *R. lauricola* T.C. Harr., Fraedrich & Aghayeva, the causal agent of laurel wilt) (Harrington, Fraedrich, & Aghayeva, 2008) in laurels, bays and other angiosperm hosts. A few Basidiomycete fungal species are associated with beetles; these include *Entomocorticium* species and *Phlebiopsis* species associated with bark beetles (Harrington, Batzer, & McNew, 2021; Hsiau & Harrington, 2003) and *Flavodon* species associated with ambrosia beetles (Li et al., 2017). Entomopathogenic fungi such as *Beauveria bassiana* (Bals.-Criv.) Vuill. and *Metarhizium anisopliae* (Metchnikoff) Sorokin are also associated with beetles and found within tree tissues (Doberski & Tribe, 1980; Kreutz, Vaupel, & Zimmermann, 2004; Wegensteiner, 2007). These entomopathogenic fungi are often introduced directly via infected beetles or passively on the surface of beetles or mites, which later become infected or infect others (Kreutz et al., 2004). Remarkably, *B. bassiana* may be able to persist within living healthy trees as an endophyte and infect beetles once they enter tree tissues (Brownbridge, Reay, Nelson, & Glare, 2012; Parsa, Ortiz, & Vega, 2013; Vega, 2018).

Some fungal species coexist within and among beetle galleries while many others appear to interact antagonistically or have little to no effect on beetles (Harrington, 2005; Hofstetter et al., 2015; Kirisits, 2004; Klepzig & Six 2004). Interestingly, most beetle species associate with multiple fungal species, even within the same gallery, that provide similar benefits to beetles (Six, 2003; Six & Wingfield, 2011). This symbiotic redundancy may allow for greater plasticity of host tree selection, geographic distribution, range of environment conditions within trees and potentially buffer some of the effects associated with climate change (Klepzig & Six 2004; Netherer et al., 2021; Six, 2012). Additionally, the complex of fungal species may provide different benefits at different stages of the beetle life cycle (Addison, Powell, Six, Moore, & Bentz, 2013; Hofstetter, Dempsey, Klepzig, & Ayres, 2007; Klepzig et al., 2001; Six & Bentz, 2007; Six & Paine, 1999).

Ambrosia beetles and many bark beetles are obligately dependent upon particular fungal species. Ambrosia beetle larvae are dependent upon their symbiotic fungi for their nutritional needs, and larvae of some bark beetle species feed on fungi to acquire nitrogen, vitamins, and sterols necessary to complete development (Batra, 1966; Kirkendall, 1983; Weber & McPherson, 1983). As the nutrient content of xylem and phloem markedly differs, the nutritional benefits of symbiotic fungi for these beetles may likewise differ markedly (Guevara-Rozo et al., 2020; Six & Elser, 2019; Vanderpool, Bracewell, & McCutcheon, 2018). Beetle-associated fungi also confer benefits such as exhaustion (Barras, 1973; Lieutier, Yart, & Salle, 2009; Lieutier, Yart, Ye, Sauvard, & Gallois, 2004) or detoxification (Hammerbacher et al., 2013; Zhao et al., 2019) of tree defenses, reduction in the prevalence of antagonistic microbes (Klepzig & Wilkens, 1997), and enhanced chemical communication by beetles (Davis, Stewart, Mann, Bradley, & Hofstetter, 2019; Hofstetter et al., 2015).

2.2 Ectosymbiotic bacteria

Bacteria, commonly associated with bark and ambrosia beetles, have been isolated from tree tissues surrounding beetle galleries, from the surfaces and interiors of beetle larvae and adults, and in oral secretions and beetle mycangia (Bridges, 1981; Cardoza, Paskewitz, & Raffa, 2006; Hulcr et al., 2011; Morales-Jiménez, Zúñiga, Ramírez-Saad, & Hernández-Rodríguez, 2012; Saati-Santamaría, Rivas, Kolařik, & García-Fraile, 2021; Scott et al., 2008). Most commonly, bacteria associated with bark beetle mycangia are found in the Burkholderiales and Pseudomonadales, in the genera *Enterobacter* and *Mycoplasma* (Bridges, 1981; Hulcr et al., 2012). Bacteria found within beetle guts are abundant and highly diverse (reviewed by Delalibera et al., 2007; Morales-Jiménez, Zúñiga, Villa-Tanaca, & Hernández-Rodríguez, 2009; and others) and include genera such as *Acinetobacter, Enterobacter, Klebsiella, Pantoea, Rahnella, Stenotrophomonas,* and many others (Popa, Déziel, Lavallée, Bauce, & Guertin, 2012). While trees attacked by bark beetles may contain endophytic bacteria, these significantly differ from those found in bark beetle guts—though some are closely related (Gonzalez-Escobedo, Briones-Roblero, Pineda-Mendoza, Rivera-Orduña, & Zúñiga, 2018).

Some bacteria may benefit beetles by defending against, or deterring growth of, insect pathogens and antagonists (Adams et al., 2009; Cardoza, Paskewitz, & Raffa, 2006; Hulcr et al., 2011; Scott et al., 2008; Zhou et al., 2016), contributing to beetle nutrition (Morales-Jiménez et al., 2009, 2013), detoxifying or altering tree defensive compounds (Adams et al., 2009, 2011, 2013; Boone et al., 2013; Boone, Aukema, Bohlmann, Carroll, & Raffa, 2011; Cheng, Xu, Xu, Lu, & Sun, 2016) and improving insect communication via pheromones (Fang et al., 2020; Xu, Lou, Cheng, Lu, & Sun, 2015). Other bacteria can be pathogenic or antagonistic to beetles (Yaman, Ertürk, & Aslan, 2010) or have direct, negative consequences on beetle reproduction (e.g., *Wolbachia*, Riegler, Sidhu, Miller, & O'Neill, 2005). The presence of gram-positive bacteria such as *Bacillus* and *Leuconostoc* species in southern pine beetle larval guts also suggests bacteria might play an important role in bark beetle growth and development, including but not limited to N fixation and concentration (Delalibera et al., 2007; Vasanthakumar et al., 2006). Some bacteria stimulate fungal spore germination or affect fungal growth (Adams et al., 2009), while some endobacteria may be permanently associated with some fungal species, forming a tightly coupled symbiosis. These bacteria could be involved with the transition of mycangial fungi from the yeast-like form in the mycangia to the filamentous form while living outside the beetle (Barras & Perry, 1972; Batra, 1966; Bleiker, Potter, Lauzon, & Six, 2009). Thus, fungi and bacteria likely promote the survival of each other, as fungi could provide a vector for bacteria (as an endosymbiont) or help mediate tree defensive compounds that improve bacteria invasion into tree tissues (Peters, Shirtliff, & Jabra-Rizk, 2010; Seneviratne, Lüthi, Litschi, & Schär, 2006). Actinomycetes, which are well known to produce antibiotics that protect insect fungal symbionts (Currie, Scott, Summerbell, & Malloch, 1999), are also associated with bark beetles (Cardoza, Paskewitz, & Raffa, 2006; Hulcr, Novotny, Maurer, & Cognato, 2008; Human, Slippers, Wilhelm de Beer, Wingfield, & Venter, 2017; Scott et al., 2008). For instance, the southern pine beetle maintains an association with an actinomycete bacterium that produces an antibiotic—mycangimycin—which suppresses the growth of the antagonist fungus *Ophiostoma minus*. However, this bacterium, stored in the adult beetle's mycangia, has no deleterious effects on the main nutritional mutualistic mycangial fungus (Scott et al., 2008). The Actinomycete bacterium, *Micrococcus luteus*, found in oral secretions of the spruce beetle was shown to negatively impact growth of opportunistic gallery fungal invaders and of their predominant ophiostomatoid fungal associate *Leptographium abietinum* (Cardoza, Paskewitz, & Raffa, 2006).

