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Forum

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A Review of the Ecology and Management of Black Turpentine Beetle (Coleoptera: Curculionidae)

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Abstract

The black turpentine beetle, *Dendroctonus terebrans* Olivier is the largest pine-infesting bark beetle native to the southern and eastern United States. It generally reproduces in fresh stumps and bases of trees weakened or killed by other biotic or abiotic agents, although it can also infest and sometimes kills apparently healthy trees. Its numbers can build when large amounts of host material become available (typically through a disturbance), and black turpentine beetle-caused mortality at a local scale can become considerable. Here, we provide a complete review of the literature on this species, including its taxonomy, host, life history, chemical ecology, arthropod and microbial associates, and management options. We also provide original data on numbers of instars, acoustic signals, and pheromone chirality in this species. Our survey of the existing literature revealed that key biological characteristics of black turpentine beetles are known, but interactions with closely associated organisms, economic and ecological impacts, and improvements to monitoring and management practices have been only partially investigated.

Key words: bark beetle, conifer, fungal associate, mite associate, semiochemical

The black turpentine beetle, *Dendroctonus terebrans* Olivier is a common and typically abundant bark beetle species in pine (*Pinus* spp.) forests of the southeastern and eastern United States. It colonizes all species of pines within its range, spanning from eastern Texas and Oklahoma eastward to the Atlantic coast and northward to Massachusetts (Pajares and Lanier 1990, Staeben et al. 2010). It is one of only two species of the highly destructive genus of bark beetles *Dendroctonus* Erichson that occur within the expanse of managed pine forests of the coastal plain and piedmont of the southern United States (Wood 1982a, Pajares and Lanier 1990), an area often called the 'wood-basket' of the United States (Fox et al. 2007). It belongs to the southern pine bark beetle guild, which includes the pine engravers (Coleoptera: Curculionidae) *Ips avulsus* (Eichhoff), *Ips calligraphus* (Germar), *Ips grandicollis* (Eichhoff), and the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae). Species in the southern pine bark beetle guild commonly co-occur on the same trees, often in large numbers. All members of the guild are capable of killing apparently healthy trees when at high densities and are thus significant pests (Nebeker 2011), particularly southern pine beetle, which periodically produces devastating and widespread outbreaks and has been the most significant pest of southern forestry. Typically, black turpentine beetle is found in the basal portions of pines that are either damaged, dying, or dead due to various abiotic and biotic factors, and they may contribute to the initial stages of the breakdown of large woody debris (Hodges and Pickard 1971, Sullivan et al. 2003). Black turpentine beetles can have important ecological and economic impacts on planted and natural forests, and also affect ornamental and shade trees in the urban environment.

Generally, black turpentine beetle is a 'secondary' pest species that rarely causes tree mortality alone, but rather acts in concert with other bark beetles and mortality factors. They tend to reproduce in either cut-over stumps or the basal portions of trees severely weakened or killed by other causes such as fire, drought, mechanical damage, lightning, disease, and/or attack by other subcortical species (Hopkins 1909, Wood 1982a, Staeben et al. 2010). Invariably, they are the most common species found on symptomatic pine trees, whether *Ips* spp. or southern pine beetle are present alone or together on the same tree (H.L.M., B.T.S., and K.J.K.G., personal observations). Historically, they were a serious pest to the naval stores industry (i.e., harvesting and processing of pine resin for turpentine, resin, and other products) in the southern states during much of the last century (Smith and Lee 1972, Merkel 1981). With traditional methods, resin harvesting causes significant damage to tees. Although the importance of black turpentine beetles as a pest has decreased with the fading of the naval stores industry of the United States (Johnson 2000), there is currently interest in reviving turpentine production in the South (Lloyd Busby, personal communication) and thus, renewed interest in its effective management. Black turpentine beetles may become a more significant mortality agent with appearance of expected increases in disturbance events and stresses from climate change; these may include drought, and wind damage due to more frequent and stronger storms, and flooding events. It is also possible that black turpentine beetles will undergo range expansion northward to regions where it has historically been restricted due to colder temperatures (as is currently happening with southern pine beetles in the northeastern United States [Lesk et al. 2017, Aoki et al. 2018]), and potentially gain access to naive host species. Finally, black turpentine beetles may have the capacity to become established as an exotic pest outside its native range, as indicated by the establishment and serious pest status of the closely related, Nearctic red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Curculionidae), in China (Yan et al. 2005). However, it is unclear if the aforementioned scenarios will result in increased pest status or if black turpentine beetles will exceed their economic injury level or threshold.

The goal of our paper is to provide an up-to-date review and synthesis of the literature on the biology and natural history of black turpentine beetle. We review its taxonomy and phylogeography, life history, chemical communication, acoustic signals, associated organisms, economic and ecological importance, and sustainable management. Additionally, some newly collected data are reported for the purpose of filling some significant knowledge gaps on this species.

Economic and Ecological Importance

At endemic levels, black turpentine beetles rarely cause pine mortality sufficient to produce a significant economic impact, but, when population densities build to high levels, mortality can be locally severe (Hopkins 1909, Smith and Lee 1972, Merkel 1981). Anthropogenic activities, such as resin harvesting (i.e., naval stores industry), forest thinning, and urban activities, can cause bark or root damage that can exacerbate attacks by black turpentine beetle and increase their pest status (Hopkins 1909, Kucera et al. 1970, Feduccia and Mann 1975, Merkel 1981, Fatzinger 1985, Cameron 1987). Reliable documentation of timber losses from black turpentine beetles is limited, likely because it can be difficult to attribute mortality to a single bark beetle species, as trees are typically colonized by multiple species of bark beetle at the same time (Birch et al. 1980, Coulson et al. 1986, Flamm et al. 1993). Between 1949 and 1951, three million board feet of pine were killed by black turpentine beetles on a single 50.6-thousand-hectare tract in Louisiana, and wet sites in Florida experienced 30–50% mortality attributed to this species (Lee and Smith 1955). In the 1980s, portions of the northern limits of the range of black turpentine beetle (Massachusetts) experienced significant losses in non-native coastal Japanese black pine (*P. thumbergiana* Franco) and Scots pine (*P. sylvestris* L.) from black turpentine beetle attacks (Highley and Tattar 1985). Conservative estimates of mortality attributed to black turpentine beetle across the southern United States during 1998–2005 were 64 million board feet at a cost of $21 million (www.sfiwc.org/publications), a value which was far less than losses attributed to either southern pine beetle or *Ips* bark beetles over the same time interval.

Secondary bark beetles such as black turpentine beetles fulfill a range of direct and indirect ecological functions, including thinning and gap formation, decomposition, nutrient cycling, and habitat creation. Accelerated natural thinning through fatal attacks on weak and senescent trees results in the reallocation of resources (i.e., water, light, and soil nutrients) to healthy trees. The resulting snags (i.e., standing dead trees) create habitat for wildlife, although occasional loss of nest-cavity trees of the near-threatened red-cockaded woodpecker, *Leuconotopicus borealis* Vieillot (Piciformes: Picidae), which nests only in living trees, have been attributed to black turpentine beetle attacks (Sullivan et al. 2003). Thinning from secondary bark beetle activity creates gaps necessary for release of understory hardwood regeneration, which creates more heterogenous vegetation on the landscape. Colonization of fresh pine stumps and other host material by black turpentine beetles creates entry points and subcortical conditions suitable for colonization by wood-decay fungi and wood-feeding insects, thereby accelerating decomposition of woody debris and enhancing nutrient cycling. For example, termites are attracted to tissue colonized by the black turpentine beetle-transmitted blue-stain fungus, *Leptographium terebrantis* Barras and Perry (Ophiostomatales: Ophiostomataceae) (Little et al. 2013).

Taxonomy and Phylogeography

Black turpentine beetle belongs to the genus *Dendroctonus*, which is comprised of 20 species of phloem-feeding bark beetles that typically reproduce in mature coniferous hosts and includes pests of great economic and ecological importance (Six and Bracewell 2015). At low population densities, *Dendroctonus* spp. are generally not the primary cause of host mortality, typically infesting only stems and stumps of fallen trees or standing trees that are weakened or dying from other causes (Wood 1963). However, local changes in abundance of susceptible hosts and other factors can lead to rapid population growth that results in severe, local mortality of healthy trees. As with other bark beetles, *Dendroctonus* colonize conifers by excavating galleries in the host phloem where they complete their life cycle (Wood 1963, Six and Bracewell 2015). Colonization results in death of the host through phloem girdling and possibly by the colonization of sapwood and phloem by weakly or moderately pathogenic fungi that are carried by the beetles into the tree. The major tree killing species are associated with aggregation pheromones that mediate rapid congregation of conspecifics on host trees, a behavior which aids in the beetles' overcoming of the host's defenses (Raffa 2001).

The genus *Dendroctonus* is morphologically distinguished by the following characters (Figs. 1 and 2): head that is visible when viewed from above; elytral declivity not impressed; elytra covered with fine, short hairs rather than scales; flattened (lentil-shaped) and segmented antennal club; an antennal funicle with five antennomeres, and a prominent epistomal process (Wood 1982a, Victor and Zuñiga 2015). Black turpentine beetles can be distinguished from other members of the same genus because of the absence of a vertical groove on the front of the head (frons), their large size (5.0–7.5 mm), their uniformly dark color (typically black), host species (almost exclusively *Pinus*), and range (southern and eastern United States) (Wood 1963, 1982a) (Figs. 1 and 2). The larvae are those typical of scolytines: white legless grubs with a yellowish-white body, and a reddish-brown sclerotized head and jaws. The eighth and ninth abdominal tergites each possess a dorsal plate armed with three teeth (Hopkins 1909, Thomas 1965). This latter feature, which occurs in black turpentine beetle, and its sibling species, *D. valens,* and *Dendroctonus rhizophagus* (Thomas and Bright) (Coleoptera: Curculionidae) (Victor and Zuñiga 2015), may facilitate movement of larvae within the open feeding chambers produced by these species (Pajares and Lanier 1990).

Sexes can be best distinguished by dimorphism of the stridulatory apparatus and to some degree by differences in the produced sounds (Godbee and Franklin 1978). The stridulatory apparatus in males consists of a bifid process with a pair of short spines protruding from the center of the posterior margin of the seventh abdominal tergite ('scraper') which can be engaged with a file on the center of the interior surface of the elytral declivity (Godbee and Franklin

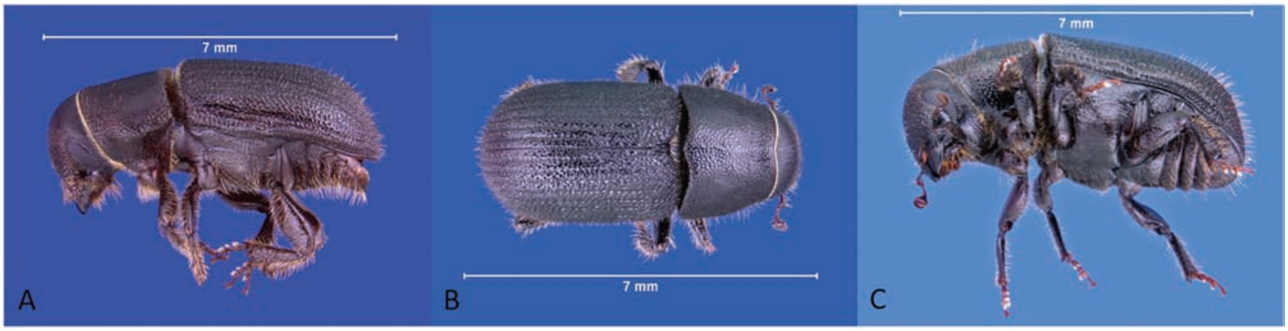


Fig. 1. Lateral (A), dorsal (B), and ventral (C) views of the black turpentine beetle, *Dendroctonus terebrans*. Images by Erich Vallery, USDA Forest Service Southern Research Station.

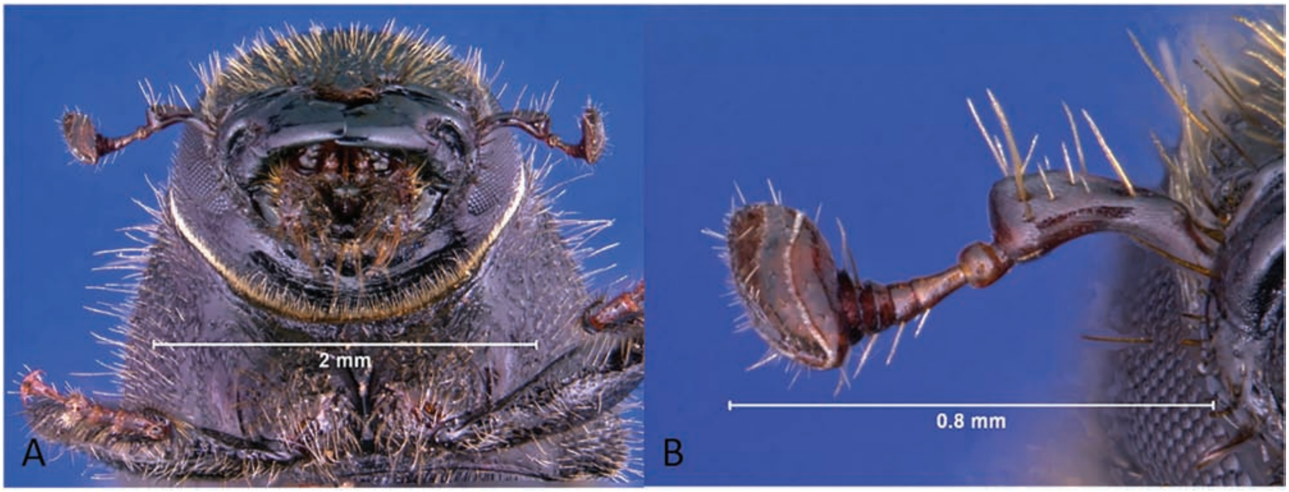


Fig. 2. Head (A) and antennae (B) of black turpentine beetle, *Dendroctonus terebrans*. Images by Erich Vallery, USDA Forest Service Southern Research Station.