2.3 Ectosymbiotic mites

As phoretic hitchhikers on bark beetles, mites can reach spectacular numbers in abundance and diversity. For example, over 110 species of mites from more than 30 families are associated with the southern pine beetle (Hofstetter, 2011; Moser & Roton, 1971). In most beetle populations, more than 75% of the beetles carry at least one mite, with some bark beetles carrying >100 mites (Pfammatter et al., 2016; Pfammatter, Moser, & Raffa, 2013). With few exceptions, these phoretic species are found exclusively in beetle-infested

tree tissues and may be transported solely by one beetle species (Hofstetter et al., 2015). Comparable phoretic mite communities can be found with carrion beetles (Wilson & Knollenberg, 1987), dung beetles (Costa, 1969), and other insects that specialize on patchy ephemeral resources (Hofstetter & Moser, 2014). However, mite communities are less studied in ambrosia beetle systems, and their abundance and richness are lower than those found associated with bark beetles (Vissa & Hofstetter, 2017). Phoretic mite taxa associated with bark beetles are reviewed by Hofstetter et al. (2015).

Effects of mites on beetles span the full spectrum of interactions, from predation to antagonism, and commensalism to cooperation and mutualism (Hofstetter, Cronin, et al., 2006; Hofstetter, Moser, & Blomquist, 2014). These impacts may extend directly to beetle population dynamics and fitness, or indirectly through interactions with other phoront species (Hofstetter & Moser, 2014; Klepzig et al., 2001; Lombardero, Ayres, Hofstetter, Moser, & Klepzig, 2003) and beetle host trees (Moser, Konrad, Blomquist, & Kirisits, 2010).

The challenge and difficulty of fully understanding the dynamics of phoretic communities (Figs. 1–2) may be illustrated by considering phoretic mite composition and abundance over time. For instance, mite abundance and composition within a beetle-infested tree (i.e., the nonphoretic community) may not correlate strongly with mite abundance and composition on emerging beetles (i.e., phoretic community). Single factors such as beetle progeny distribution, density, or development stage significantly affect phoretic mite numbers on emerging beetles. Given equal mite populations within two trees, the number of emerging beetles directly affects phoretic mite levels and composition

FIG. 2 Coexistence of biotic community in bark beetle ecosystems. Animal, plant, and microbial species occupy overlapping niches within the tree and when associated with bark beetles. Disturbing the communities that occupy these niches, for example, by reduced fitness or removal of key members, may alter beetle tree colonization success, fitness, and population dynamics. Changes in temperature and other environmental factors can disrupt and alter the system.

(Hofstetter, Mahfouz, Klepzig, & Ayres, 2005; Vissa, Soderberg, & Hofstetter, 2021). Similar effects take place with all ectosymbionts within the tree that need to attach to emerging beetles. For additional complexity, differences in fungal composition may translate to differences in mite community composition across beetle populations. Feeding and reproduction of mites are favored by some fungi, and not by others, drastically altering mite populations within trees and relative abundances of phoretic mites on emerging beetles (Cardoza et al., 2008; Lombardero et al., 2003).

Interestingly, some studies measuring a single generation of mites in a tree have shown little effect of mites on beetle fitness (Hodgkin, Elgar, & Symonds, 2010; Peralta Vázquez, 2018; Pfammatter, 2015). However, these mites themselves likely altered the communities within the tree, affecting the ectosymbiotoic community on emerging progeny (Fig. 1). Multigenerational studies of mites and beetles tend to show more significant effects of mites on beetle fitness and population growth. For example, Wilson and Knollenberg (1987) studied the effect of mites on the fitness of carrion beetles and initally found no (or a "neutral") effect of mites on beetle progeny survival or size. However, a closer look at emerging beetles revealed a sixfold increase in the number of nematodes clinging to the beetle bodies when mites were removed from the system. Without the phoretic mites, fewer beetles survived to have a second brood, fewer of their broods survived, and successful broods had a smaller number of offspring (Wilson & Knollenberg, 1987). Studies of phoretic mites over multiple bark beetle generations have not been performed yet.

2.4 Ectosymbiotic nematodes

Bark and ambrosia beetles serve as phoretic hosts (described as ectophoronts, and free living within the tree) or as trophic hosts (described as endoparasites) for nematodes (Grucmanová & Holuša, 2013; Hofstetter et al., 2015; Massey, 1974; Wegensteiner et al., 2015). Some nematodes species are also well-known tree pathogens causing wilts and dieback diseases of plants (Cobb, 1914; Mamiya, 1984). Over 50 nematode species are associated with bark beetles (Massey, 1974), feeding within and among beetle galleries upon fungi, bacteria, other arthropods, or tree tissues (reviewed in Grucmanová & Holuša, 2013; Hofstetter et al., 2015; Kaya, 1984; Kurashvili, Kakulia, & Devdariani, 1980; Lieutier, Mendel, & Faccoli, 2016; Massey, 1962, 1974; Polyanina, Mandelshtam, & Ryss, 2019; Rühm, 1956; Wegensteiner et al., 2015) and many are obligate endoparasites of beetles and can impact beetle fitness and general population growth (Wegensteiner et al., 2015). Generally, these nematodes do not kill their host but reduce fecundity, longevity, and flight distance, alter host behavior, and delay beetle emergence (Cardoza et al., 2008; Kaya, 1984). Nematodes are also known to feed upon and disperse microbes within beetle-infested trees (Cardoza, Paskewitz, & Raffa, 2006; Steiner & Buhrer, 1934; Wingfield, 1987).

The relative abundance of nematodes within beetles and between beetle populations varies greatly. Reported prevalence of nematodes in bark beetle populations ranges from 1 to 100% of beetles carrying nematodes within a given population (Cardoza, Klepzig, & Raffa, 2006; Grucmanová & Holuša, 2013; Massey, 1974; Meirmans, Skorping, Løyning, & Kirkendall, 2006; Takov & Pilarska, 2008). Nematode abundance may be especially high

(up to 99%) within tree tissues surrounding beetle galleries (Burjanadze & Goginashvili, 2009; Cardoza et al., 2008; Hoffard & Coster, 1976; Kereselidze, Wegensteiner, Goginashvili, Tvaradze, & Pilarska, 2010; Tenkáčová & Mituch, 1986, 1987; Tenkácová & Mituch, 1991). Significant differences have been documented in parasitization and phoretic rates between the spring and summer beetle generations (Choo, Kaya, Shea, & Noffsinger, 1987; Tenkáčová & Mituch, 1986) but not between male and female beetles (e.g., Takov & Pilarska, 2008; Zitterer, 2002).

2.5 Whole community interactions

Although beetles are the primary phoretic host for most of the ectosymbiotic communities, ectosymbionts themselves can play a phoretic role in introducing and spreading species within beetle-colonized trees (Hofstetter et al., 2015). For instance, many mycophagous mites have structures, termed sporothecae (Moser, 1985) used to collect and transport fungal spores (Ebermann & Hall, 2004; Moser et al., 2010; Moser, Perry, & Solheim, 1989) to new tree hosts. Fungi and bacteria are also introduced through feces of mites, nematodes, and other animals (Bridges, 1981; Popa et al., 2012; Xu, Lu, Xu, Chen, & Sun, 2016) or as endosymbionts of fungi (Gibson & Hunter, 2010). Given the complexity and diversity of species, it is not surprising that all types of interactions occur. Ultimately, for each species to move from tree to tree and persist in this community, it must either coexist or outcompete with other species, using adaptations and mechanisms for their propagules or offspring to successfully attach to beetle hosts when tree conditions deteriorate.

In general, we describe the ectosymbiotic species complex as a "community" (Fig. 2). This may be taken to imply that members of the community are all mutualistic or at least function in a manner to promote the community. However, the presence or absence of a mutualism is governed by dynamic ecological situations and contexts. In an evolutionary context, a phoretic association will not be mutualistic unless its carrier is faced with a need that the phoretic organism can solve adaptively. For example, as reviewed above, mycangial fungi provide an improved nutritional resource for ambrosia beetles, while for bark beetles, associated fungi may assist in detoxifying host chemistry, exhausting host defenses, and concentrate needed nutrients (Klepzig & Hofstetter, 2011; Netherer et al., 2021). As a result, beetles and their mycangial fungi form an elaborate multispecies mutualism (Bracewell & Six, 2015). Mites provide benefits to beetles if they reduce the presence of parasitic nematode loads on beetle offspring, but other species such as bacteria can affect those interactions and change associations from commensal to mutualistic, or even mutualistic to antagonistic (Cardoza et al., 2008; Wilson & Knollenberg, 1987). Interestingly, many ectosymbionts probably have little effect on beetles when the system is stable and only when the environment shifts do they cause significant effects, either positive or negative to their beetle host. Variation in species composition and genotypes of ectosymbionts of beetles within trees, stands and at the landscape scale, provides a foundation for natural selection to function on these communities and to affect bark and ambrosia beetle ecology.

3 Ectosymbiotic communities and their relationship with climate variables

Wilson (1980) argued that phoretic associations are elegant communities for studying the evolutionary consequences of indirect effects. Like all biotic communities, the responses of species associated with bark and ambrosia beetles to abiotic (e.g., climate change) and biotic (e.g., tree host species) factors can be dynamic and diverse, making it difficult, at best, to predict how communities will function in a nonanalog future (Williams & Jackson, 2007; Williams & Liebhold, 2002). Because these phoretic species are primarily dependent upon insects for transport and dispersal between habitats, understanding and modeling the community over time must include consideration of the complexity of interactions, phoretic relationships, and ecology of beetle hosts. Ectosymbiotic communities associated with bark beetles within trees in temperate and boreal habitats are well adapted to seasonal and typical year-to-year fluctuations in climate (Hofstetter, Klepzig, Moser, & Ayres, 2006; Khadempour, LeMay, Jack, Bohlmann, & Breuil, 2012; Roe, James, Rice, Cooke, & Sperling, 2011; Six & Bentz, 2007). However, climate change is expected to shift species ranges, phenology, and relative abundances, with resulting changes in species interactions (Dawson, Jackson, House, Prentice, & Mace, 2011; Waring et al., 2009). At the organismal level, metabolic, behavioral, or evolutionary mechanisms may drive ecto-symbiotic population responses to altered temperatures (and other factors) within trees, but responses of phoronts must match those of their phoretic hosts for the associations to persist. Community-level responses, in other words, are complex, and changing temper-atures may differentially affect demographic attributes of all species in these systems (Bentz et al., 2009, 2010; Elmendorf et al., 2012). The magnitude or sign (positive or neg-ative) of species interactions may also change, thereby disrupting mutualisms, trophic interactions, competition, and ultimately species coexistence of ectosymbiotic commu-nities (Blois et al., 2013; Gedan & Bertness, 2009; Six & Bentz, 2007; Sorte & White, 2013).

Many beetle species may have hedges against such disruptive forces, by maintaining redundant mutualistic associations (e.g., multiple mycangial fungi), which provide sources of resiliency to changes in climate, host tree species, and biotic interactions, and may protect beetle hosts from local extinction (Francke-Grosmann, 1967; Harrington, 2005; Paine, Raffa, & Harrington, 1997; Six, 2003, 2013; Villari et al., 2012). However, even in the past and present, climate extremes can have drastic effects on beetle survival and fit-ness (e.g., Evans, Hofstetter, Ayres, & Klepzig, 2011), which in some cases could result in poor performance by the ectosymbiotic species the beetles depend upon and vice versa (Bentz & Six, 2006; Klepzig & Six 2004; Netherer et al., 2021). Beetle population and distri-bution models typically do not account for interspecific biotic interactions among the ectosymbiotic community (e.g., Bentz & Jönsson, 2015; Wermelinger & Seifert, 1999), partly because of the complexity of interactions and partly because of lack of information about outcomes among these interactions. Thus, much of the data and interpretation pre-sented in this chapter relate to studies that have looked at direct climate effects on beetles and/or ectosymbiotic species across one generation (e.g., Evans et al., 2011; Hofstetter

et al., 2007) or just effects of climate on individual or groups of species, rather than the entire community (e.g., Vissa et al., 2021). It is clear from demographic studies of ectosymbionts that many species covary in their response to changes in temperature and slight changes in these responses could have long-term effects on beetles. Additionally, because most species covary in their response, this can compromise attempts to infer causality (e.g., Tylianakis, Didham, Bascompte, & Wardle, 2008) to patterns of beetle population dynamics (Soderberg, Mock, Hofstetter, & Bentz, 2020; Vissa et al., 2021).

In the following sections, we describe the effects of, and responses to, temperature in particular taxonomic groups commonly associated with bark and ambrosia beetles and later discuss effects of temperature on the ectosymbiotic community as a whole.

4 Direct effects of temperature of ectosymbionts

Temperature affects biochemical, physiological, and behavioral processes in animals and microbes, for which growth, competition, movement, and reproduction are sensitive to changes in temperature and environmental variability. Many of the ectosymbiotic species associated with bark beetles are no exception and their performance (growth, reproduction, competitiveness, etc.) is affected by temperature. Most species have an asymmetrical thermal performance profile, as shown in Fig. 3.

4.1 Direct effects of temperature on growth and reproduction of fungi

Most fungi associated with beetles have a left-skewed bump-shaped pattern (like Fig. 3) in growth rate in response to temperature (Addison et al., 2013; Hofstetter et al., 2007; Hofstetter et al., 2005; Klepzig et al., 2001). Additionally, fungal species and isolates within
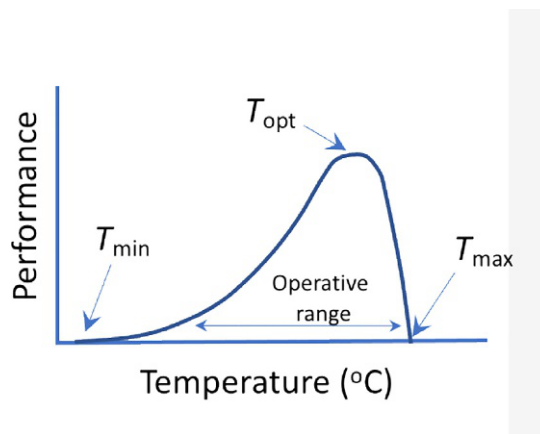

FIG. 3 Typical asymmetrical performance profile (e.g. growth or feeding rate) in relation to temperature. Upper (T_{max}) and lower critical temperatures (T_{min}) and the temperature at which performance is maximum (T_{opt}).