1978, Wood 1982a). Females possess a file, but the scraper is absent (Pajares and Lanier 1990). Wood (1982a) indicated that females have a median frontal elevation at the upper level of the eyes that is absent in males, but the utility of this character in distinguishing the sexes is uncertain (Godbee and Franklin 1978). Karyologically, sex determination in black turpentine beetles occurs through the parachute bivalent sex chromosome (XYP) (Zuñiga et al. 2002a,b, Dutrillaux 2017).

The geographic distribution of black turpentine beetle overlaps with that of the sibling species *D. valens* in the Appalachian Mountains south of Maryland and in coastal New England. Shared traits of black turpentine beetle and *D. valens* include specialization on *Pinus*; formation of a broad, relatively short parent gallery; larvae that feed communally in a broad feeding chamber; colonization generally restricted to the lower portions of the tree as well as stumps and roots; a strong attraction to odors of host resin; and production of the pheromone component frontalin by females (Wood 1963, Bentz 1986, Pajares and Lanier 1990, Erbilgin et al. 2007, Liu et al. 2013). Generally, these otherwise very similar species can be distinguished one from the other by the reddish-brown versus black body color of *D. valens* and black turpentine beetle, respectively. However, black turpentine beetle callow adults can be reddish in color, and one study observed that almost 20% of adults trapped on baited trees in the piedmont of Georgia were red in color (Godbee and Franklin 1976). Additional taxonomic characters useful for distinguishing the two species include (in black turpentine beetles): 1) larger punctures on the lateral areas of the pronotum; 2) more abundant granules on the elytral declivity; 3) a narrower epistomal process; 4) less abundant hairs on the anterior dorsal area of the elytra; 5) larger and less variably arranged metatibial spurs; 6) sterna 5 plus 6 always less than 7 in black turpentine beetle females (sterna 5 plus 6 equal to or longer than sternum 7 in *D. valens*); 7) seminal valve U-shaped in black turpentine beetles (bell-shaped in *D. valens*); and 8) broader elytral pars stridens (file) in females (Hopkins 1909, Wood 1982a, Pajares and Lanier 1990).

Life Cycle

Females initiate the gallery construction (Pajares and Lanier 1990), and males that locate the female entrance will chirp audibly at the threshold (H.L.M. and B.T.S., personal observations), possibly to gain acceptance from the female (Ryker 1988). Once joined by the male, the two beetles, one female and one male, construct an irregular gallery that is typically much wider than the beetle itself; it extends upward a few cm and then turns downward for typically less than 30 cm resulting in a reverse J-like shape (Hopkins 1909, Mayfield and Foltz 2005). The male clears the gallery of frass. Over a span of approximately two weeks, the female lays dozens of eggs into elongated pockets along one or both sides of the parent gallery and then fills these areas with a tightly-packed layer of frass (Staeben et al. 2010). After hatching, the larvae feed side-by-side on the phloem (i.e., feed gregariously), consuming it entirely while enlarging a chamber under the bark. This chamber may fill with resin and the larvae will continue feeding despite being immersed in it (Hopkins 1909). To our knowledge, the number of black turpentine beetle larval instars has not been reported previously. We collected head capsule measurements of 229 larvae from the bases of approximately 10 black turpentine beetle-infested trees in southwestern Mississippi, and data suggested the existence of four instars (Fig. 3). Pupation generally occurs in pockets formed by larvae within the frass that has accumulated within the larval feeding chamber, and pupation is completed over the course of 2 wk (Hopkins 1909). Some pupal cells may extend into the phloem or outer bark. After pupation, enclosed adults congregate within the larval feeding chamber (Hopkins 1909), and emergence can occur either through holes previously formed by the parents or through newly chewed exit holes; multiple individuals may exit through the same hole for dispersal (Merkel 1981). Hopkins (1909) reported that the beetles mated prior to emergence, but he did not indicate any evidence, and there is no mention of this behavior by later authors.

Abiotic factors, such as temperature, wind, and precipitation, have been shown to alter black turpentine beetle reproduction and dispersal. Black turpentine beetles can be multivoltine in warmer climates (with one generation lasting approximately 3–4 mo from parent attack until brood emergence) and univoltine or semivoltine in the northern portions of their range (Hopkins 1909, Merkel 1981, Wood 1982a, Fatzinger 1985). In a laboratory study using pine bolts as the rearing substrate, black turpentine beetles required just 2.5 mo to complete development at 23°C, and development was estimated to require 1,302-degree days (Godbee and Franklin 1978). Generations overlap, and all life stages are capable of overwintering in the host (Godbee and Franklin 1976). Flight dispersal appears to occur throughout the warmer months (Sullivan et al. 2003), and flight activity may be governed by their minimum flight temperature (17°C) (Vité et al. 1964). A peak spring dispersal has been reported in March and April for the South, and this may be slightly later in the cooler northern portion of their range (Hopkins 1909). In northern Florida, appearance of newly attacked trees and new attacks were concentrated from April through October and peaked in July (Smith 1957). During summer, black turpentine beetle flight activity is concentrated at sunset, with some activity occurring also in the hours after sunrise (Vité et al. 1964, Fatzinger 1985), while in spring or on heavily overcast days, flight may occur throughout the afternoon. Furthermore, Fatzinger (1985) observed that black turpentine beetles were not able to orient to attractant-baited traps at wind speeds >8 km/h, and highest catches occurred when wind was nearly calm (<0.8 km/h). In the same study, it was also noted that light or sporadic rain reduced flight activity.

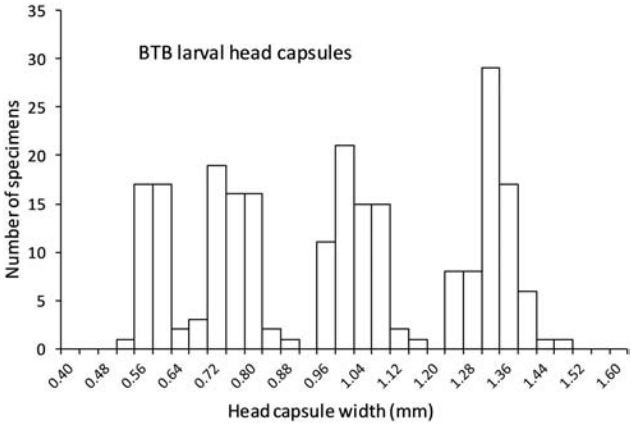


Fig. 3. Head capsule widths of 229 black turpentine beetles, *Dendroctonus terebrans,* larvae removed from the bases of ~10 infested pines.

Host Tree Interactions

Host Trees

Except during dispersal, black turpentine beetles spend their entire life cycle in the phloem tissue of their host. Black turpentine beetles colonize all species of pine within its range, showing preference for pitch (*Pinus rigida* Mill.), loblolly (*Pinus taeda* L.), shortleaf (*Pinus echinata* Mill.), and slash (*Pinus elliottii* Englm.)pines, but has also been documented to attack red spruce (*Picea rubens* Sargent) when these are >10 cm diameter (Wood 1982a, Staeben et al. 2010). Also, they show a preference for older trees and those weakened by fire, mechanical damage from logging or construction operations, disease, lightning strike, or colonization by other forest pests (Hopkins 1909, Kucera et al. 1970, Merkel 1981, Mayfield and Foltz 2005, Zanzot et al. 2010).

Host Colonization Behavior

Initial attacks occur at the base of the tree below 46 cm, and subsequent attacks gradually increase in height to approximately 2 m (Smith 1957) or more if bark thickness is adequate to support gallery excavation. Black turpentine beetle attacks on roots have been observed at a depth of 150 cm, although reproduction was not observed below about 50 cm (Lee and Smith 1955). New attacks on a single tree can accumulate for 5–7 mo both above and below the soil line (Smith 1963, Fatzinger 1985), and in one study, trees succumbing to black turpentine beetle attacks had a mean of 28.4 attacks per tree (Smith 1957). On living trees, entrance holes are associated with large (sometimes several centimeters in diameter), white pitch masses that often incorporate red boring dust (Hopkins 1909, Merkel 1981, Mayfield and Foltz 2005). The color of pitch masses can vary with the time elapsed since attack, with older pitch masses turning gray to purple (Staeben et al. 2010). Trees can survive BTB infestation and multiple BTB attacks; however, it is reported that attacks on trees that ultimately survive infrequently result in emerging brood (Pajares and Lanier 1990). Although trees may survive attacks, the residual damage renders them more susceptible to fire injury (Hopkins 1909). Black turpentine beetle attacks on stumps and on bases of trees killed by other insect species or diseases produce inconspicuous pitch tubes, accompanied by copious, coarse, red boring dust scattered on the bark, and root collar below the beetle entrances (H.L.M., B.T.S., and K.J.K.G., personal observations). Fading of foliage on infested, dying trees may not be apparent until 4–8 mo after the initial attack (Merkel 1981).

Black turpentine beetles display primary olfactory attraction to their host (attraction to odors of the host in the absence of insect-produced compounds), which is a common trait in nonaggressive, secondary bark beetle species that attack only weakened, stressed trees (Schroeder and Lindelow 1989, Lindelow et al. 1992, Miller and Rabaglia 2009). The trait appears to be relatively rare in aggressive bark beetle species that commonly kill healthy hosts, rather, in these species host odors commonly function as synergists for attractive pheromone components (Raffa et al. 1993, Skillen et al. 1997, Raffa et al. 2015).

Black turpentine beetle initially locates host trees by attraction to the volatile components of the host's constitutive resin. Conifers produce resin as a defensive mechanism against invasion by insects and fungi, and this is released after the rupture of living tissues (Phillips and Croteau 1999, Franceschi et al. 2005). This attraction likely plays a role in the tendency for black turpentine beetle attacks to occur on hosts that are releasing resin at high rates such as those subjected to physical damage or treated with herbicide (Merkel 1981, Siegfried et al. 1986, Phillips et al. 1989), and explains their attraction to recently cut logs (Flechtmann et al. 1999). Turpentine, the product of distillation of pine resin, is highly attractive to this species (Clements and Williams 1981, Fatzinger 1985, Siegfried et al. 1986, Fatzinger et al. 1987, Payne et al. 1987, Phillips et al. 1988, Phillips et al. 1989). Composition of turpentine varies according to the host species from which the resin is derived, and with geographic origin within a species (Mirov 1961, Squillace and Fisher 1965). Chemical analyses of turpentines attractive to black turpentine beetle have shown them to be dominated by the hydrocarbon monoterpenes α- and β-pinene, with lesser quantities of camphene, limonene, myrcene, and β-phellandrene (Siegfried et al. 1986, Phillips et al. 1988). This blend, in varying proportions, reflects the monoterpene composition of the resin of the common host species for black turpentine beetle (Mirov 1961). In electroantennogram studies, both sexes of black turpentine beetle exhibited olfactory sensitivity to α- and β-pinene, but they had a much lower response threshold (i.e., greater olfactory sensitivity) to whole turpentine than either monoterpene singly (Delorme and Payne 1990). Consistent with these findings, whole turpentine was significantly more attractive to flying black turpentine beetles than any of the major monoterpenes in its composition, and single monoterpenes caught beetles in very low numbers (Siegfried et al. 1986). Further, these authors found that a synthetic blend, mimicking turpentine, although composed of all six predominant monoterpenes, was nonetheless less attractive than the turpentine after which it was modeled. This suggests that turpentine may contain additional attractive components not included in the synthetic blend, or that potential differences in the enantiomeric composition (i.e., the blend of the two optical isomers) of chiral host monoterpenes used in the synthetic mixture may have impacted black turpentine beetle responses. This latter explanation is supported by the finding that enantiomeric composition of host monoterpenes influences behavioral responses of some other *Dendroctonus* species (Hobson et al. 1993, Staeben 2015). However, a (−) enantiomer dominated solution of α-pinene [i.e., >95% (−)] has been shown to be attractive to black turpentine beetles (Miller and Rabaglia 2009).

Ethanol can act synergistically with turpentine in increasing attraction of black turpentine beetle when the two are released as a mixture from a single device (Fatzinger 1985, Fatzinger et al. 1987, Phillips et al. 1988), but apparently not when released from separate lures (Phillips et al. 1988). The explanation for this difference is unknown. Ethanol is released by stressed and initially decaying plants, and it is attractive to many secondary bark, wood, and root-infesting beetle species presumably because it signifies a susceptible host tree or suitable host tissue (Moeck 1970, Kelsey and Joseph 2001, Ranger et al. 2010).

Evidence that visual cues are important to host orientation has been reported in several *Dendroctonus* species (Strom et al. 1999, Strom and Goyer 2001, Strom et al. 2001, Campbell and Borden 2006). Successful trap designs for black turpentine beetle have all included a large (i.e., thousands of cm^2), black, typically vertically oriented visual impression, but the specific importance of visual cues has not been tested for black turpentine beetles. Fatzinger (1985) compared traps with cylindrical (vertical) and conical shapes but found no significant differences in their catches.