a species show considerable variability in response to temperature (Fig. 4) (Moore, 2013; Moore & Six, 2015; Roe et al., 2011). Fungal growth rate generally peaks between 20°C and 30°C, declines quickly above 32°C, and gradually below 10°C. Fungi associated with bark beetles are not believed to grow below 0°C nor above 43°C. Differences in growth rates in response to slight changes in temperature influence the relative proportion of fungal species within a forest stand or beetle population (Adams & Six, 2007; Dysthe, Bracewell, & Six, 2015; Hofstetter et al., 2007; Hofstetter, Klepzig, et al., 2006; Linnakoski et al., 2016; Six & Bentz, 2007), and this proportion can shift seasonally year after year (Addison et al., 2013; Addison, Powell, Bentz, & Six, 2015; Hofstetter, Klepzig, et al., 2006). Although not studied, the lower threshold that fungal hyphae can survive likely varies by species but probably falls between −10°C and −20°C, based on the lower threshold of most beetles,
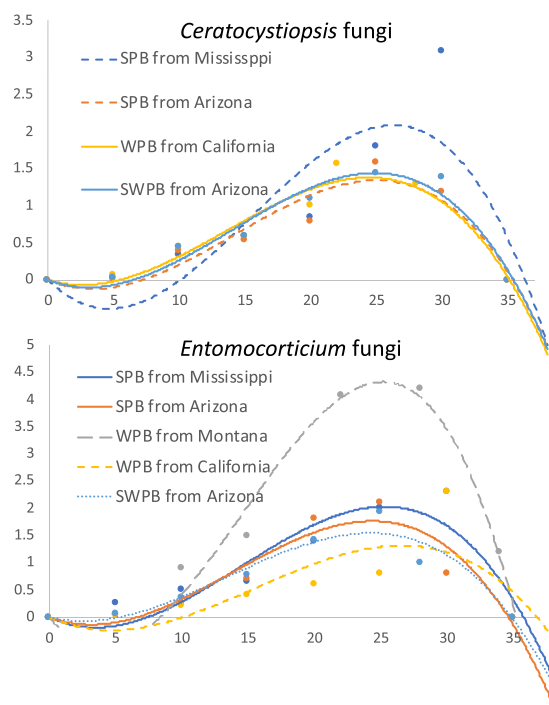

FIG. 4 Growth rate of mycangial fungi associated with bark beetles in response to temperatures. (top figure) Shows growth of *Ceratocystiopsis* fungi associated with the southern pine beetle (MS, AZ), western pine beetle (CA) and southwestern pine beetle (AZ). (bottom figure) Shows growth of *Entomocorticium* fungi associated with southern pine beetle (MS, AZ), western pine beetle (CA), and southwestern pine beetle (AZ). *Data adapted from Klepzig, K.D., Moser, J. C., Lombardero, M. J., Ayres, M. P., Hofstetter, R. W. & Walkinshaw, C. J. (2001). 13 Mutualism and antagonism: Ecological interactions among bark beetles, mites and fungi.* Biotic interactions in plant-pathogen associations *(p. 237).; Davis, T. S., Hofstetter, R. W., Klepzig, K. D., Foster, J. T. & Keim, P. (2010). Interactions between multiple fungi isolated from two bark beetles, Dendroctonus brevicomis and Dendroctonus frontalis (Coleoptera: Curculionidae).* Journal of Yeast and Fungal Research, *1(7), 118–126.; Bracewell, R. R., Pfrender, M. E., Mock, K. E. & Bentz, B. J. (2013). Contrasting geographic patterns of genetic differentiation in body size and development time with reproductive isolation in Dendroctonus ponderosae (Coleoptera: Curculionidae, Scolytinae).* Annals of the Entomological Society of America, *106(3), 385–391.*

typically −5°C to −22°C (Chansler, 1966; Friedenberg, Powell, & Ayres, 2007; Friedenberg, Sarkar, Kouchoukos, Billings, & Ayres, 2014; Koštál et al., 2011; Lombardero, Ayres, Ayres, & Reeve, 2000; Sømme, 1982). One of the lowest survival thresholds recorded for a bark beetle is −38.4°C for the mountain pine beetle (Rosenberger, Aukema, & Venette, 2017). Fungi appear to have an upper threshold around 35–40°C, and lethal exposure time varies by species and isolate. Field observations by Beal (1933) suggest that the upper lethal limit for fungal hyphae may match that of their beetle hosts, which is >43°C for the southern pine beetle. It may be lower for more long-term exposure, as Evans et al. (2011) observed low beetle survival and fungal growth when exposed to continuous 32°C. Additional studies are needed to determine if conidia or ascospores can survive in greater temperature extremes.

Temperature can affect the reproductive mode (e.g., sexual vs asexual) of fungi and thus affect fungal genetic diversity as sexual reproduction creates mosaic sequences and a means of creating new genetic combinations (Barrett, Thrall, Burdon, Nicotra, & Linde, 2008). Some fungal species associated with bark beetles show great diversity in levels of recombination, ranging from low variation seen in asexual lineages (e.g., *Leptographium longiclavatum* S.W. Lee, J.J. Kim & C. Breuil, *Entomocorticium*) to high variation seen in obligate out-crossers (e.g., *Ophiostoma montium* (Rumbold) von Arx, *Ceratocystiopsis ranaculosus* Perry and Bridges) (Bracewell & Six, 2014; Ojeda Alayon et al., 2017). Additionally, temperature affects spore production of fungi growing within trees (Moore & Six, 2015). Fungal species and isolates vary in the timing and abundance of sporulation, and responses to temperature may be different than that for optimal growth (Moore & Six, 2015; Roe et al., 2011). Effects of temperature on the timing of sporulation will thus influence fungal and beetle fitness and the maintenance of symbioses (Moore & Six, 2015); fungi must sporulate at the time beetles eclose so that their spores are available to beetles for packing in mycangia prior to emergence and dispersal, and adult feeding if needed (Moore & Six, 2015; Six & Bentz, 2007). Spore production also influences interactions with mites as they too carry spores between trees and disperse spores within trees (Levieux, Lieutier, Moser, & Perry, 1989; Lombardero et al., 2003; Moser, 1985; Moser et al., 1989).

Resource capture by fungi is closely tied to their growth rate as many fungi exhibit exploitation competition (Bleiker & Six, 2009a, 2009b; Harrington, 2005; Lockwood, 1992). Interestingly, many of the mutualistic fungal species associated with bark beetles do not exhibit "interference" competition with each other but exhibit "exploitative" competition in which growth rate is more important for resource capture (Moore & Six, 2015). However, this does not imply that fungi cannot affect each other's growth and resource acquisition (Hofstetter et al., 2015), nor that interference competition between beetle associated fungi does not exist (Klepzig, 1998; Klepzig & Wilkens, 1997).

From beetle studies that monitor fungal species exposed to various temperatures in trees (e.g., Evans et al., 2011; Hofstetter et al., 2007; Hofstetter, Klepzig, et al., 2006; Roe et al., 2011), it is clear that temperature affects species abundances in ways that are not predicted based solely on autecological responses of individual species (Hofstetter

et al. 2005; Klepzig et al., 2001; Klepzig, Flores-Otero, Hofstetter, & Ayres, 2004; Six & Bentz, 2007). Growth, spore production, and dispersal of species will be varied in their response to temperature (Moore & Six, 2015) thus affecting the nature of interactions and composition of species within communities over time. However, shifts in fungal species performance in relation to changing temperatures provide a mechanism that allows multiple fungi to persist in long-term symbioses with their beetle hosts. By growing at different rates across temperatures at different times of the year, fungi may minimize competition. In turn, beetles benefit by exploiting multiple fungal symbionts, whose growth optima span a wide range of environmental conditions (Davis et al., 2010; Hofstetter et al., 2007; Six & Bentz, 2007). However, more extreme high temperatures could lead to a reduction in community richness and a predominance of a few species able to persist at high temperatures (Davis et al., 2010). Alternatively, increased variability in mean temperatures might counter this trend and promote symbiont diversity and community complexity. It is also important to note that nonmycangial fungi (including potential antagonists to beetles and mutualistic fungi) may increase due to environmental changes and may deplete resources available to beetles and their obligate associates (Ayres, Wilkens, Ruel, Lombardero, & Vallery, 2000; Wang et al., 2012, 2013).