Chemical Communication

Pheromone System

Some bark beetles, including many in the genus *Dendroctonus*, produce pheromones following landing and/or mining into the host. These act as 'secondary' attractants (i.e., produced by organisms other than the host itself) to host-seeking members of the same species (Wood 1982b, Byers 1989a), and these pheromones also bring the sexes together for mating and joint gallery formation. Further, secondary attractants play a key role in the capacity of the more aggressive bark beetle species to kill healthy trees, since successful colonization requires a synchronized attack by typically hundreds or thousands of insects in order to overwhelm host defenses (Borden 1982, Raffa 2001). Evidence that secondary attraction influences colonization of trees by black turpentine beetles includes: 1) a higher incidence of beetle attacks on trees with previous attacks (Smith 1963); 2) attraction of flying beetles to logs artificially infested with conspecifics (Godbee and Franklin 1976, Phillips et al. 1989); and 3) production by black turpentine beetles of compounds attractive to conspecifics (i.e., pheromones, discussed below). Although black turpentine beetles typically form conspicuously spatially aggregated attacks at the bases of living hosts (Godbee and Franklin 1976), they do not 'mass attack' as more aggressive, aggregating species do. Their attacks accumulate over weeks or months rather than days, and in a single year attacks will typically not exceed a few dozen on any single tree (Smith 1957, Godbee and Franklin 1976). Also, differently from infestations of other bark beetle species that utilize aggregation pheromones, attacked trees tend to be scattered in a stand rather than tightly clustered together (Merkel 1981). It is likely that secondary attractants are more important for mediating interactions between the sexes than in aggregating conspecifics for the purpose of reducing host defenses and increasing host susceptibility (Phillips et al. 1989). Aggregation pheromones, unlike sex pheromones, are typically strong attractants (or attractive synergists) to the producing sex as well as the opposite sex (Cardé 2014), however same-sex attraction is limited or absent in black turpentine beetles (see below).

Black turpentine beetles utilize a multicomponent pheromone system for intraspecific communication, and their pheromone components, as well as those of associated bark beetle species, may function as kairomones in interspecific interactions (Table 1). The pheromone accumulates in the hindguts of this species and generally in pheromone-producing bark beetles (White et al. 1980). It is detectable in both sexes collected in traps or mining in a host and may be released in small amounts while the beetle is active outside the bark (Payne et al. 1987, Phillips et al. 1989). As with other bark beetles (Byers 1989b), pheromone presumably is also released by defecation when the adult is feeding/mining. Each sex produces a single, distinct bicyclic ketal pheromone component: females produce frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane), whereas males produce *exo*-brevicomin (*exo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane) and possibly traces of *endo*-brevicomin (*endo*-7-ethyl-5-methyl-6,8-dioxabicyclo[3.2.1]octane) (Payne et al. 1987, Phillips et al. 1989; however, the authors have failed to detect *endo*-brevicomin in their own studies). These were found in the hindguts of dispersing beetles (caught in traps) as well as of beetles excised from galleries (Payne et al. 1987, Phillips et al. 1989). Frontalin and both *exo*- and *endo*-brevicomin occur widely in *Dendroctonus* species and are components of the aggregation pheromone for many species (Skillen et al. 1997, Symonds and Elgar 2004); they are produced de novo and not from a host-derived precursor (Blomquist et al. 2010).

Electroantennogram studies have demonstrated that black turpentine beetles have olfactory sensitivity to all three bicyclic ketals, and theywere found to be particularly sensitive to *endo*-brevicomin despite its scarcity or absence in this species (Payne et al. 1987, Delorme and Payne 1990). In an olfactometer study, walking black turpentine beetles were attracted to *endo*-brevicomin and frontalin when presented singly, however, beetles do not appear to be attracted

Table 1. Semiochemicals relevant to the biology of the black turpentine beetle (BTB), *Dendroctonus terebrans*

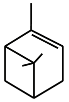
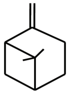
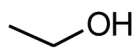
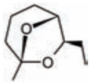
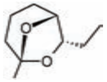
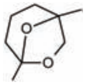
Compound name	Natural origin	Producing sex	Antennal response	Attractive alone[1]		Enhances attraction	Reduces attraction	Active enantiomer	Likely behavioral function for BTB	Possible role with bark beetle associates[4]	References
				Walking[2]	Flying[3]	Flying[3]	Flying[3]				
Turpentine (volatile component of pine resin)	Host	-[5]	♀♂	♂	♀♂	-	-	-	Primary host attractant	-	1,2,3,7,8
α-pinene 	Host	-	♀♂	-	✓[6]	-	-	-	Primary host attractant	-	1,6
β-pinene 	Host	-	♀♂	-	-	-	-	-	-	-	1
Ethanol 	Host	-	-	-	no	yes[6]	-	-	Primary host attractant	-	2,3,8
exo-brevicomin 	BTB	♂	♀♂	-	no	♀	♂	(+)>(−)	Sex/aggregation pheromone	✓	7,9,10
endo-brevicomin 	BTB (and associate, *D. frontalis)*	♂ ≤trace	♀♂	♀♂	no	♀>♂	♂	(+)	Associate-produced secondary attractant	✓	1,7,9,10
Frontalin 	BTB (and associate, *D. frontalis)*	♀	♀♂	♀♂	no	♀>♂	♀	(−)>(+)	Sex/aggregation pheromone	✓	1,7,9,10

Table 1. *Continued*

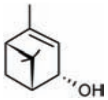
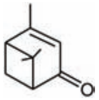
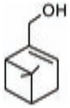
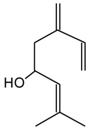
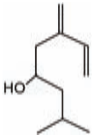
Compound name	Natural origin	Producing sex	Antennal response	Attractive alone[1]		Enhances attraction	Reduces attraction	Active enantiomer	Likely behavioral function for BTB	Possible role with bark beetle associates[4]	References
				Walking[2]	Flying[3]	Flying[3]	Flying[3]				
trans-verbenol 	BTB and bark beetle associates	♀♂	♀♂	♂	no	~[7]		-	-	✓	1,2,7,9
Verbenone 	BTB and bark beetle associates	♀♂	♀♂	-	no	-	♂	-	Possible multifunctional	✓	1,9,11
Myrtenol 	BTB and bark beetle associates	♀♂	-	-	no	-	-	-	-	✓	7,9
Ipsdienol 	*Ips* spp. Bark beetle associates	-	♀♂	-	no	✓[6]	-	-	Associate-produced secondary attractant	✓	1,5

Table 1. *Continued*

Compound name	Natural origin	Producing sex	Antennal response	Attractive alone[1]		Enhances attraction	Reduces attraction	Active enantiomer	Likely behavioral function for BTB	Possible role with bark beetle associates[4]	References
				Walking[2]	Flying[3]	Flying[3]	Flying[3]				
Ipsenol 	*Ips* spp. (associate)	-	♀♂	-	no	-	-	-	-	-	1,5
Other oxygenated monoterpenes	BTB and bark beetle associates	♀♂	-	-	-	-	-	-	-	✓	9

[1] Attractive in the absence of any other semiochemical.

[2] Laboratory olfactometer results with walking beetles exposed to an odor source.

[3] Responses to baited traps.

[4] Compounds produced by BTB and eliciting a behavioral response in an associate (or vice versa). Associate behavioral responses summarized in Skillen et al. (1997).

[5] Dash indicates that the category is not applicable, or data does not exist.

[6] Sexes not counted separately.

[7] Activity apparent in minority of trials.

[8] Sympatric species *Ips avulsus* and *Ips calligraphus*.

[9] Myrtenal, *trans*-pinocarveol, *cis*-verbenol.

References: 1: Delorme and Payne 1990, 2: Fatzinger 1985, 3: Fatzinger et al. 1987, 4: Hughes 1975, 5: Miller et al. 2005, 6: Miller and Rabaglia 2009, 7: Payne et al. 1987, 8: Phillips et al. 1988, 9: Phillips et al. 1989, 10: Phillips et al. 1990, 11: Sun et al. 2003.

in flight (i.e., to baited traps) to any pheromone components in the absence of host monoterpenes (Payne et al. 1987, Phillips et al. 1989, Payne et al. 1991, Staeben 2015). Males display a greater attraction for the female-produced frontalin than to male-produced *exo*-brevicomin, whereas females display the reciprocal response (Payne et al. 1987, Phillips 1989). The natural context in which females would be attracted to males in nature is unclear since females are the gallery-establishing sex. Additionally, in some trap lure tests, attractant inhibition by these compounds was observed in the producing sex (Payne et al. 1987, Phillips 1989). The alternately observed attractive/absent/inhibitory effects of these compounds in different trials may be attributable to use of different release rates of these compounds or their host odor synergists.

The bicyclic ketal pheromone components are chiral molecules (with two possible enantiomers). The authors performed coupled gas chromatography–mass spectrometry analyses with a chiral column (Supelco gamma-Dex 225 column; 30 m length × 0.25 mm diam. × 0.25 µm film thickness; program 40° for 1 min, then 5°/min to 70°, then 2°/min to 155°; retention times and mass spectra compared to identified standards) of samples derived by static headspace collections (methods in Sullivan et al. 2007) of odors released by female black turpentine beetles ($n = 9$) that had been feeding in a pine log for one day. These analyses indicated an enantiomeric ratio of frontalin of 90.7:9.3 (−):(+). In similar analyses of samples from males ($n = 10$) that had been paired in a bolt one day with a female, we detected only (+)-*exo*-brevicomin, and, based on our estimated threshold of detection of the (−)-enantiomer, we estimate conservatively that males produce >98% of the (+)-enantiomer. The overwhelming predominance of the (−)-enantiomer of frontalin and (+)-enantiomer of brevicomin also occurs in sympatric southern pine beetle and other *Dendroctonus* species that produce these compounds (Stewart et al. 1977, Pureswaran et al. 2000, Sullivan et al. 2007, Niño-Domínguez et al. 2015). In field trapping assays, black turpentine beetles were more attracted to the (−)-enantiomer of frontalin, and the (+)-enantiomers of both *endo*- and *exo*-brevicomin, than to their antipodes (Phillips 1990). Simultaneously, presence of the antipodes does not reduce response to the more attractive enantiomer.

There is limited evidence for a behavioral role for the oxygenated monoterpenes that are produced by both sexes (Table 1), although all of the oxygenated monoterpenes detected in black turpentine beetles have been reported as having behavioral activity in at least some species of *Dendroctonus* (Skillen et al. 1997, Sullivan 2011). Black turpentine beetles have olfactory sensitivity to *trans*-verbenol and verbenone, and walking males were attracted to *trans*-verbenol in olfactometer assays (Payne et al. 1987, Delorme and Payne 1990). In one trapping study, *trans*-verbenol produced a weak synergistic effect with lures consisting of turpentine and ethanol, but it had no behavioral effect in several other studies (Fatzinger et al. 1987, Payne et al. 1987, Phillips et al. 1989). Verbenone is an attraction inhibitor in many species of *Dendroctonus* as well as other bark and ambrosia beetles (Etxebeste and Pajares 2011, Hughes et al. 2017, Byers et al. 2018, Seybold et al. 2018). It has been proposed to function as an antiaggregation pheromone in many species or a repellant kairomone that indicates an unsuitable host, and in this role, it deflects beetle arrivals from hosts or host portions that are fully colonized and no longer suitable for colonization, or dead hosts in early stages of decay (Byers 1989b, Lindgren and Miller 2002). However, verbenone proved inconsistent in its ability to reduce attraction of black turpentine beetles to traps and appeared to enhance attacks on baited trees (Phillips et al. 1989, T.W. Phillips, personal communication). All these oxygenated monoterpenes in the hindgut of black turpentine beetles likely arise from metabolic oxidation of hydrocarbon monoterpenes ingested or inhaled from host resin and are possibly the result of detoxification processes rather than pheromone metabolism per se (Seybold et al. 2006, Blomquist et al. 2010). Production of these compounds by both sexes (pheromone components are typically sexually dimorphic) and their presence in both larval and adult black turpentine beetles supports this hypothesis (Hughes 1975).

Semiochemical Interactions with Sympatric Bark Beetles

Semiochemicals likely mediate interactions between black turpentine beetles and other bark beetle species, and in particular those in the southern pine bark beetle guild (Smith et al. 1990), since these insects share some of the same pheromone components or respond to pheromone components produced by other species. In this context, these semiochemicals may: 1) allow for 'eavesdropping' on other species that have located a suitable host; 2) through mutual attraction, mediate multispecies mass attacks to ensure that tree defenses are overcome; and/or 3) through mutual repellency, promote resource partitioning when these species are colonizing the same host tree (Birch et al. 1980, Svihra et al. 1980, Smith et al. 1990, Payne et al. 1991). Although it has not been demonstrated under natural conditions, attacks by black turpentine beetle and southern pine beetle are presumably cross-attractive, since black turpentine beetles produce attractants and attractant-synergists for southern pine beetles (frontalin, *exo*-brevicomin, and *trans*-verbenol) and vice versa (southern pine beetles produce frontalin and *endo*-brevicomin) (Smith et al. 1990, Sullivan 2016). Attraction of southern pine beetles to attacks by black turpentine beetles may be significant for its epidemiology. Southern pine beetles do not appear to respond to primary host attractants (i.e., host odors are unattractive in the absence of pheromone components [Sullivan 2016]), and no host-produced semiochemical cues are known to attract pioneer female southern pine beetles to host trees. Black turpentine beetles are typically the first bark beetle species arriving opportunistically on pines weakened by a lightning strike (Hodges and Pickard 1971), and lightning-struck trees are also commonly the initial foci for the establishment of beetle infestations (Coulson et al. 1983, Lovelady et al. 1991). Pheromone released by these initially arriving black turpentine beetles could function as kairomones that allow southern pine beetle to locate these particularly susceptible hosts and initiate mass colonization. Likewise, other members of the southern pine bark beetle guild (in particular *I. grandicollis*, which is attracted to frontalin) (Werner 1972, Staeben 2015) may be attracted to the pheromone components released by black turpentine beetles, and these may instigate colonization by these species on lightning-struck or otherwise disturbed trees. Conversely, black turpentine beetles may be attracted to pheromone components of *Ips* bark beetles. Electroantennogram studies indicated that black turpentine beetles have olfactory sensitivity to the *Ips* pheromone components ipsenol and ipsdienol (Delorme and Payne 1990). Moreover, ipsdienol, which is produced by both guild members *I. avulsus* and *I. calligraphus*, enhanced black turpentine beetle attraction to traps in Florida (Miller et al. 2005).

Trapping

Trap designs reported as effective for catching black turpentine beetles when deployed with semiochemical lures include various pipe traps (e.g., a black plastic or metal cylinder of ~1 m height and ~15–30 cm diameter erected vertically above a catch funnel or water-filled catch basin of much larger diameter), the 'Lindgren'-type black multiple-funnel trap (Lindgren 1983), and black cross-vane panel traps (Clements and Williams 1981, Fatzinger 1985, Miller and Crowe 2011). Among these, the cross-vane trap has been reported as the most effective, although trap attributes such as surface area, visual height and width were not the same during comparison studies (Miller and Crowe 2011). 'Drainpipe traps', which are effective with some species of bark beetles, but require that the beetles enter small holes in the trap surface to be caught, were not successful for black turpentine beetles (Fatzinger 1985). Rather than landing, beetles were observed to fly into and 'bounce' off of trap surfaces, falling to the substrate underneath hence, a large diameter catch surface or funnel beneath the trap's barrier (i.e., panel or cylinder) increases trapping efficiency (Fatzinger 1985). Catches of black turpentine beetles were not significantly different in multiple-funnel traps of either 8 or 16 funnels (Miller and Crowe 2009), and in two out of three experiments, black turpentine beetle catches were greater in funnel traps with liquid-filled, rather than dry (but containing a fumigant insecticide) collection cups (Miller and Duerr 2008).

Acoustic Signals

Both sexes of black turpentine beetle produce sounds that presumably function during interactions between the beetles at close range, as demonstrated with other *Dendroctonus* (Rudinsky et al. 1976, Liu et al. 2017). Males produce a high pitched 'chirp' apparently via friction between the aforementioned scraper and file (Barr 1969, Godbee and Franklin 1978). However, some males do not stridulate, while a small percentage of females do but produce a low-pitched 'rasping' sound (Godbee and Franklin 1978). Female stridulation may occur by means of a pars stridens located on the enfolded surface of the terminal abdominal sternite (a feature present in both sexes) which is apparently rubbed by the distal edge of the pygidium (Pajares and Lanier 1990). Since both sexes produce sound, morphological sex identification should be considered more reliable than auditory (Godbee and Franklin 1978).

The authors conducted investigations of acoustic signals produced by black turpentine beetles. Females that had emerged from naturally infested logs collected in southwestern Mississippi were infested in the laboratory onto fresh logs, and both before and after addition of males, sounds were recorded by placing a subminiature high-performance electret microphone (Knowles model FG-3652-P15, Itaska, IL) <1 mm from the gallery opening. The microphone was connected to a preamplifier (M-Audio model DMP3, Cumberland, RI) and a laptop computer operating with its internal sound card (16-bit, 96 kHz). Recordings and their analyses were performed with Raven Lite 2.0.0 software (Cornell Lab of Ornithology, Ithaca, NY). Sounds were also recorded by placing one or two males into a large gelatin capsule with fresh female frass and inserting the microphone into the capsule. Additionally, soft forceps were used to hold males within 1–2 mm from the microphone to record sounds produced during stress.

As noted in earlier studies, the sounds produced by the sexes differed. When alone in the gallery, females were generally quiet but began stridulating either when disturbed (by exerting pressure with a finger on the bark surrounding the gallery entrance), or after a male was introduced into the gallery (Fig. 4A and B). In the presence of a male, females would produce 'chirps' that were typically 0.2 s long and consisted of, on average, widely (mean 39/s) but irregularly spaced toothstrikes. (Here, 'toothstrike' is used to refer to a single oscillogram spike. In isolation, these spikes possessed the sound of a single 'click', and all black turpentine beetle vocalizations by both sexes were composed of these spikes. A stridulation mechanism is not necessarily implied.) Toothstrikes ascended then descended in amplitude over the duration of a single female chirp, and these chirps sometimes lacked an audible pause between them. The female typically produced these continuously while the male was present and regardless of whether the male was stridulating or not. Audibly, the sound was toneless and resembled that made by stroking the tines of a comb. Chirps produced by solitary females disturbed in the gallery generally resembled those produced in the presence of a male, but they occurred at a slower rate and with fewer toothstrikes and wider gaps in-between.

Males most commonly produced a sequence of repeated 'singlet' chirps (1.6–7.0/s), each consisting of an uninterrupted series of four to 31 rapid toothstrikes produced at rate of approximately 180–670/s, with each chirp lasting from 0.006 to 0.105 s (Fig. 4C,D,F; Supp Table 1 [online only]). The production of the chirps was regular and rhythmic, with consecutive chirps tending to be similar in duration and rate. Toothstrike amplitude of the male singlet chirps declined approximately linearly during the final 0.01 s (insets Fig. 4D and F), and short chirps had a distinctly triangular appearance in the oscillogram. These singlet chirps were produced by males held in forceps, those in contact with female frass (alone or with another male present), and those in a female gallery entrance. However, the singlet chirps produced in these varying circumstances differed somewhat in rate, duration, and numbers of toothstrikes (Suppl Table 1 [online only]). For example, males introduced to a female's gallery typically produced longer chirps at a slower rate and with greater numbers of toothstrikes, than those exposed to female frass (either alone or with a male) (Supp Table 1 [online only]). Three of six males introduced into a female's gallery also produced compound 'multiplet' chirps that consisted of 2–6 singlet-like components (≤16 toothstrikes in an unbroken series) separated by gaps of a mean of 0.04 s (Fig. 4E; Supp Table 2 [online only]). Audibly, these multiplet chirps possessed a trilled sound that was very distinct from the sound of the singlet chirps. The multiplet chirps were generated at a typical rate of 2 per second, or about half the rate of singlet chirps. This sound was detected in males only when in the female gallery, and typically the male's vocalization alternated between series of singlet and multiplet chirps.

We did not investigate the origins of the sounds, however the singlet chirps produced by males when held in forceps were coincident with twitching of the tip of the abdomen downward and away from the elytra, a movement presumably associated with scraping of the bifid process of the seventh abdominal tergite against the elytral file. We encountered only a single female out of dozens that stridulated when held in forceps, and no movement of the insect was observed in association with the sounds.

Associated Organisms

Southern Pine Bark Beetle Guild

As mentioned earlier, black turpentine beetles are part of the southern pine bark beetle guild, which includes four other bark beetle species that are often found colonizing the same trees: the small southern pine engraver (*I. avulsus*), the eastern five-spined ips (*I. grandicollis*), the six-spined ips (*I. calligraphus*), and the southern pine beetle (*D. frontalis*) (Thatcher 1960, Nebeker 2011). All but southern pine beetle are relatively nonaggressive species that prefer weakened or dying trees (Thatcher 1960, Flamm et al. 1993, Nebeker 2011) and commonly arrive following or during mass attacks on vigorous trees apparently initiated by *D. frontalis* (Dixon and Payne 1980, Svihra et al. 1980, Flamm et al. 1993). All southern pine species are potential hosts for members of the guild (Wood 1982b). These beetle species compete for the same phloem resource, but competition is

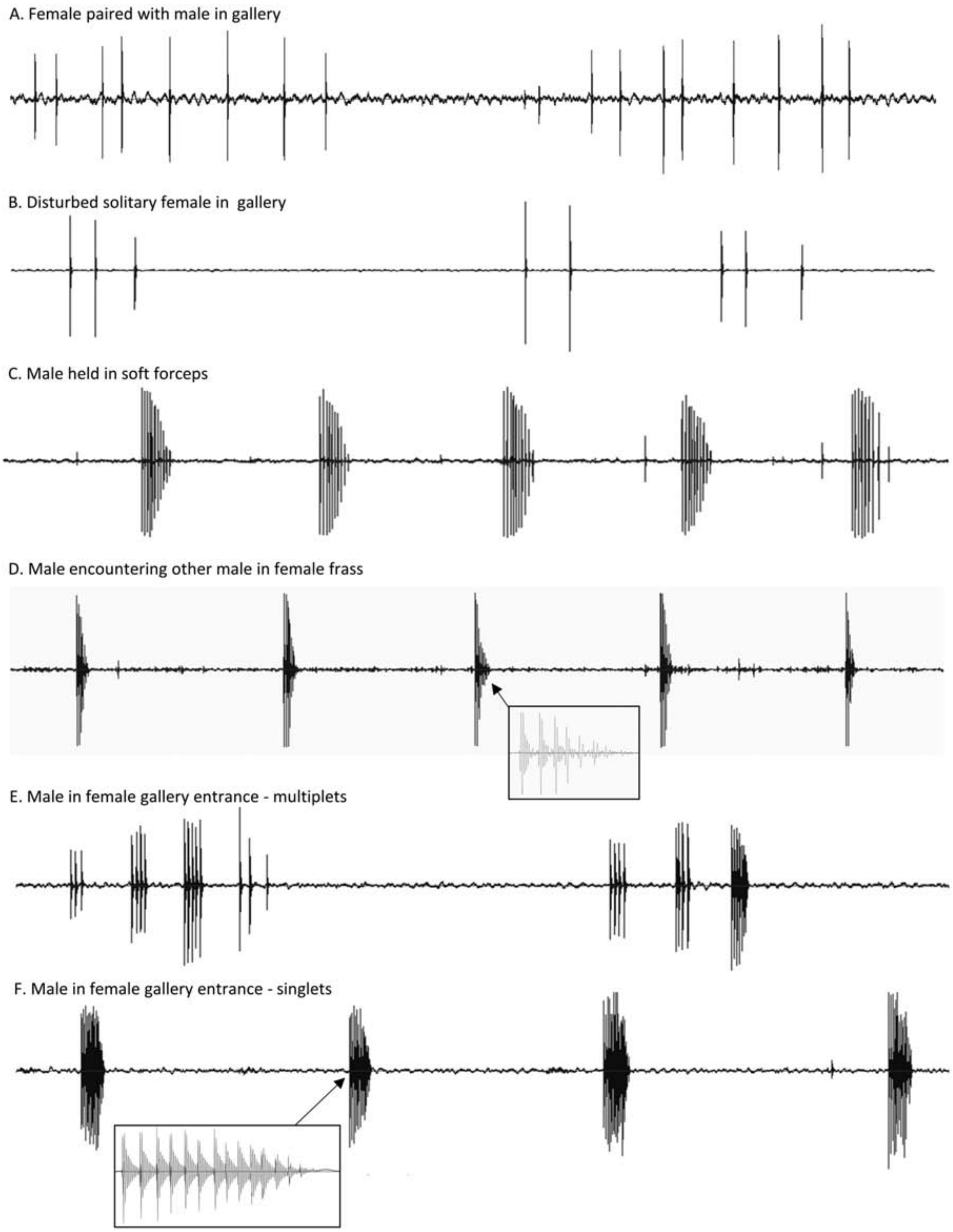


Fig. 4. Oscillograms (1 s duration) of vocalizations of black turpentine beetle, *Dendroctonus terebrans.* (A) Female in 1-d-old gallery after male introduced into entrance. Two complete 'chirps' are shown. (B) Solitary female in 1-d-old gallery after pressure was exerted on the bark near the gallery entrance. (C) Singlet chirps produced by a male held in soft forceps. (D) Singlet chirps produced by a male encountering another male in the presence of female frass. (E) Two multiplet chirps produced by a male following entry into the gallery of a solitary female. (F) Singlet chirps produced by a male following entry into the gallery of a solitary female.

apparently reduced through their exploitation of different regions of the same host, although with some spatial overlap (Paine et al. 1981, Wagner et al. 1985, Flamm et al. 1987). Black turpentine beetles appear to be the only species in the guild that will colonize the root collar and upper roots, although it may overlap with other species in the lower portions of the bole (Lee and Smith 1955, B.T.S., personal observations). It is possible that joint attack of trees may increase success of host colonization because greater numbers of attacks can more quickly deplete host defenses (Svihra et al. 1980, Økland et al. 2009) and thereby balance some of the negative impacts resulting from direct competition for phloem. Members of the guild will jointly colonize trees damaged or disturbed by natural lightning strikes or by induced damage that duplicates the effects of a lightning strike (Coulson et al. 1986, Flamm and Coulson 1988, Lovelady et al. 1991, Flamm et al. 1993).

Fungi and Other Microorganisms

Bark beetles are commonly associated with fungi that are carried into the host either externally or in mycangia (organs adapted for the transport of fungi). Fungal growth in the host tissue sometimes provides nutrition for parent adults and their brood, and in various ways may enhance conditions in the phloem for brood development (Paine et al. 1997, Ayres et al. 2000, Klepzig et al. 2001b, Six 2003). However, certain fungi, carried incidentally on the cuticle or by phoronts, can compete with the beetles for the phloem resource (Klepzig et al. 2001a) or compete with the beetles' mutualistic fungi (Klepzig and Six 2004, Six 2012) and thereby negatively impact brood development. Fungal associates of *Dendroctonus* bark beetles often include both nonpathogenic species and weak-to-moderate plant pathogens, and although some authors have argued that these play a significant role in assisting beetles in overcoming host defenses (Lieutier et al. 2009), others have cast doubt on their importance in facilitating initial bark beetle establishment on living hosts (Six and Wingfield 2011).

The fungal associates of black turpentine beetle have received less attention than other *Dendroctonus* species with greater pest status, and only eight fungal associates have been identified (Table 2). Black turpentine beetles are not known to possess a mycangium for transporting fungi (Victor and Zuñiga 2015). The most commonly reported fungal associate of black turpentine beetle is the bluestaining ascomycete, *Leptographium terebrantis* Barras & Perry, for which a sexual form has not been identified (Barras and Perry 1971, Eckhardt et al. 2007). This fungus can be isolated from stained sapwood adjacent to black turpentine beetle attacks (Highley and Tattar 1985). Conidia are carried externally on the cuticle of the beetle, and the fungus can be cultured from adults walking on agar plates (Barras and Perry 1971, Highly and Tattar 1985). Stalked conidiophores of this fungus, which bear heads of sticky conidia, often line black turpentine beetle pupal chambers, and spores presumably adhere to the exoskeleton of the newly eclosed brood adults on contact. *Leptographium terebrantis* is considered a pathogen since seedlings died at a high rate after inoculation in controlled experiments (Harrington and Cobb 1983, Rane and Tattar 1983, Wingfield 1986, Owen et al. 1987). However, no pathogenicity tests have been conducted on mature pine trees. It is commonly isolated from roots of trees within stands experiencing red pine decline or loblolly pine decline syndromes (Klepzig et al. 1991, Erbilgin and Raffa 2002, Eckhardt et al. 2007), but a causative relationship between decline and death of plants and presence of the fungus has not been sufficiently established (Coyle et al. 2015). However, given that black turpentine beetles have been collected (along with other root-feeding beetles) in stands experiencing loblolly pine decline (Matusick et al. 2013), the beetle presumably may play a role in the transmission and dispersal of this suspected decline agent.