4.2 Direct effects of temperature on the growth and reproduction of bacteria

Most work on bacteria associated with bark and ambrosia beetles involves surveys of species (Cardoza, Paskewitz, & Raffa, 2006; Cardoza et al., 2009) or investigations on the effects of bacteria on tree defenses or interactions with fungi (Adams et al., 2009, 2011; Cardoza, Paskewitz, & Raffa, 2006; Zhou et al., 2016). To date, no one has conducted temperature studies on growth rates of bacteria associated with bark and ambrosia beetles. Studies on effects of temperature on soil bacteria (Baath, 2018; Pietikäinen, Pettersson, & Bååth, 2005) show similar growth rate patterns to soil fungi. Temperature-growth patterns of bacteria and fungi in soil appear to be similar to those of fungi associated with bark beetles. Optimal growth of soil bacteria, with the exclusion of extremophiles, is generally between 20°C and 30°C (Barcenas-Moreno, Gomex-Brandon, Rousk, & Bååth, 2009) and likely similar for bacteria associated with beetles that colonize trees. Minimum temperatures for bacteria growth found in soil ranges from −8.4°C to −12.1°C and maximum temperatures for soil bacteria are around 45°C. Differences in minimum and maximum temperatures of particular species often relate to temperature patterns of their respective habitats. Based on soil studies, it appears that low temperatures are more detrimental to bacteria than fungi, and high temperatures (above 30°C) are more detrimental to fungi than bacteria (Pietikäinen et al., 2005). Given strong effects of temperature on bacteria growth rate, we would expect seasonal variation in bacteria growth and differences between years, associated with changes in average annual temperatures (Hofstetter, Klepzig, et al., 2006).

Additionally, maximum and minimum temperatures should affect bacteria growth, survival and composition.

4.3 Direct effects of temperature on growth and reproduction of mites

Mites, like beetles, are ectothermic, their metabolic activity and developmental rates increase with increasing temperature (Schowalter, 2006). Temperature is a key abiotic factor affecting the development of individuals and populations of mites, from those in stored products (Błoszyk & Robbert, 1985; Kawamoto, Sinha, Muir, & Woods, 1991) to those associated with bark beetles (Hofstetter & Moser, 2014). The few studies that have looked at the effects of temperature on population growth of mites associated with bark beetles (Evans et al., 2011; Hofstetter et al., 2007; Lombardero et al., 2003) show a bump shaped pattern in growth rate in response to temperature, similar to that of fungi and bacteria shown earlier. Similar to fungi, reproduction and growth rate of mites are highly sensitive to temperature (Lombardero et al., 2003). Temperatures below 8°C result in no mite egg production or hatching, limited movement and no population growth (Lombardero et al., 2003). High temperatures above 30°C increase mite metabolic rates but result in low or no egg production and shortened lifespans (Lombardero et al., 2003).

For mites, successful attachment to emerging phoretic hosts is highly dependent on being at the right developmental stage at the right time. Basically, the window of opportunity for mite reproduction and population growth within the tree is set by the generation time of its beetle hosts (Bentz et al., 2010). However, mites are more sensitive to changes in temperature than are some bark beetles (Lombardero et al., 2003). For example, southern pine beetle larvae can continue development during the winter (Thatcher, 1981), and adult beetles fly at temperatures as low as 7°C (Thompson & Moser, 1986). At these same temperatures, mites barely move, feed, or lay eggs (Lombardero et al., 2003). This difference in temperature sensitivity produces a surprisingly narrow range of temperatures (centered around 27°C) in which mite reproduction per beetle generation can be high. At temperatures of 23°C or 30°C, mite reproductive potential is less than half its maximum (Lombardero et al., 2003).

Differential responses to temperature affect the relative proportion and abundances of phoretic mites associated with bark beetles (Vissa et al., 2021). Hofstetter, Klepzig, et al. (2006) observed that the relative abundance of mite species within beetle populations changed through time, with some mite species being abundant in warm seasons and others in colder seasons. Species-level differences in mites leads to drastic changes in phoretic mite composition from beetle generation to generation, whether within years (e.g., southern pine beetle system, Evans et al., 2011; Hofstetter et al., 2007; Hofstetter, Klepzig, et al., 2006) or from year to year (e.g., mountain pine beetle system, Vissa et al., 2020). Additional studies are needed to determine environmental effects on mite sex ratio or triggers for morphological shifts in mite preparation for phoretic stages.

4.4 Direct effects of temperature on growth and reproduction of nematodes

Nematode numbers within bark beetle-colonized tree tissues and phoretic rates on beetles are influenced by a multitude of factors including temperature and moisture (Choo et al., 1987; Massey, 1974; Shimizu et al., 2013). Given that nematodes perform better in moist environments, this factor is likely the key driver in nematode abundance within beetle-infested materials (Massey, 1974). Rühm (1956) stated that temperature during the summer months would be crucial for the occurrence of some nematode species for which their larval stages are outside their beetle hosts during this period and thus most vulnerable to microclimate conditions. The prevalence of endoparasitic nematodes is also strongly correlated with spring and summer temperatures (Meirmans et al., 2006). Rühm (1956) and Meirmans et al. (2006) found that ectoparasitic nematodes have lower tolerance for cold than endoparasitic nematodes. Thus, it is possible that differences in temperature would affect the relative abundances and success of particular nematode species.

5 Effects of climate change on tree condition (secondary defenses, nutrition, moisture) and the symbiotic community

In most parts of the world, climate change is resulting in elevated temperatures, higher CO_2, and increased overall carbon fixation (Mullin et al., 2021; Robinson, Ryan, & Newman, 2012). However, the majority of this additional fixed carbon is predicted to be accumulated in nonstructural carbohydrates and carbon-based secondary metabolites because nitrogen and phosphorous will remain limiting factors for growth (Cook, Shirley, & Zambino, 2010; Hammerbacher, Wright, & Gershenzon, 2020; Lindroth, 2010). Elevated temperatures will also increase evaporative demand or vapor pressure deficits, creating longer and more intense periods of drought stress on trees (Andrus, Chai, Harvey, Rodman, & Veblen, 2021; Breshears et al., 2009, 2013; Williams et al., 2013). Severe drought conditions increase the susceptibility of trees to pests and pathogens (Anderegg et al., 2015; Desprez-Loustau, Marcais, Nageleisen, Piou, & Vannini, 2006; Koricheva, Larsson, & Haukioja, 1998; Larsson, 1989; Mattson & Haack, 1987; Sturrock et al., 2011), but under moderate drought conditions, trees tend to actually increase the production of defense metabolites (Ferrenberg, Kane, & Langenhan, 2015; Lorio, 1986; McDowell, 2011; Netherer et al., 2021).