Very little research has focused on other microorganisms associated with black turpentine beetles. In the only available study, bacteria belonging to the *Streptomyces* genus were found to be associated with black turpentine beetles and their galleries and were hypothesized to have a role in mediating beetle-fungus interactions (Hulcr et al. 2011).

Mites

Pine bark beetles, including black turpentine beetles, are generally associated with phoretic mites that attach to the cuticle of adult beetles and are transported between host trees during beetle dispersal. They then become established in the beetles' new parent and larval galleries, which provide a favorable environment for their feeding and reproduction (Woodring et al. 1970, Moser and Roton 1971, Langor 1991, Klepzig et al. 2001a,b, Moser et al. 2005, Pernek et al. 2008). Some mites have a commensalistic relationship with bark beetles as they feed on the fungi, nematodes, and other small arthropods associated with bark beetles (Hofstetter 2011, Hofstetter et al. 2014), while others are predators of immature stages of bark beetles (Hofstetter et al. 2015). Given the role that some mites have in transporting and inoculating fungal species that can negatively

Table 2. Fungal species associated with the black turpentine beetle (*Dendroctonus terebrans*)

Species	Order: Family	Association	Reference
Grosmannia aureum-like	--	Beetle exoskeleton	1
Grosmannia huntii Robinson-Jeffrey	Ophiostomatales: Ophiostomataceae	Beetle exoskeleton	1
Heterobasidion annosum Brefeld*	Russulales: Bondarzewiaceae	Beetle exoskeleton	2
Leptographium terebrantis Barras and Perry	Ophiostomatales: Ophiostomataceae	Beetle exoskeleton; larval feeding galleries; sapwood of beetle-infested trees; inner bark tissue of beetle-infested trees	3,4,5,6,7
Leptographium procerum Wingfield	Ophiostomatales: Ophiostomataceae	Beetle exoskeleton; inner bark tissue of beetle-infested trees; larval feeding galleries	1,7,8,9
Ophiostoma ips Rumbold	Ophiostomatales: Ophiostomataceae	Beetle exoskeleton; inner bark tissue of beetle-infested trees; larval feeding galleries	1,7,9
Ophiostoma minus Hedgcock	Ophiostomatales: Ophiostomataceae		9
Pesotum spp.	Ophiostomatales: Ophiostomataceae	Beetle exoskeleton	1

**Heterobasidion* is not normally associated with insects, so association may be incidental.

1: Zanzot et al. 2010, 2: Otrosina and Cobb 1989, 3: Barras and Perry 1971, 4: Eckhardt et al. 2007, 5: Highley and Tattar 1985, 6: Raffa and Smalley 1988, 7: Rane and Tattar 1987, 8: Harrington 1983, 9: Little et al. 2013

Table 3. Mite species associated with the black turpentine beetle (*Dendroctonus terebrans*)

Species	Order: Family	Feeding Guild	Reference
Acarocheyla impolita Smiley & Moser	Acarina: Cheyletidae	Mite predator	1,2
Cunaxa Taurus Kramer	Prostigmata: Cunaxidae	Predator	1,3
Dendrolaelaps carolinensis McGraw and Robert	Mesostigmata: Digamasellidae	Predator	4
Dendrolaelaps nocornutus Hurlbutt	Mesostigmata: Digmasellidae	Predator	1
Dendrolaelaps neodisetus Hurlbutt	Mesostigmata: Digmasellidae	Nematode predator	1
Ereynetoides scutulis Hunter	Trombidiformes: Ereynetidae	Predator	1
Eugamasus lyriformis McGraw & Farrier	Mesostigmata: Parasitidae	Mite and nematode predator	1
Eupelops sp.		--	1
Fuscuropoda Americana		Mite Predator	1
Gaeolaelaps ninabregus McGraw and Farrier	Mesostigmata: Laelapidae	--	4
Haemolaelaps megaventralis (Strandtmann)	Mesostigmata: Laelapidae	--	4
Heterotarsonemus lindquisti Smiley	Trombidiformes: Tarsonemidae	Mycetophagous	1
Histiogaster arborsignis Woodring	Sarcoptiformes: Acaridae	Mycetophagous	1,5
Histiostoma media Woodring and Moser	Sarcoptiformes: Histiostomatidae	--	1,4,6
Histiostoma varia Woodring	Sarcoptiformes: Histiostomatidae	Microflora feeder	1,6,7
Lasioseius ometes (Oudemans)	Mestigmata: Ascidae	Predator	4
Lasioseius safroi Ewing	Mestigmata: Ascidae	Predator	4
Lasioseius tubiculiger (Berlese)	Mestigmata: Ascidae	Predator	4
Leptus n. sp.		--	1
Macrocheles boudreauxi Krantz	Mesostigmata: Macrochelidae	Predator	1
Neojordensia tennesseensis De Leon	Mesostigmata: Blattisociidae	--	4
Oodinychus sp.	Mesostigmata: Trematuridae	--	1
Paraleius n. sp.	Sarcoptiformes: Oribatulidae	--	1
Proctolaelaps bickleyi Bram	Mesostigmata: Melicharidae	Predator	4
Proctolaelaps fiseri Samsinak	Mesostigmata: Melicharidae	Predator	4
Proctolaelaps hystricoides Lindquist & Hunter	Mesostigmata: Melicharidae	Omnivorous	4
Proctolaelaps hystrix (Vitzthum)	Mesostigmata: Melicharidae	Predator	1,8
Proctolaelaps dendroctoni Lindquist & Hunter	Mesostigmata: Melicharidae	Predator	1
Proctolaelaps pygmaeus (Muller)	Mesostigmata: Melicharidae	Omnivorous	4
Scapheremaeus palustris (Sellnick)		--	1
Schizosthetus lyriformis (McGraw & Farrier)	Mesostigmata: Parasitidae	--	4
Tarsonemus subcorticalis Lindquist	Trombidiformes: Tarsonemidae	Mycetophagous	1
Tarsonemus terebrans n. sp.	Trombidiformes: Tarsonemidae	--	9
Trichoribates sp.		--	1
Trichouropoda australis Hirschmann	Mesostigmata: Trematuridae	Omnivorous	1,4
Uroobovella americana Hirschmann	Mesostigmata: Urodinychidae	Predator	4

Adapted from Hoffstetter et al. 2015.

1: Moser and Roton 1971, 2: Smiley and Moser 1970, 3: Whitcomb 1974, 4: Hofstetter et al. 2015, 5: Woodring 1966, 6: Woodring and Moser 1970, 7: Stone and Simpson 1991, 8: Lindquist and Hunter 1965, 9: Magowski and Moser 2003.

impact development of bark beetles, their ecological importance on population cycles of bark beetles may be considerable (Lombardo et al. 2003, Hofstetter et al. 2006). Of the 36 identified mite species associated with black turpentine beetle (Table 3), 17 species are considered predators, while the remaining species are fungus feeders or omnivores, or the feeding guild has yet to be identified. The known life histories of these different taxa suggest a diversity of possible ecological relationships with black turpentine beetles; however, there is no published research specifically on beetle–mite interactions.

Natural Enemies

There is very limited information on the identities or impacts of insect natural enemies associated with black turpentine beetles (Frank and Foltz 1997). The sympatric bark beetle predator *Thanasimus dubius* (Fabricius) (Coleoptera: Cleridae) has been observed attacking black turpentine beetles (Staeben et al. 2010) and they consumed black turpentine beetles in petri dish assays (B.T.S., personal observations). They can be found foraging at tree bases colonized by black turpentine beetle and ambrosia beetles, although the target prey for *T. dubius* in this situation is unclear (Clarke and Menard 2006). Their presence on these trees is perhaps due to the predator's strong attraction to the black turpentine beetle pheromone component frontalin (also produced by southern pine beetle prey) as well as to the host monoterpenes associated with pitch tubes (Mizell et al. 1984, Reeve et al. 2009, Staeben et al. 2015). Bark beetle predators (e.g., larvae of *T. dubius* and *Temnoscheila* spp.) have occasionally been encountered in the feeding chambers of black turpentine beetles, but it was not evident whether these were feeding on black turpentine beetle rather than associates (C. Wayne Berisford, personal communication).

A diverse complex of hymenopterous parasitoids (particularly in the families Braconidae and Pteromalidae) attack larvae and pupae of the other members of the southern pine beetle guild (Berisford et al. 1970, Berisford 2011), however, parasitism has not been reported for black turpentine beetle. The thick bark at the bases of trees where black turpentine beetle colonization occurs would likely interfere with host location and oviposition (Gargiullo and Berisford 1981), and the resinous environment where the larvae feed may not be tolerated. Woodpeckers have not been observed foraging on bark infested by black turpentine beetles (Lee and Smith 1955).

During the 1980s, initial investigations were performed on whether black turpentine beetle might be managed through inoculative release of the exotic predator *Rhizophagus grandis* Kugelann (Coleoptera: Monotomidae), a native to Europe (Moser 1989). In its native range, *R. grandis* prey on the larvae of *Dendroctonus micans* (Kugelmann), which, similarly to larvae of black turpentine beetle, feed gregariously in a chamber within the phloem, predominantly at the bases of their hosts (Hopkins 1909). *Rhizophagus grandis* was shown to be attracted to black turpentine beetle frass in walking bioassays (Miller et al. 1987) and fed on their brood under laboratory conditions (Moser 1989). A small field release occurred in Louisiana in 1988 (Moser 1989), but there is no evidence that these predators ever became established. During attacks on stumps and trees killed by other bark beetle species, competition with and/or predation by other subcortical phloem feeders, particularly the larvae of *Monochamus* spp. beetles, likely reduces the numbers of surviving beetle brood (Coulson et al. 1976, Coulson et al. 1980).

Management

Preventative Management

Prevention management strategies are often preferred over direct control enacted after attacks have been detected. Such management includes harvesting during fall and winter, keeping stump heights low, thinning overstocked stands (while minimizing damage to residual trees), harvesting damaged trees, and prescribed burns, all of which aim to enhance the health of pine stands (Staeben et al. 2010). However, prescribed fire is the only preventative management recommendation for black turpentine beetle in the existing literature with quantitative data. Prescribed fire is often used in pine stands to reduce hazardous fuel buildup, augment nutrient cycling, restore pine ecosystems, and improve wildlife habitat (Barnett 1999, Fernandes and Botelho 2003), and it may be a preventative measure against beetle attacks. Some prior research indicated a decrease in numbers of black turpentine beetle attacks following prescribed burns (Hanula et al. 2002), whereas other studies indicated an increase in attacks following prescribed burns but no accompanying increase in tree mortality (Campbell et al. 2008a,b). Black turpentine beetles do not appear to be attracted to burned stands, since trap catches did not differ among longleaf (*Pinus palustris* Mill.) pine stands receiving burn treatments of three different levels of severity or no burn (Sullivan et al. 2003). However, significant levels of tree mortality were observed in subsequent years in the more severe burns, and the first signs observed in the affected trees typically were attacks by black turpentine beetles. Evidence suggested that these severe burn areas experienced root injury and consequent fungal infection, and that the gradually weakened and susceptible trees were ultimately killed by black turpentine beetles and other bark beetles (Ostrosina et al. 2002).

Direct Management

Several insecticides such as lindane, chlorpyrifos, and fenitrothion have been tested and deployed successfully for black turpentine beetle management in the past. For example, lindane sprayed on stumps and damaged trees was shown to drastically reduce black turpentine beetle attacks and damage (Bennett 1965, Kucera et al. 1970). Nearly all insecticides demonstrated to be effective against black turpentine beetle in past research contain compounds now banned in the United States and elsewhere in the world. The insecticide carbaryl, which is currently labeled in the United States for use as a preventative treatment against bark beetles, has demonstrated efficacy in reducing black turpentine beetle attacks on loblolly pines (Burke et al. 2012). This insecticide is readily broken down by microbes, however, it has shown slight toxicity to birds and mammals and is highly toxic to fish, amphibians, and other insects, such as honey bees and stoneflies (Branch and Jacqz 1986, Zinkl et al. 1987, Relyea and Mills 2001, Singh et al. 2007). The use of chemical control for black turpentine beetles in forestry settings is not likely to be cost effective; however, insecticide use has merit in urban areas where black turpentine beetles can cause considerable damage to individual, high value trees. Additionally, insecticides are currently being deployed to protect pines used in development of novel, mechanized procedures for tapping resin, as black turpentine beetle attacks can result from this tapping (Lloyd Busby, personal communication).

Conclusions

Black turpentine beetles are not considered obligate tree killers and rarely cause extensive tree mortality in healthy pine trees. It appears to be a characteristic *r*-selection strategist, as it is multivoltine and produces many offspring, yet it rarely meets the carrying capacity of pine-dominated forests. Nevertheless, introduction to new areas may pose a concern, in particular because its sibling species *D. valens,* which is considered a secondary pest in its native range, became a major mortality agent of pines following introduction into China (Yan et al. 2005). Warming temperatures due to climate change are expected to result in extended flight and breeding seasons, increased number of generations per year, and range expansion for bark beetles (Gaylord et al. 2008, Waring et al. 2009, Bentz et al. 2010, Lesk et al. 2017). Climate change-driven northerly range expansion of southern pine beetle is having catastrophic impacts on unmanaged pine stands in the northeastern United States, and this major bark beetle pest is projected to come into contact with naive host species within the next half century, with potentially devastating results (Cudmore et al. 2010, Cullingham et al. 2011, Lesk et al. 2017, Heuss et al. 2019). If black turpentine beetles have similar temperature constraints as southern pine beetle, as suggested by their similar northern range limits, we might expect a comparable potential for northward range expansion.