Resin production in conifers, for instance, can be severely impacted by water deprivation (Dunn & Lorio, 1993), but Lombardero, Ayres, Lorio, and Ruel (2000) showed that the effect would depend on whether constitutive or induced resin production is considered. In fact, when drought conditions limited growth, the constitutive resin volume of loblolly pine was higher, while resin induction was lower. Similarly, in experiments where either lodgepole pine (Arango-Velez et al., 2016) or jack pine (Klutsch, Shamoun, & Erbilgin, 2017) were inoculated with *Grosmannia clavigera* (Robinson-Jeffrey and Davidson)

Zipfel, Z.W.de Beer & M.J.Wingf., the common fungal associate of the mountain pine beetle, drought increased constitutive levels of several monoterpenes, but decreased their induction. The results of both experiments are in accordance with the growth-differentiation balance hypothesis prediction that mild resource limitations will produce an increase of constitutive carbon-based defense metabolites and a decrease of induced ones (Herms & Mattson, 1992; Lorio, 1986). The effect of climate on resin production will also depend on the location of the forest affected; oleoresin flow, for instance, may increase with climate warming in cool mesic and boreal forests whose growth and secondary metabolites production is currently limited most strongly by low temperature (Boisvenue & Running, 2006; Littell et al., 2010). Temperature and moisture changes as well as exposure to fire may also affect resin viscosity and consequently alter resin volumetric flow (Davis, Jarvis, Parise, & Hofstetter, 2011; Gaylord, Kolb, Wallin, & Wagner, 2007).

As reviewed in Hammerbacher et al. (2020), higher CO_2 levels generally result in higher accumulation of phenolic compounds in angiosperms (Robinson et al., 2012), while warmer temperatures have an opposite effect (Kuokkanen, Julkunen-Tiitto, Keinänen, Niemelä, & Tahvanainen, 2001). In conifers, however, the effects of increased CO_2 levels on production of phenolic compounds are not as clear, with discording results within and between different species (Gebauer, Strain, & Reynolds, 1997; Sallas, Luomala, Utriainen, Kainulainen, & Holopainen, 2003; Zhang et al., 2018). Higher temperature will reduce phenolic compounds in conifers, similarly to what observed for angiosperms (Riikonen et al., 2012; Sallas et al., 2003; Zhang et al., 2018). Drought will generally increase accumulation of constitutive phenolic compounds (see Hale, Herms, Hansen, Clausen, & Arnold, 2005 and Mechri, Tekaya, Hammami, & Chehab, 2020 for experiments in poplar and olive tree, respectively), which is consistent with their role as antioxidants in plants (Kumar et al., 2020; Sharma et al., 2019). However, Chakraborty et al. (2014) found that drought had no effect on either the constitutive or induced content of phenolic compounds in ash species, while Roth, MacDonald, and Lindroth (1997) reported a decrease of phenolic glycoside concentrations in drought quacking aspen, suggesting that the response might be system specific.

Huang et al. (2020) have recently proposed a comprehensive framework to better address the complex interactions between tree defenses and bark beetles under water stress. Allocation of nonstructural carbohydrates to defense-related secondary metabolites has a nonlinear behavior under drought conditions, and it depends on a variety of factors including the class of the chemical compounds, plant tissue, tree characteristics, age and health status, and timing and intensity of the stress. Hence, it is not surprising that experiments carried out with bark beetle fungal symbionts have given contrasting results, with instances where mild drought increased overall resistance of adult trees (measured as shorter lesion length) (Arango-Velez, Gonzalez, Meents, et al., 2014; Christiansen & Glosli, 1996), and others, performed on seedlings, where drought decreased tree resistance to fungi (Devkota, Enebak, & Eckhardt, 2018; Linnakoski et al., 2017).

   In addition to the abovementioned changes in their secondary metabolism and pro-
duction of defense compounds, whose effects on bark beetles and their symbiotic com-
munities are intuitive, plants cope with drought and other climatic disturbances with a
variety of physiological alterations of their primary metabolism (Bhargava & Sawant,
2013; Chaves, Maroco, & Pereira, 2003), which can increase susceptibility to fungal path-
ogens (Mann & Davis, 2020; Schoeneweiss, 1975). The accumulation of osmolytes such as
the amino acid proline (Hare, Cress, & Van Staden, 1998), for instance, has been shown to
produce the unwanted secondary effect of triggering a shift to aggressive behavior in an
otherwise entophytic fungal species in Austrian pine (Sherwood, Villari, Capretti, & Bone-
llo, 2015). Changes in tree primary metabolites could hence affect the bark beetle's sym-
biotic community in ways that are difficult to predict without further investigations.
Drought conditions and higher temperatures will also reduce moisture within tree tissues
and negatively impact ectosymbionts as well as beetle development and survival (Klepzig
et al., 2004; Klepzig & Hofstetter, 2011). However, excessively high moisture in tree tissues
can also have negative effects on beetle growth and survival (Webb & Franklin, 1978).
   In summary, changes in host tree chemistry, moisture, and nutritional content can
affect distribution and prevalence of ectosymbionts within trees. Fungus, bacteria, nem-
atode and mite abundance and composition shift dramatically within beetle generations
and across seasons. In addition to temperature-growth responses, shifts in ectosymbionts
can be driven by changes in tree defenses, primary metabolism, and moisture content and
can even occur through systemic cross-induction of susceptibility (Klutsch et al., 2017).
Variation in reproduction (spores, offspring) among ectosymbionts affect the rate of
growth, abundance, and synchrony with exiting beetles. Changes in tree defenses affect
colonization success but also succession patterns of ectosymbionts within the tree. For
instance, some fungi might be highly competitive in one set of conditions but poor com-
petitors under others. Thus, changes in tree defenses over time could influence not only
relative rates of growth and primary resource capture but also the outcome of direct com-
petition among the various ectosymbionts which could ultimately affect beetle fitness
over time.

6 Projected effects of climate (temperature regimes, drought) and changes to the ectosymbiotic community on bark beetle ecology

Climate strongly effects the outcome of interactions and species performance, and each
species ability to persist within the bark beetle system will depend on their response (Fig.
5) to the range of climate factors during each beetle generation (Bentz & Powell, 2014; Bie-
dermann et al., 2019; Moore & Six, 2015). High thermal thresholds for development vary
across ectosymbiotic species and bark beetles species (Fig. 5). For instance, optimal devel-
opment rates for the adult southern pine beetle are between 27°C and 30°C (Wagner,
Gagne, Sharpe, & Coulson, 1984), near 28°C for adult eastern larch beetle (McKee &
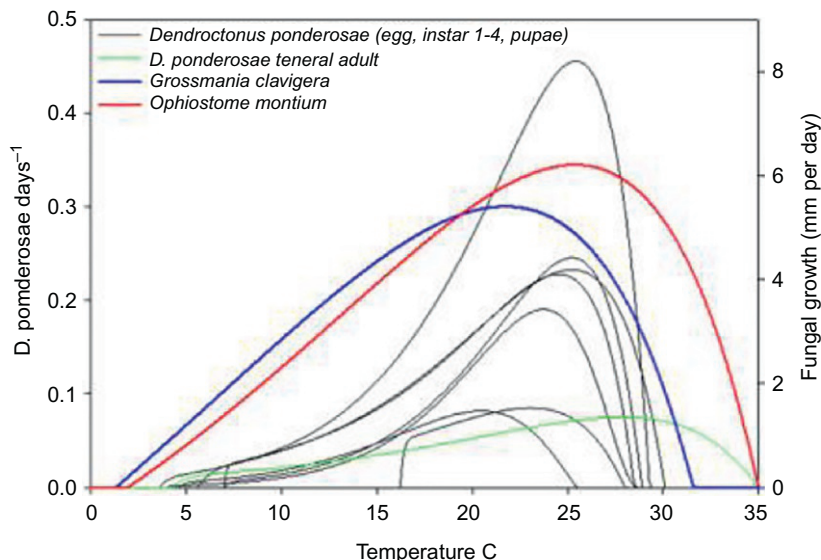
FIG. 5 Growth rates of the mountain pine beetle (*Dendroctonus ponderosae)* life stages (*black lines*) and associated mycangial fungi in response to temperature. *Figure adapted from Moore, M.L., & Six, D.L. (2015). Effects of temperature on growth, sporulation, and competition of mountain pine beetle fungal symbionts.* Microbial Ecology, 70*(2), 336–347.; Bentz, B. J. & Powell, J. A. (2014). Mountain pine beetle seasonal timing and constraints to bivoltinism: A comment on Mitton and Ferrenberg (2012).* The American Naturalist, 184*(6), 787–796; Régnière, J., Powell, J., Bentz, B. & Nealis, V. (2012). Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling.* Journal of Insect Physiology, 58*(5), 634-647, created by Barbara Bentz and Jim Powell.*