There is very little literature with black turpentine beetles as its primary focus, and most research is outdated. Black turpentine beetles is a very understudied species, likely due to its weak responses to semiochemical lures for use in detection and monitoring, and its being often overshadowed by more aggressive bark beetle species, primarily the sympatric southern pine beetle.

Review of the existing literature revealed knowledge gaps as below. A focus on these major gap areas will assist with long-term sustainability and management of future pine forests (especially commercial plantations) under variable and enhanced natural and anthropogenic disturbances in the southern forests:

1. Interactions of black turpentine beetle with sympatric bark beetles and associates: Black turpentine beetles have a close relationship with their associates; however, it is unclear what role they have in assisting their associates with locating suitable host trees, overcoming tree defenses, and exacerbating outbreaks. Bark beetles are commonly associated with fungi that may play a significant role in overcoming host tree defenses, yet little to no research has investigated the black turpentine

beetle—fungi relationship. Further, black turpentine beetles can be found colonizing the same trees as the southern pine bark beetle guild and it's possible that their pheromone plumes are serving as secondary attractants to other species (Payne 1987). It is likely that a complex exists between bark beetles, fungi, mites, and other associates, and they are indirectly or directly working in consort to overcome tree defenses. These interactions may influence the success of each species and the functioning of the ecosystem, and a more thorough examination of these relationships may inform forest management practices.

2. The economic and ecological impacts of black turpentine beetles: The most recent estimates of black turpentine beetle-caused pine mortality across the southern United States were from 1998 to 2005 (www.sfiwc.org/publications), and pest risk can be strongly influenced by revisions to forestry practices and land usage. More accurate means of measuring black turpentine beetle-caused losses may be needed since it is difficult to assess the role of single agents in causing pine mortality. Killed trees discovered with black turpentine beetle attacks usually have evidence of colonization by other bark beetles, pathogens, and additional agents that may or may not have contributed to tree mortality; and for this reason, previous damage estimates may have significantly underestimated impacts of black turpentine beetles.
3. Direct and indirect management strategies: Nearly all demonstrated direct control methods of black turpentine beetles involve insecticides that are now restricted or banned. Current recommendations for indirect control and prevention are largely inferred from findings for other bark beetle species or basic knowledge of black turpentine beetle biology; none have been directly investigated for their efficacy. There are currently no commercially-available trapping systems (i.e., lures and trapping devices) for black turpentine beetles that are sufficiently effective for ecological research or use as detection and management tools, which will be needed if this species was to become a more significant pest.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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References Cited

Aoki, C. F., M. Cook, J. Dunn, D. Finley, L. Fleming, R. Yoo, and M. P. Ayres. 2018. Old pests in new places: effects of stand structure and forest type on susceptibility to a bark beetle on the edge of its native range. Forest Ecol. Manag. 419: 206–219.

Ayres, M. P., R. T. Wilkens, J. J. Ruel, M. J. Lombardero, and E. Vallery. 2000. Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. Ecology 81: 2198–2210.

Barnett, J. P. 1999. Longleaf pine ecosystem restoration: the role of fire. J. Sustainable Forestry. 9: 89–96.

Barr, B. A. 1969. Sound production in Scolytidae (Coleoptera) with emphasis on the genus *Ips*. Can. Entomol. 101: 636–672.

Barras, S. J., and T. J. Perry. 1971. *Leptographium terebrantis* sp. nov. associated with *Dendroctonus terebrans* in loblolly pine. Mycopathologia et Mycologia Applicata. 43: 1–10.

Bennett, W. H. 1965. Benzene hexachloride emulsion for controlling black turpentine beetle in logging areas. J. Econ. Entomol. 58: 358.

Bentz, B. J., and M. W. Stock. 1986. Phenetic and phylogenetic relationships among ten species of *Dendroctonus* bark beetles (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 79: 527–534.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience. 60: 602–613.

Berisford, C. W. 2011. Parasitoids of the southern pine beetle, pp. 129–139. *In* R. N. Coulson and K. D. Klepzig (eds.), Southern Pine Beetle II. USDA Forest Service Southern Research Station. General Technical Report SRS-140, Asheville, NC.

Berisford, C. W., H. M. Kulman, and R. L. Pienkowski. 1970. Notes on the biologies of hymenopterous parasites of *Ips* spp. bark beetles in Virginia. Can. Entomol. 102: 484–490.

Birch, M. C., P. Svihra, T. D. Paine, and J. C. Miller. 1980. Influence of chemically mediated behavior on host tree colonization by four cohabiting species of bark beetles. J. Chem. Ecol. 6: 395–414.

Blomquist, G. J., R. Figueroa-Teran, M. Aw, M. Song, A. Gorzalski, N. L. Abbott, E. Chang, and C. Tittiger. 2010. Pheromone production in bark beetles. Insect Biochem. Mol. Biol. 40: 699–712.

Borden, J. H. 1982. Aggregation pheromones, pp. 74–139. *In* J. B. Mitton and K. B. Sturgeon (eds.), Bark beetles in North American conifers: a system for the study of evolutionary biology. University of Texas Press, Austin, TX.

Branch, R. A., and E. Jacqz. 1986. Subacute neurotoxicity following long-term exposure to carbaryl. Am. J. Med. 80: 741–745.

Burke, J. L., J. L. Hanula, S. Horn, J. P. Audley, and K. J. Gandhi. 2012. Efficacy of two insecticides for protecting loblolly pines (*Pinus taeda* L.) from subcortical beetles (Coleoptera: Curculionidae and Cerambycidae). Pest Manag. Sci. 68: 1048–1052.

Byers, J. A. 1989a. Behavioral mechanisms involved in reducing competition in bark beetles. Holarct. Ecol. 12: 466–476.

Byers, J. A. 1989b. Chemical ecology of bark beetles. Experientia, 45: 271–283.

Byers, J. A., Y. Maoz, D. Wakarchuk, D. Fefer, and A. Levi Zada. 2018. Inhibitory effects of semiochemicals on the attraction of an ambrosia beetle *Euwallacea* nr. *fornicatus* to Quercivorol. J. Chem. Ecol. 44: 565–575.

Cameron, R. S. 1987. Southern pine bark beetles in the urban environment. J. Arboric. 13: 145–151.

Campbell, S. A., and J. H. Borden. 2006. Integration of visual and olfactory cues of hosts and non-hosts by three bark beetles (Coleoptera: Scolytidae). Ecol. Entomol. 31: 437–449.

Campbell, J. W., J. L. Hanula, and K. W. Outcalt. 2008a. Effects of prescribed fire and other plant community restoration treatments on tree mortality, bark beetles, and other saproxylic Coleoptera of longleaf pine, *Pinus palustris* Mill., on the Coastal Plain of Alabama. Forest Ecol. Manag. 254: 134–144.

Campbell, J. W., J. L. Hanula, and T. A. Waldrop. 2008b. Effects of prescribed fire and fire surrogates on saproxylic coleoptera in the Southern Appalachians of North Carolina. J. Entomol. Sci. 43: 57–75.

Cardé, R. T. 2014. Defining attraction and aggregation pheromones: teleological versus functional perspectives. J. Chem. Ecol. 40: 519.

Clarke, S. R., and R. D. Menard. 2006. Predation of an ambrosia beetle (Coleoptera: Platypodidae) by a checkered beetle (Coleoptera: Cleridae) congregating on pines containing brood adult southern pine beetles (Coleoptera: Curculionidae). J. Entomol. Sci. 41: 257–260.

Clements, R. W., and H. G. Williams. 1981. Attractants, techniques, and devices for trapping bark beetles, USDA Forest Service Research Note. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC.

Coulson, R. N., A. M. Mayyasi, J. L. Foltz, and F. P. Hain. 1976. Interspecific competition between *Monochamus titillator* and *Dendroctonus frontalis*. Environ. Entomol. 5: 235–247.

Coulson, R. N., D. N. Pope, J. A. Gagne, W. S. Fargo, P. E. Pulley, and L. J. Edson. 1980. Impact of foraging by *Monochamus titillator* (Col.: Cerambycidae) on within-tree populations of *Dendroctonus frontalis* (Col.: Scolytidae). Entomophaga. 25: 155–170.

Coulson, R. N., P. B. Hennier, R. O. Flamm, E. J. Rykiel, L. C. Hu, and T. L. Payne. 1983. The role of lightning in the epidemiology of the southern pine beetle. Zeitschrift für angewandte Entomologie. 96: 182–193.

Coulson, R. N., R. O. Flamm, P. E. Pulley, T. L. Payne, E. J. Rykiel, and T. L. Wagner. 1986. Response of the southern pine bark beetle guild (Coleoptera: Scolytidae) to host disturbance. Environ. Entomol. 15: 850–858.

Coyle, D. R., K. D. Klepzig, F. H. Koch, L. A. Morris, J. T. Nowak, S. W. Oak, W. J. Otrosina, W. D. Smith, and K. J. K. Gandhi. 2015. A review of southern pine decline in North America. Forest Ecol. Manag. 349: 134–148.

Cudmore, T. J., N. Björklund, A. L. Carroll, and B. S. Lindgren. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. J. Appl. Ecol. 47: 1036–1043.

Cullingham, C. I., J. E. Cooke, S. Dang, C. S. Davis, B. J. Cooke, and D. W. Coltman. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. Mol. Ecol. 20: 2157–2171.

Delorme, J. D., and T. L. Payne. 1990. Antennal olfactory responses of black turpentine beetle, *Dendroctonus terebrans* (Olivier), to bark beetle pheromones and host terpenes. J. Chem. Ecol. 16: 1321–1329.

Dixon, W. N., and T. L. Payne. 1980. Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Texas Agricultural Experiment Station Bulletin Miscellaneous Publication No. 1432.

Dutrillaux, A. M., and B. Dutrillaux. 2017. Evolution of the sex chromosomes in beetles. I. The loss of the Y chromosome. Cytogenet. Genome Res. 152: 97–104.

Eckhardt, L. G., A. M. Weber, R. D. Menard, J. P. Jones, and N. J. Hess. 2007. Insect-fungal complex associated with loblolly pine decline in central Alabama. Forest Sci. 53: 84–92.

Erbilgin, N., and K. F. Raffa. 2002. Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. Forest Ecol. Manag. 164: 221–236.

Erbilgin, N., S. R. Mori, J. H. Sun, J. D. Stein, D. R. Owen, L. D. Merrill, R. C. Bolaños, K. F. Raffa, T. M. Montiel, D. L. Wood, *et al*. 2007. Response to host volatiles by native and introduced populations of *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae) in North America and China. J. Chem. Ecol. 33: 131–146.

Etxebeste, I., and J. Pajares. 2011. Verbenone protects pine trees from colonization by the six-toothed pine bark beetle, *Ips sexdentatus* Boern. (Col.: Scolytinae). J. Appl. Entomol. 135: 258–268.

Fatzinger, C. W. 1985. Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest coleopteran to turpentine-baited traps. Environ. Entomol. 14: 768–775.

Fatzinger, C. W., B. D. Siegfried, R. C. Wilkinson, and J. L. Nation. 1987. *trans*-Verbenol, turpentine, and ethanol as trap baits for the black turpentine beetle, *Dendroctonus terebrans*, and other forest Coleoptera in North Florida. J. Entomol. Sci. 22: 201–209.

Feduccia, D. P., and W. F. Mann. 1975. Black turpentine beetle infestations after thinning in a loblolly pine plantation. US Dept. of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA.

Fernandes, P. M., and H. S. Botelho. 2003. A review of prescribed burning effectiveness in fire hazard reduction. Int. J. Wildland Fire 12: 117–128.

Flamm, R. O., and R. N. Coulson. 1988. Traumatized hosts: their influence on the population dynamics of the southern pine beetle guild, pp. 345–358. *In* W. J. Matson, J. Levieux and C. Bernard-Dagan (eds.), Mechanisms of woody plant defenses against insects. Springer-Verlag, New York.

Flamm, R. O., T. L. Wagner, S. P. Cook, P. E. Pulley, R. N. Coulson, and T. M. McArdle. 1987. Host colonization by cohabiting *Dendroctonus frontalis*, *Ips avulsus*, and *I. calligraphus* (Coleoptera: Scolytidae). Environ. Entomol. 16: 390–399.

Flamm, R. O., P. E. Pulley, and R. N. Coulson. 1993. Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera, Scolytidae). Environ. Entomol. 22: 62–70.

Flechtmann, C. A. H., M. J. Dalusky, and C. W. Berisford. 1999. Bark and ambrosia beetle (Coleoptera: Scolytidae) responses to volatiles from aging loblolly pine billets. Environ. Entomol. 28: 638–648.

Fox, T. R., E. J. Jokela, and H. L. Allen. 2007. The development of pine plantation silviculture in the Southern United States. J. Forest. 105: 337–347.

Franceschi, V. R., P. Krokene, E. Christiansen, and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytol. 167: 353–375.

Frank, J. H., and J. L. Foltz. 1997. Classical biological control of pest insects of trees in the southern united states: a review and recommendations. USDA Forest Service Forest Health Technology Enterprise Team Publication FHTET-1996-20, Morgantown, WV.

Gargiullo, P. M., and C. W. Berisford. 1981. Effects of host density and bark thickness on the densities of parasites of the southern pine beetle. Environ. Entomol. 10: 392–399.

Gaylord, M. L., K. K. Williams, R. W. Hofstetter, J. D. McMillin, T. E. Degomez, and M. R. Wagner. 2008. Influence of temperature on spring flight initiation for southwestern ponderosa pine bark beetles (Coleoptera: Curculionidae, Scolytinae). Environ. Entomol. 37: 57–69.

Godbee, J. F., and R. T. Franklin. 1976. Attraction, attack patterns and seasonal activity of the black turpentine beetle. Ann. Entomol. Soc. Am. 69: 653–655.

Godbee, J. F., and R. T. Franklin. 1978. Sexing and rearing the black turpentine beetle (Coleoptera: Scolytidae). Can. Entomol. 110: 1087–1089.

Hanula, J. L., J. R. Meeker, D. R. Miller, and E. L. Barnard. 2002. Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. Forest Ecol. Manag. 170: 233–247.

Harrington, T., and F. Cobb Jr. 1983. Pathogenicity of *Leptographium* and *Verticicladiella* spp. isolated from roots of western North American conifers. Phytopathology. 73: 596–599.

Heuss, M., A. W. D'Amato, and K. J. Dodds. 2019. Northward expansion of southern pine beetle generates significant alterations to forest structure and composition of globally rare *Pinus rigida* forests. Forest Ecol. Manag. 434: 119–130.

Highley, L., and T. A. Tattar. 1985. *Leptographium terebrantis* and black turpentine beetles associated with blue stain and mortality of black and scots pines on Cape Cod, Massachusetts. Plant Dis. 69: 528–530.

Hobson, K. R., D. L. Wood, L. G. Cool, P. R. White, T. Ohtsuka, I. Kubo, and E. Zavarin. 1993. Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. J. Chem. Ecol. 19: 1837–1846.

Hodges, J. D., and L. S. Pickard. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). Can. Entomol. 103: 44–51.

Hofstetter, R. W. 2011. Mutualists and phoronts of the southern pine beetle, pp. 161–181. *In* Coulson, R. N., and K. D. Klepzig (eds.). Southern pine beetle II. Gen. Tech. Rep. SRS-140, 140. US Department of Agriculture Forest Service, Southern Research Station, Asheville, NC.

Hofstetter, R. W., J. T. Cronin, K. D. Klepzig, J. C. Moser, and M. P. Ayres. 2006. Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. Oecologia. 147: 679–691.

Hofstetter, R. W., J. Moser, and S. Blomquist. 2014. Mites associated with bark beetles and their hyperphoretic ophiostomatoid fungi. Biodiversity Series. 12: 165–176.

Hofstetter, R. W., J. Dinkins-Bookwalter, T. S. Davis, and K. D. Klepzig. 2015. Symbiotic associations of bark beetles, pp. 209–245. *In* F. E. Vega, and R. W. Hofstetter (eds.), Bark beetles - Biology and ecology of native and invasive species. Academic Press, Cambridge, MA.

Hopkins, A. D. 1909. Contributions toward a monograph of the scolytid beetles: the genus *Dendroctonus* (No. 17). US Government Printing Office, US Bureau of Entomology Technical Series.

Hughes, P. R. 1975. Pheromones of *Dendroctonus:* origin of α-pinene oxidation products present in emergent adults. J. Insect Physiol. 21: 681–691.

Hughes, M. A., X. Martini, E. Kuhns, J. Colee, A. Mafra-Neto, L. Stelinski, and J. Smith. 2017. Evaluation of repellents for the redbay ambrosia beetle, *Xyleborus glabratus*, vector of the laurel wilt pathogen. J. Appl. Entomol. 141: 653–664.

Hulcr, J., A. S. Adams, K. Raffa, R. W. Hofstetter, K. D. Klepzig, and C. R. Currie. 2011. Presence and diversity of Streptomyces in *Dendroctonus* and sympatric bark beetle galleries across North America. Microb. Ecol. 61: 759–768.

Johnson, R. N. 2000. Declining industries and the persistence of government support programs: the quiet decline of gum naval stores production in the United States. J. Econ. Hist. 60: 995–1016.

Kelsey, R. G., and G. Joseph. 2001. Attraction of *Scolytus unispinosus* bark beetles to ethanol in water-stressed Douglas-fir branches. Forest Ecol. Manag. 144: 229–238.

Klepzig, K. D., and D. Six. 2004. Bark beetle-fungal symbiosis: context dependency in complex associations. Symbiosis 37: 189–205.

Klepzig, K. D., K. F. Raffa, and E. B. Smalley. 1991. Association of an insect-fungal complex with red pine decline in Wisconsin. Forest Sci. 37: 1119–1139.

Klepzig, K. D., J. C. Moser, M. J., Lombardero, M. P. Ayres, R. W. Hofstetter, and C. J. Walkinshaw. 2001a. Mutualism and antagonism: ecological interactions among bark beetles, mites and fungi, pp. 237–267. *In* M. J. Jeger and N. J. Spence (eds.) Biotic Interactions in Plant-Pathogen Associations. CAB International, Oxford, NY.

Klepzig, K. D., J. C. Moser, F. J. Lomardero, R. W. Hofstetter, and M. P. Ayres. 2001b. Symbiosis and competition: complex interactions among beetles, fungi and mites. Symbiosis. 30: 83–96.

Kucera, D. R., J. D. Ward, and H. N. Wallace. 1970. Effectiveness of chemical control for the black turpentine beetle in Central Louisiana. J. Econ. Entomol. 63: 104–106.

Langor, D. W. 1991. Arthropods and nematodes co-occurring with the Eastern Larch Beetle, *Dendroctonus simplex* [Col, Scolytidae], in Newfoundland. Entomophaga. 36: 303–313.

Lee, R. E., and R. H. Smith. 1955. The black turpentine beetle, its habits and control, USDA Forest Service Southern Forest Experimental Station. Occasional Paper. USDA Forest Service, Southern Forest Experimental Station.

Lesk, C., E. Coffel, A. W. D'Amato, K. Dodds, and R. Horton. 2017. Threats to North American forests from southern pine beetle with warming winters. Nat. Clim. Change 7: 713.

Lieutier, F., A. Yart, and A. Salle. 2009. Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. Annals of Forest Sci. 66: 801.

Lindelow, A., B. Risberg, and K. Sjodin. 1992. Attraction during flight of scolytids and other bark-dwelling and wood-dwelling beetles to volatiles from fresh and stored spruce wood. Can. J. For. Res. 22: 224–228.

Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles. Can. Entomol. 115: 299–302.

Lindgren, B. S., and D. R. Miller. 2002. Effect of verbenone on five species of bark beetles (Coleoptera: Scolytidae) in lodgepole pine forests. Environ. Entomol. 31: 759–765.

Lindquist, E. E., and P. E. Hunter. 1965. Some mites of the genus *Proctolaelaps Berlese* (Acarina: Blattisociidae) associated with forest insect pests. Can. Entomol. 97: 15–32.

Little, N. S., T. P. Schultz, S. V. Diehl, D. D. Nicholas, A. J. Londo, F. R. Musser, J. J. Riggins. 2013. Field evaluations of subterranean termite preference for sap-stain inoculated wood. J. Insect Behav. 26: 649–659.

Liu, Z., B. Xu, Z. Miao, and J. Sun. 2013. The pheromone frontalin and its dual function in the invasive bark beetle *Dendroctonus valens*. Chem. Senses 38: 485–495.

Liu, Z., B. Xu, Y. Guo, K. F. Raffa, and J. Sun. 2017. Gallery and acoustic traits related to female body size mediate male mate choice in a bark beetle. Anim. Behav. 125: 41–50.

Lombardero, M. J., M. P. Ayres, R. W. Hofstetter, J. C. Moser, and K. D. Klepzig. 2003. Strong indirect interactions of *Tarsonemus* mites (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). Oikos. 102: 243–252.

Lovelady, C. N., P. E. Pulley, R. N. Coulson, and R. O. Flamm. 1991. Relation of lightning to herbivory by the southern pine bark beetle guild (Coleoptera: Scolytidae). Environ. Entomol. 20: 1279–1284.

Magowski, W. L., and J. C. Moser. 2003. Redescription of *Tarsonemus minimax* and definition of its species-group in the Genus *Tarsonemus* (Acari: Tarsonemidae) with descriptions of two new species. Ann. Entomol. Soc. Am. 96: 345–368.

Matusick, G., R. D. Menard, Y. Zeng, and L. G. Eckhardt. 2013. Root-inhabiting bark beetles (Coleoptera: Curculionidae) and their fungal associates breeding in dying loblolly pine in Alabama. Fla. Entomol. 96: 238–241.

Mayfield, A. E., III, and J. L. Foltz. 2005. The black turpentine beetle, *Dendroctonus terebrans (*Olivier) (Coleoptera: Curculionidae: Scolytinae). Division of Plant Industry, FDACS. Entomology Circ. 405: 4.

Merkel, E. P. 1981. Control of the black turpentine beetle. Georgia Forest Research Paper 15. Georgia Forestry Commission, Macon, GA.

Miller, D. R., and C. M. Crowe. 2009. Length of multiple-funnel traps affects catches of some bark and wood boring beetles in a slash pine stand in northern Florida. Fla. Entomol. 92: 506–508.

Miller, D. R., and C. M. Crowe. 2011. Relative performance of Lindgren multiple-funnel, Intercept panel, and Colossus pipe traps in catching Cerambycidae and associated species in the southeastern United States. J. Econ. Entomol. 104: 1934–1941.

Miller, D. R., and D. A. Duerr. 2008. Comparison of arboreal beetle catches in wet and dry collection cups with Lindgren multiple funnel traps. J. Econ. Entomol. 101: 107–113.

Miller, D. R., and R. J. Rabaglia. 2009. Ethanol and (-)-alpha-Pinene: attractant kairomones for bark and ambrosia beetles in the southeastern US. J. Chem. Ecol. 35: 435–448.

Miller, M. C., J. C. Moser, M. McGregor, J. Gregoire, M. Baisier, D. L. Dahlsten, D. L., and R. A. Werner. 1987. Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 80: 417–428.

Miller, D. R., C. Asaro, and C. W. Berisford. 2005. Attraction of southern pine engravers and associated bark beetles (Coleoptera: Scolytidae) to ipsenol, ipsdienol, and lanierone in southeastern United States. J. Econ. Entomol. 98: 2058–2066.

Mirov, N. T. 1961. Composition of gum turpentines of pines, pp. 25. USDA Forest Service Pacific Southwest Forest and Range Experiment Station.

Mizell, R. F., 3rd, J. L. Frazier, and T. E. Nebeker. 1984. Response of the clerid predator *Thanasimus dubius* (F.) to bark beetle pheromones and tree volatiles in a wind tunnel. J. Chem. Ecol. 10: 177–187.

Moeck, H. A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum* (Coleoptera: Scolytidae). Can. Entomol. 102: 985–995.

Moser, J. C. 1989. Inocluative release of an exotic predator for the biological control of the black turpentine beetle, pp. 189–200. In D. L. Kulhavy and M. C. Miller (eds.), Potential for biological control of *Dendroctonus* and *Ips* bark beetles. Stephen F. Austin State University, Nacogdoches, TX.

Moser, J. C., and L. M. Roton. 1971. Mites associated with the southern pine bark beetles in Allen Parish, Louisiana. Can. Entomol. 103: 1775–1798.

Moser, J. C., H. Konrad, T. Kirisits, and L. K. Carta. 2005. Phoretic mites and nematode associates of *Scolytus multistriatus* and *Scolytus pygmaeus* (Coleoptera: Scolytidae) in Austria. Agr. Forest Entomol. 7: 169–177.

Nebeker, T. 2011. Southern pine bark beetle guild, pp. 199–209. *In* R. N. Coulson and K. D. Klepzig (eds.). Southern pine beetle II. USDA Forest Service Southern Research Station General Technical Report SRS-140, Asheville, NC.

Niño-Domínguez, A., B. T. Sullivan, J. H. López-Urbina, and J. E. Macías-Sámano. 2015. Pheromone-mediated mate location and discrimination by two syntopic sibling species of *Dendroctonus* bark beetles in Chiapas, Mexico. J. Chem. Ecol. 41: 746–756.

Økland, B., O. Skarpaas, and K. Kausrud. 2009. Threshold facilitations of interacting species. Popul. Ecol. 51: 513–523.

Otrosina, W. J., and F. W. Cobb. 1989. Biology, ecology, and epidemiology of *Heterobasidion annosum*. Proceedings of the symposium on research and management of annosus root disease (*Heterobasidion annosum*) in western North America 1989. Monterey, CA. Gen. Tech. Rep.

PSW-GTR-116. Pacific Southwest Forest and Range Experiment Station, Forest Service, US Department of Agriculture, Berkeley, CA.

Ostrosina, W. J., C. H. Walkinshaw, S. J. Zarnoch, S. J. Sung, and B. T. Sullivan. 2002. Root disease, longleaf pine mortality, and prescribed burning, pp. 551–557. In K.W. Outcalt (ed.), Proceedings of the eleventh biennial southern silvicultural research conference 2002. USDA Forest Service Southern Research Station, Asheville, NC. Gen. Tech. Rep. SRS-48.

Owen, D. R., K. Q. Lindahl, Jr, D. L. Wood, and J. R. Parmeter, Jr. 1987. Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. Phytopathology. 77: 631–636.

Paine, T. D., M. C. Birch, and P. Švihra. 1981. Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). Oecologia. 48: 1–6.

Paine, T. D., K. F. Raffa, and T. C. Harrington. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. Annu. Rev. Entomol. 42: 179–206.

Pajares, J. A., and G. N. Lanier. 1990. Biosystematics of the turpentine beetles *Dendroctonus terebrans* and *D. valens* (Coleoptera, Scolytidae). Ann. Entomol. Soc. Am. 83: 171–188.

Payne, T. L., R. F. Billings, J. D. Delorme, N. A. Andryszak, J. Bartels, and W. Francke. 1987. Kairomonal-pheromonal system in the black turpentine beetle, *Dendroctonus terebrans* (Ol.). J. Appl. Entomol. 103: 15–22.

Payne, T., M. Smith, M. Birch, and A. Ascoli. 1991. Interspecific olfactory communication in the southern pine bark beetle guild, pp. 352–370. *In* Y. N. Baranchikov, W. J. Mattson, F. P. Hain, T. L. Payne (eds.) Forest insect guilds: patterns of interaction with host trees; 1989 August 13–17; Abakan, Siberia, USSR Gen. Tech. Rep. NE-153. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA.

Pernek, M., B. Hrasovec, D. Matosevic, I. Pilas, T. Kirisits, and J. C. Moser. 2008. Phoretic mites of three bark beetles (*Pityokteines* spp.) on Silver fir. J. Pest Sci. 81: 35–42.