Aukema, 2015), and 25–35°C for different stages of the mountain pine beetle (Régnière, Powell, Bentz, & Nealis, 2012), and optimal fungal growth for their respective fungal mutualists are between 20°C and 30°C (Adams & Six, 2007; Hofstetter et al., 2007; Hofstetter, Klepzig, et al., 2006; Linnakoski et al., 2016; Six & Bentz, 2007). Information on response at the extremes is important, particularly when predicting the impacts of climate change, and nonlinear descriptions are critical (Régnière et al., 2012). Examining low and high temperature thresholds in nature can be complicated by nonlinearities that occur at thresholds and reduced survival at temperature extremes. Because of these difficulties, low and high temperature thresholds are unclear for many bark beetle species (Bentz & Jönsson, 2015).

A warming climate will have variable effects on ectosymbionts and host beetle population dynamics. Species already living at or near their thermal maximum (i.e., small "thermal safety margin") may be more impacted by climate warming as temperatures exceed optimal thresholds, especially those with sharp declines in development rate at temperatures above the optimum (e.g., Figs. 3 and 5). Populations in cooler environments typically have thermal optima higher than their current environment (i.e. large "thermal safety margin") relative to populations in warmer environments (Deutsch et al., 2008) and,

therefore, may initially respond positively to warming temperatures. For example, at many cool, high elevation sites, recent temperature increases remain in the thermal range of increasing development rate for mountain pine beetles, resulting in a decrease in their generation time (Marini, Ayres, Battisti, & Faccoli, 2012; Mitton & Ferrenberg, 2012). At warm, low-elevation sites, however, historical temperatures were already at or near the threshold for optimal development and increased warming could have little effect on generation time (Bentz et al., 2014) and may also improve beetle performance (Mitton & Ferrenberg, 2012; Soderberg et al., 2020).

Increases in beetle development rate may have negative consequences for beetle survival and population growth. For example, Jönsson, Harding, Bärring, and Ravn (2007) and Bentz et al. (2015) reported that accelerated development rates render *Ips typographus* L. (DeGreer, 1775) and *D. ponderosae* more susceptible to mortality because of cold winter temperatures. Increases in abundances of microbes or mites that are less favorable to beetles can occur with increased temperatures (Evans et al., 2011). For example, Moore and Six (2015) suggest that, as temperatures increase due to climate change, the relatively less beneficial mycangial fungus *O. montium* may become a more common associate of the mountain pine beetle, while the more beneficial *G. clavigera* may be lost in areas that experience even moderate warming (Rice, Thormann, & Langor, 2008; Roe et al., 2011). While redundancy of nutritional symbionts in this system likely has supported a broad ecological resilience for the host beetle, the loss of the nutritionally superior symbiont could mean that mountain pine beetle populations would increasingly depend upon *O. montium*, resulting in lower beetle fitness and reduced population growth potential (Bleiker & Six, 2014). This could be exacerbated by tree defense reduction driven by warming which will translate to short term effects in beetle population dynamics (Bentz et al., 2010; Raffa et al., 2015) and increased tree mortality. In the long-term, however, beetle population growth, range expansion, competitiveness, and resilience may decline. Unfortunately, continued stress due to drought and temperature extremes on host trees will result in high tree mortality, regardless of beetle population growth potential.

7 Conceptual model

The most important determinant of ectosymbionts success and persistence within a system is the ability to consistently be picked up and transferred (i.e., dispersal ability) by a phoretic host to the next tree (i.e., resource) (Hofstetter & Moser, 2014). To do this, ectosymbionts must survive and/or reproduce within the timespan of the beetle life cycle (Klepzig & Six 2004; Six, 2020). Survival and reproduction depend upon the ability of organisms to acquire resources, avoid predation, be competitive or avoid competition, and mechanisms or adaptations (e.g., diapause, spores, etc.) to allow propagules or offspring to be present when beetles exit the resource (Hofstetter et al., 2015). Relative effects of temperature on survival, reproduction/development rate, nutrition, predation, or competition will, of course, impact the ectosymbiotic community as a whole (Fig. 6). A change
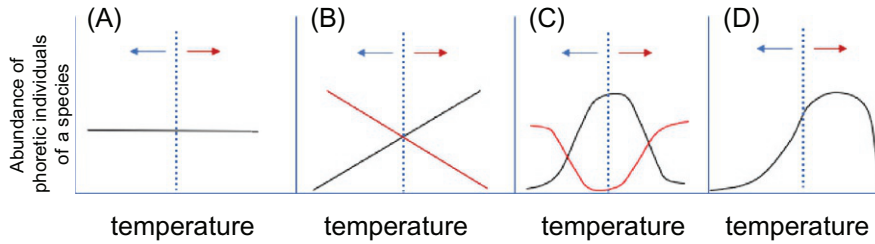
FIG. 6 Examples of performance profiles of ectosymbiotic species. The *dotted line* could represent the annual mean temperature, and the *arrows* represent a change in mean temperature (*blue arrow* indicating reduced mean temperature and *red arrow* for increased mean temperature). If a species is insensitive to temperature or its abundance is not sensitive to this temperature range, the resulting profile (A) is flat. However, such insensitivity to temperature might be true only of very few species or be representative of a limited temperature range. More typical is some kind of positive (*black lines*) or negative (*red lines*) response, which can be linear (B) or more complex (C and D). Linear profiles appear to result where the range of temperature is still small relative to the operative ranges (see Fig. 3). Exploring effects of temperature across a wider range that encompasses a greater proportion of the thermal performance profiles, and even exceeds the operative ranges, generally reveals more complex nonlinear responses. The most common profile is likely shown in (C) or (D) (*black lines*), as performance is generally low at cool and hot temperatures, and an optimal range is at moderate temperatures. Short-term exposures to extreme temperatures could result in a local extension of a species.

in any of these factors has the potential to facilitate climate change-induced local extinctions of ectosymbionts. Significant reductions in just one symbiotic community member may drastically decrease the total number of future phoretic individuals, potentially decoupling dependencies and collapsing symbiotic communities.

Variation in climate, host defenses, and other factors (e.g., moisture, competitors, CO_2, etc.), whether at the local or regional scale, influences ectosymbiotic communities. As long as it falls within a defined, tolerable range, variation in environment parameters seems to promote the coexistence of multiple species. For example, seasonal variations in temperature have apparently favored the co-occurrence of multiple mycangial mutualistic fungi and southern, western, and mountain pine beetles. While beetles in more tropical environments with less temperature variation or environments with less change in plant defenses (e.g., secondary beetles or ambrosia beetles) may favor single dominate mycangial fungal associates.