Phillips, T. W. 1990. Responses of *Hylastes salebrosus* to turpentine, ethanol, and pheromones of *Dendroctonus* (Coleoptera: Scolytidae). Fla. Entomol. 73: 286–292.

Phillips, M. A., and R. B. Croteau. 1999. Resin-based defenses in conifers. Trends Plant Sci. 4: 184–190.

Phillips, T. W., A. J. Wilkening, T. H. Atkinson, J. L. Nation, R. C. Wilkinson, and J. L. Foltz. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). Environ. Entomol. 17: 456–462.

Phillips, T. W., J. L. Nation, R. C. Wilkinson, and J. L. Foltz. 1989. Secondary attraction and field activity of beetle-produced volatiles in *Dendroctonus terebrans*. J. Chem. Ecol. 15: 1513–1533.

Pureswaran, D. S., R. Gries, J. H. Borden, and H. D. Pierce, Jr. 2000. Dynamics of pheromone production and communication in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). Chemoecology. 10: 153–168.

Raffa, K. F. 2001. Mixed messages across multiple trophic levels: The ecology of bark beetle chemical communication systems. Chemoecology. 11: 49–65.

Raffa, K. F., and E. B. Smalley. 1988. Host resistance to invasion by lower stem and root infesting insects of pine: response to controlled inoculations with the fungal associate *Leptographium terebrantis*. Can. J. Forest Res. 18: 675–681.

Raffa, K. F., T. W. Phillips, and S. M. Salom. 1993. Strategies and mechanisms of host colonization by bark beetles, pp. 103–128. *In* R. D. Schowalter and G. M. Filip (eds.), Beetle-pathogen interactions in conifer forests. Academic Press, London.

Raffa, K. F., J. C. Gregoire, and B. S. Lindgren. 2015. Natural history and ecology of bark beetles, pp. 1–40, Bark Beetles. Elsevier, London, UK.

Rane, K. K., and T. A. Tattar. 1983. Pathogenicity of *Leptographium* sp. associated with *Dendroctonus terebrans*. Phytopathology. 73: 1346.

Rane, K. K., and T. A. Tattar. 1987. Pathogenicity of blue-stain fungi associated with *Dendroctonus terebrans*. Plant Dis. 71: 879–882.

Ranger, C. M., M. E. Reding, A. B. Persad, and D. A. Herms. 2010. Ability of stress-related volatiles to attract and induce attacks by *Xylosandrus germanus* and other ambrosia beetles. Agr. Forest Entomol. 12: 177–185.

Reeve, J. D., B. L. Strom, L. K. Rieske, B. D. Ayres, and A. Costa. 2009. Geographic variation in prey preference in bark beetle predators. Ecol. Entomol. 34: 183–192.

Relyea, R. A., and N. Mills. 2001. Predator-induced stress makes the pesticide carbaryl more deadly to gray treefrog tadpoles (*Hyla versicolor*). Proc. Natl. Acad. Sci. USA 98: 2491–2496.

Rudinsky, J. A., L. C. Ryker, R. R. Michael, L. M. Libbey, and M. E. Morgan. 1976. Sound production in Scolytidae: female sonic stimulus of male pheromone release in two *Dendroctonus* beetles. J. Insect. Physiol. 22: 1675–1681.

Ryker, L. C. 1988. Acoustic studies of *Dendroctonus* bark beetles. Fla. Entomol. 71: 447–461.

Schroeder, L. M., and A. Lindelöw. 1989. Attraction of scolytids and associated beetles by different absolute amounts and proportions of α-pinene and ethanol. J. Chem. Ecol. 15: 807–817.

Seybold, S. J., D. P. W. Huber, J. C. Lee, A. D. Graves, and J. Bohlmann. 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. Phytochemistry. Rev. 5: 143–178.

Seybold, S. J., B. J. Bentz, C. J. Fettig, J. E. Lundquist, R. A. Progar, and N. E. Gillette. 2018. Management of western North American bark beetles with semiochemicals. Annu. Rev. Entomol. 63: 407–432.

Siegfried, B. D., C. W. Fatzinger, R. C. Wilkinson, and J. L. Nation. 1986. In-flight responses of the black turpentine beetle (Coleotera: Scolytidae) to individual monoterpenes, turpentine, and paraquat-treated slash pines. Environ. Entomol. 15: 710–714.

Singh, B. P., L. Singhal, and R. S. Chauhan. 2007. Immunotoxicity of carbaryl in chicken. Indian J. Exp. Biol. 45: 890–895.

Six, D. L. 2003. Bark beetle-fungus symbioses. Insect Symbiosis. 1: 97–114.

Six, D. L. 2012. Ecological and evolutionary determinants of bark beetle -fungus symbioses. Insects. 3: 339–366.

Six, D. L., and R. Bracewell. 2015. *Dendroctonus*, pp. 305–350. *In* F. Vega and R. Hofstetter (eds.), Bark beetles: biology and ecology of native and invasive species. Elsevier Academic Press, The Netherlands.

Six, D. L., and M. J. Wingfield. 2011. The role of phytopathogenicity in bark beetle-fungus symbioses: a challenge to the classic paradigm. Annu. Rev. Entomol. 56: 255–272.

Skillen, E. L., C. W. Berisford, M. A. Camaan, and R. C. Reardon. 1997. Semiochemicals of forest and shade tree insects in North America and management applications. USDA Forest Service Forest Health Technology Enterprise Team Publication FHTET-96-15, Morgantown, WV.

Smiley, R. L., and J. C. Moser. 1970. Three cheyletids found with pine bark beetles (Acarina: Cheyletidae). *In* Proceedings of Entomological Society of Washington. 72: 229–235.

Smith, R. H. 1957. Habits of attack by the black turpentine beetle on slash and longleaf pine in north Florida. J. Econ. Entomol. 50: 241–244.

Smith, R. H. 1963. Preferential attack by *Dendroctonus terebrans* on *Pinus elliottii*. J. Econ. Entomol. 56: 817–819.

Smith, R. H., and R. E. Lee, III. 1972. Black turpentine beetle. USDA Forest Service Forest Pest Leaflet 12, pp. 1–8.

Smith, M. T., T. L. Payne, and M. C. Birch. 1990. Olfactory-based behavioral interactions among five species in the southern pine bark beetle group. J. Chem. Ecol. 16: 3317–3331.

Squillace, A. E., and G. S. Fisher. 1965. Evidences of the inheritance of turpentine composition in slash pine. Joint Proceedings, Second Genetics Workshop of the Society of American Foresters and the Seventh Lake States Forest Tree Improvement Conference, October 21–23, 1965, research paper No. NC-6. North Central Forest Experiment Station, US Department of Agriculture Forest Service, St. Paul, MN.

Staeben, J. C. 2015. Southern pine beetle (*Dendroctonus frontalis* Zimmermann): Semiochemical ecology, relationship between outbreak populations and lightning strike, and ecological impacts of suppression and control techniques. Ph.D dissertation, University of Georgia, Athens.

Staeben, J. C., S. Clarke, and K. J. K. Gandhi. 2010. The Black Turpentine Beetle. USDA Forest Service, Forest Insect and Disease Leaflet 12, 8 p.

Staeben, J. C., B. T. Sullivan, J. T. Nowak, and K. J. K. Gandhi. 2015. Enantiospecific responses of southern pine beetle (*Dendroctonus frontalis*) and its clerid predator, *Thanasimus dubius*, to α-pinene. Chemoecology. 25: 73–83.

Stewart, T. E., E. L. Plummer, L. L. McCanless, J. R. West, and R. M. Silverstein. 1977. Determination of enantiomer composition of several bicyclic ketal insect pheromone components. J. Chem. Ecol. 3: 27–43.

Stone, C., and J. A. Simpson. 1991. Effect of six chemicals on the insects, mites, nematodes and fungi associated with *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in northeastern New South Wales. Australian J. Entomol. 30: 21–28.

Strom, B. L., L. M. Roton, R. A. Goyer, and J. R. Meeker. 1999. Visual and semiochemical disruption of host finding in the southern pine beetle. Ecol. Appl. 9: 1028–1038.

Strom, B. L., and R. A. Goyer. 2001. Effect of silhouette color on trap catches of *Dendroctonus frontalis* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 94: 948–953.

Strom, B. L., R. A. Goyer, and P. J. Shea. 2001. Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. Entomol. Exp. Appl. 100: 63–67.

Sullivan, B. T. 2011. Southern pine beetle behavior and semiochemistry, pp. 25–50. *In* R. N. Coulson and K. D. Klepzig (eds.), Southern pine beetle II. USDA Forest Service Southern Research Station Gen. Tech. Rep. SRS-140, Asheville, NC.

Sullivan, B. T. 2016. Chapter Four - Semiochemicals in the natural history of southern pine beetle *Dendroctonus frontalis* Zimmermann and their role in pest management. Adv. Insect Physiol. 50: 129–193.

Sullivan, B. T., C. J. Fettig, W. J. Otrosina, M. J. Dalusky, and C. W. Berisford. 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. Forest Ecol. Manag. 185: 327–340.

Sullivan, B. T., W. P. Shepherd, D. S. Pureswaran, T. Tashiro, and K. Mori. 2007. Evidence that (+)-*endo*-brevicomin is a male-produced component of the Southern pine beetle aggregation pheromone. J. Chem. Ecol. 33: 1510–1527.

Sun, J., N. E. Gillette, Z. Miao, L. Kang, Z. Zhang, D. R. Owen, J. D. Stein. 2003. Verbenone interrupts attraction to host volatiles and reduces attack on *Pinus tabuliformis* (Pinaceae) by *Dendroctonus valens* (Coleoptera: Scolytidae) in the People's Republic of China. Can. Entomol. 135: 721–732.

Svihra, P., T. D. Paine, and M. C. Birch. 1980. Interspecific olfactory communications in southern pine beetles. Naturwissenschaften. 67: 518–520.

Symonds, M. R. E., and M. A. Elgar. 2004. Species overlap, speciation and the evolution of aggregation pheromones in bark beetles. Ecol. Lett. 7: 202–212.

Thatcher, R. C. 1960. Bark beetles affecting southern pines: a review of current knowledge, pp. 25 pp. USDA Forest Service Southern Forest Experiment Station Occ. Pap. 180, Pineville, LA.

Thomas, J. 1965. The immature stages of Scolytidae: the genus *Dendroctonus* Erichson. Can. Entomol. 97: 374–400.

Victor, J., and G. Zuñiga. 2015. Phylogeny of *Dendroctonus* bark beetles (Coleoptera: Curculionidae: Scolytinae) inferred from morphological and molecular data. Syst. Entomol. 41: 162–177.

Vité, J. P., and H. D. Von Scheller. 1964. Field observations on the response to attractants of bark beetles infesting southern pines. Contrib. Boyce Thompson Inst. 22: 461–470.

Wagner, T. L., R. O. Flamm, and R. N. Coulson. 1985. Strategies for cohabitation among the southern pine bark beetle species: comparisons of life-process biologies. USDA Forest Service. GTR SO-56: 87–101.

Waring, K. M., D. M. Reboletti, L. A. Mork, C. H. Huang, R. W. Hofstetter, A. M. Garcia, P. Z. Fulé, and T. S. Davis. 2009. Modeling the impacts of two bark beetle species under a warming climate in the southwestern USA: ecological and economic consequences. Environ. Manage. 44: 824–835.

Werner, R. A. 1972. Response of the beetle, *Ips grandicollis,* to combinations of host and insect produced attractants. J. Insect Physiol. 18: 1403–1412.

Whitcomb, W. H. 1974. Natural populations of entomophagous arthropods and their effect on the agroecosystem, pp. 150–164. *In* Proceedings of the Summer Institute of Biological Control of Plant, Insects and Diseases. University Press of Mississippi, Jackson, MI.

White, R. A., Jr, M. Agosin, R. T. Franklin, and J. W. Webb. 1980. Bark beetle pheromones: evidence for physiological synthesis mechanisms and their ecological implications. Zeitschrift für Angewandte Entomologie, 90: 255–274.

Wingfield, M. J. 1986. Pathogenicity of *Leptographium procerum* and *L. terebrantis* on *Pinus stobus* seedlings and established trees. Eur J Forest Pathol. 16: 299–308.

Wood, S. L. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Nat. 23: 1–117.

Wood, S. L. 1982a. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph, pp. 159–167. Brigham Young University. United State of North America, Provo, UT.

Wood, D. L. 1982b. The role of pheromones, kairomones, an allomones in the host selection and colonization behavior of bark beetles. Annu. Rev. Entomol. 27: 411–446.

Woodring, J. P. 1966. North American Tyroglyphidae (Acari) III: the genus *Histiogaster*, with descriptions of four new species. Proceedings of Louisana Academy of Science. 29: 113–136.

Woodring, J. P., and J. C. Moser. 1970. Some anoetid mites associated with North American Scolytidae. Can. Entomol. 102: 1238–1257.

Yan, Z. L., J. H. Sun, O. Don, and Z. N. Zhang. 2005. The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. Biodivers. Conserv. 14: 1735–1760.

Zanzot, J. W., G. Matusick, and L. G. Eckhardt. 2010. Ecology of root-feeding beetles and their associated fungi on longleaf pine in Georgia. Environ. Entomol. 39: 415–423.

Zinkl, J. G., P. J. Shea, R. J. Nakamoto, and J. Callman. 1987. Brain cholinesterase activity of rainbow trout poisoned by carbaryl. Bull. Environ. Contam. Toxicol. 38: 29–35.

Zuñiga, G., R. Cisneros, J. L. Hayes, and J. Macias-Samano. 2002a. Karyology, geographic distribution, and origin of the Genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 95: 267–275.

Zuñiga, G., J. L. Hayes, J. C. Grégoire, and R. Cisneros. 2002b. Chromosome number in *Dendroctonus micans* and karyological divergence within the genus *Dendroctonus* (Coleoptera: Scolytidae). Can. Entomol. 134: 503–510.