Extremes in water availability and temperatures (e.g., T_{min} and T_{max} for a species, Fig. 3), drastically affect the ectosymbiotic community (Fig. 7). Diversity decreases when most local populations of ectosymbiont species become extinct due to their inability to recover from disturbances (when mortality outstrips reproduction). If the disturbance is extreme and regional in scale, the ectosymbionts (and bark beetle population) will remain low in density and diversity (Fig. 8). These two different situations (i.e., constant conditions vs extreme disturbances) will result in low species diversity of ectosymbionts, while in intermediate conditions (i.e., moderate variation in conditions or minimal disturbances) a more variable (and likely more resilient) ectosymbiotic community may persist.
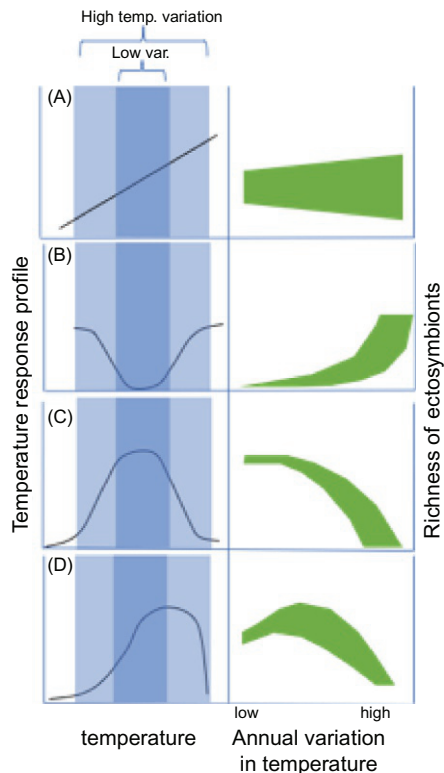
FIG. 7 Examples of performance profiles of ectosymbiotic species and how they might affect species richness (*green shaded areas*) of ectosymbionts within bark beetle symbiotic communities. Plots on the left of the figure represent low (*dark blue*) or high variation (*light blue*) in temperature and subsequent species responses (*black lines*). Plots on the right represent the effects of temperature variation on ectosymbiont richness. (A) Species that have a positive linear response to temperature (within a given range), would result in variable effects on species richness, depending upon whether high temperature variation included more high or low temperature extremes. (B) Although not common, this graph represents species that perform poorly at moderate temperatures but better at temperature extremes, resulting in an increase in richness as temperature variation increases. (C) Species with a humped-shaped response to temperature would result in a gradute decline in species richness as temperature variation increases. (D) The most common profile is likely a left-skewed hump shape temperature profile, resulting in a slight increase with some temperature variation and then decreasing as temperature variation extremes are reached.

8 Testable hypotheses

Given the rich literature on symbiotic relationships between bark and ambrosia beetles and their phoronts, we are able to generalize how they might respond to continued climatic changes. However, much is still unknown, and several testable hypotheses come to mind:

1. **Intermediate disturbance hypothesis:** Ectosymbiotic community is most diverse in habitats with intermediate "levels" of disturbance. "Level" refers to the intensity, frequency, size, or time frame of the disturbance.
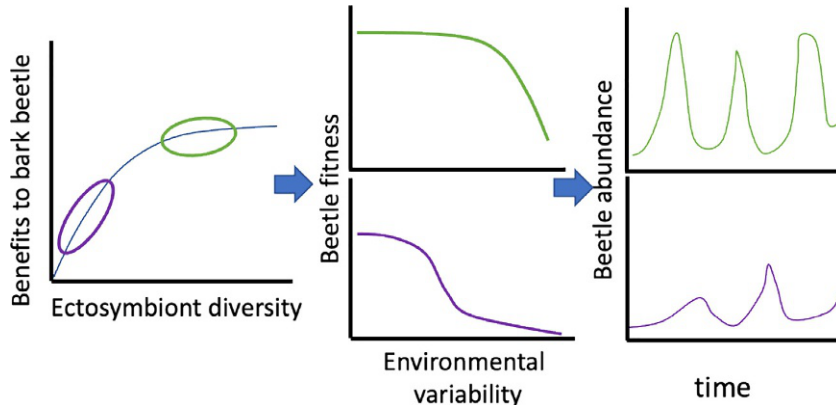
FIG. 8 (Left) Relationship between ectosymbionts diversity (low, *purple line*; high, *green line*) and benefits (growth, survival, reproduction) to bark beetles. (Middle) Effects of environmental variability on beetle fitness in systems with low diversity (*purple line*) and high (*green line*) of ectosymbionts. (Right) Bark beetle population dynamics with low (*purple line*) and high (*green line*) ectosymbiont diversity. Beetle populations are predicted to have slow population growth resulting in few outbreaks and less severe outbreaks due to reduced benefits from low ectosymbiont pool.

2. **Variable resource hypothesis:** High variability in environmental conditions (host tree species, temperature, etc.) promotes a greater diversity of ectosymbiotic species (e.g., across these host tree species) associated with a given beetle population. This variability could include factors such as climate, local beetle population size and density, host tree condition, and predators and competitors.
3. **Ecological niche restrictions hypothesis:** Limited ecological niches in ectosymbionts more readily lead to extinctions due to climate/disturbance extreme events.
4. **High mutualistic dependence hypothesis:** Loss of obligate (mutualistic) associations leads to coextinction cascades (e.g., a loss of a mutualist could lead to the establishment of exploiters and other bark beetle antagonists).

9 Critical research needs

The diversity and identities of bark beetle ectosymbiotic partners are well documented for some bark beetle systems, but for many other beetle systems—especially secondary beetles—we still have limited knowledge of these interactions. Even defining a species or strain of fungus can be challenging for bark beetle systems. Changes in ectosymbiotic species across scales further complicate our understanding of these interactions and how they affect bark beetle population dynamics. Research is needed to understand mutualistic networks (e.g., multiple obligate mycangial fungi vectored by numerous arthropod associates), how they respond to environmental variables, and how they may buffer potential effects on their bark beetle hosts. Laboratory studies are needed to examine the comprehensive ectosymbiont community and its effects on bark beetle fitness in response to individual and combined factors (e.g., temperature-host defenses-wood moisture ranges) over multiple beetle generations.

System models, including population dynamics of all symbiotic community members, require accurate data, including results from controlled laboratory studies. Future research would also benefit from a network of geographically diverse and comparable long-term field experiments that allow for additional investigator-driven experiments/observations. Some recommended minimum protocols and techniques should be created to improve the collection, isolation and identification of ectosymbionts across beetle systems (Hulcr et al., 2020). Quantitative models are needed to better understand and test hypotheses related to the effects and changes that ectosymbionts have on bark beetle dynamics. Discrepancies between models and field observations will drive improvements in our understanding of how climate change affects beetle patterns.

Some of the most important areas in which we lack a general or even basic understanding include (i) the importance of ectosymbionts on bark beetle survival, reproduction, or development, (ii) the magnitude of the effects of an ectosymbiont on beetle fitness, (iii) nonadditive effects of multiple ectosymbionts on beetle performance, (iv) population-level implications of variable environmental impacts on ectosymbiont communities, (v) the scope for population- or species-level adaptation to environmental change by ectosymbionts, and (vi) ecological responses of ectosymbionts at the level of communities (e.g. within trees) and ecosystems (within forest stands), including tipping points and beetle populations phases.

The influence of interactions between ectosymbionts, beetle hosts, and the host plants on beetle population dynamics and ecology is increasingly recognized; This chapter summarizes our current knowledge of the complex interactions among ectosymbionts of bark and ambrosia beetles and how they significantly influence beetle reproduction, growth, survival and dispersal, and how changes in temperature may affect beetle ecology. Although we focused on ectosymbionts in this chapter many factors discussed throughout this book such as forest management, host tree ecology, and competition with other beetles have equal or greater effects on beetle populations. Predicting the dynamics and distribution of beetle populations associated with global changes will likely require an understanding of beetle-ectosymbiotic communities, interspecific competition, forest stand dynamics, host plant ecology, and the suite of interacting traits associated with these species and how they response to the many changes in the future.

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