Chapter 3
Ecology and Conservation of Passalidae

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Abstract Consisting of about 1000 species globally, beetles of the family Passalidae feed on decomposing wood in tropical and subtropical forests throughout the world. Passalids live in subsocial family groups within their galleries, characterized by overlapping generations, cooperative brood care, and a complex communication system involving stridulations. In what has been referred to as an "external rumen," larval passalids feed on the microbe-rich frass and finely chewed wood paste produced by the wood-feeding adults. Endosymbionts found within the guts of passalids include a variety of microbes, including nitrogen-fixing prokaryotes and yeasts that aid in the digestion of wood. In addition to wood consumption, passalids fragment large amounts of wood in the process of creating extensive tunnel systems and are, among saproxylic insects, perhaps rivaled only by termites in their importance to wood decomposition. Although a number of laboratory studies have measured the amount of wood processed by various passalid species, no attempt has been made to quantify their contributions to wood decomposition under natural conditions. Passalids, along with their many microbial and invertebrate associates, are of considerable conservation concern given high levels of endemism and flightlessness. Many species appear sensitive to forest loss and disturbance and they have been used as indicator taxa in the creation of protected natural areas.

3.1 Introduction

Passalidae is a mostly tropical scarabaeoid family of shiny black beetles ranging from about 1 to 8 cm in length (Fig. 3.1). The family consists of two subfamilies [Aulacocyclinae (old world, two tribes) and Passalinae (pantropical, five tribes)] and approximately 1000 species (Boucher 2005). Each of the seven tribes recognized by Boucher (2005) is restricted to a particular region of the world. Passalini and

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Fig. 3.1 Museum specimens representing <3% (28 spp.) of global passalid diversity: *Aceraius grandis* (Burmeister) (Taiwan) (28); *Chondrocephalus* sp. (Guatemala) (3); *Heliscus tropicus* (Percheron) (Mexico) (4); *H. yucatanus* (Bates) (Mexico) (5); *Leptaulax* sp. (Philippines) (6); *Odontotaenius disjunctus* (Illiger) (USA) (31); *Od. striatopunctatus* (Percheron) (Honduras) (9); *Oileus sargi* (Kaup) (Honduras) (8); *Passalus bucki* (Luederwaldt) (Trinidad) (7); *Pas. caelatus* (Erichson) (Panama) (24); *Pas. elfriedae* (Luederwaldt) (Trinidad) (25); *Pas. interstitialis* (Eschscholtz) (Guatemala) (12); *Pas. punctatostriatus* (Percheron) (Panama) (13); *Pas. punctiger* (LePeletier and Serville) (Mexico) (1,2,16); *Pas. spiniger* (Bates) (Panama) (17); *Paxillus borellii* (Pangella) (Brazil) (20,30); *Pax. camerani* (Pangella) (Peru) (11); *Pax. jamaicensis* (Hincks) (Jamaica) (18); *Pax. leachi* (MacLeay) (Mexico) (19); *Proculus goryi* (Melly) (Guatemala) (14); *Pr. mniszechi* Kaup (Honduras) (15); *Ptichopus angulatus* (Percheron) (Mexico) (26); *Publius crassus* (Smith) (S. America) (10); *Spurius bicornis* (Truqui) (Mexico) (23); *Verres corticola* (Truqui) (Costa Rica) (27); *V. deficiens* Kuwert (Costa Rica) (29); *V. furcilabris* (Eschscholtz) (Trinidad) (21); *V. hageni* (Kaup) (Costa Rica) (22)

Proculini are restricted to the Americas, Solenocyclini are found in Africa and Madagascar, Ceracupini are found in Asia, Aulacocyclini and Macrolinini occur throughout Southeast Asia and eastern Australia, and Leptaulacini are found throughout Southeast Asia (Boucher 2005). Passalid richness typically decreases with increasing latitude or elevation, with the family being most diverse in moist lowland tropical forests (Schuster 1978; Moreno-Fonseca and Amat-García 2016; Castillo and Reyes-Castillo 2003). The number of passalid species present varies widely among locations within the tropics, ranging from 1 to 22 in Central and South

America, for example (Castillo and Reyes-Castillo 2003). Passalids exhibit high levels of endemism, including giant flightless species restricted to tropical cloud forests (Schuster et al. 2003), those occurring only in Andean foothills (Fonseca and Reyes-Castillo 2004), and species found only on particular islands (Jimenez-Ferbans et al. 2015) or at locations that were once islands separated from the mainland (Schuster 1994). Howden (1977) found passalids in driftwood on beaches in Australia, demonstrating the potential to colonize islands, and one island species consists almost entirely of females and has been shown to reproduce parthenogenetically (Boucher et al. 2015). Although passalid diversity is highest in tropical forests, a number of species occur in temperate zones, and these are among the best-studied taxa. These include *Odontotaenius disjunctus* (Illiger) in North America (extending as far north as Canada), *Cylindrocaulus* spp. in Japan and Northern China (Kon et al. 1999; Mishima et al. 2016), *Leptaulax koreanus* Nomura in Korea (Kim and Kim 2014), and *Pharochilus politus* (Burmeister) in Tasmania (Dibb 1938).

While a few species are known from other habitats [e.g., leaf-cutter ant nests, termite colonies, caves containing colonies of fruit-eating oilbirds, in detritus among the roots of epiphytes or from the decomposing debris of non-woody plants (Schuster 1978)], most passalid species are saproxylic, spending their entire life cycle within or beneath decomposing wood. Unlike the incredible diversity in form and coloration exhibited by other saproxylic scarabaeoid families (e.g., Lucanidae, Scarabaeidae), the body shape of passalids varies remarkably little among species (Arrow 1950) (Fig. 3.1). Moreover, whereas the males of many saproxylic lucanid and scarab (e.g., Dynastinae and Cetoniinae) species are famous for their exaggerated armaments (e.g., mandibles and horns), sexual dimorphism is largely absent among passalids. This may be due in part to the fact that passalids remain within decomposing logs as adults where giant mandibles and horns would be a hindrance to movement. The absence of sexual dimorphism in passalids may also be related to their monogamy and sociality, i.e., living in small family groups characterized by overlapping generations, cooperative brood care, and a complex communication system involving various stridulations. Compared to the amount of attention researchers have paid to passalid sociality, the importance of these insects to wood decomposition remains a relatively neglected topic. This is unfortunate considering that, among saproxylic insects, passalids are probably exceeded only by termites in their importance to decomposition in tropical and subtropical forests. These and other aspects of passalid biology are reviewed below, followed by some considerations for conservation.

3.2 Ecology

3.2.1 Subsocial Behavior

Passalids live in subsocial family groups within tunnels they excavate in moderately decomposed wood. Tunnel systems, or galleries, which often exceed a meter in length (Gray 1946; Galindo-Cardona et al. 2007), are initiated by a single female or male which is later joined by a member of the opposite sex. Copulation typically occurs within the galleries (Castillo and Reyes-Castillo 2009) although exceptions have been documented, e.g., MacGown and MacGown (1996) observed nuptial flights of *O. disjunctus* in Mississippi. Passalids are monogamous after gallery establishment, and both sexes contribute to the creation of galleries. These efforts result in the production of large amounts of fragmented wood, some of which gets pushed out of the log near the tunnel entrance (Fig. 3.2d). Eggs are laid upon a nest of finely chewed wood within the galleries and the adults attend to them. Larvae eat wood that is shredded and chewed by the adults as well as the frass of mature adults. In what Mason and Odum (1969) referred to as an "external rumen," the gut microbes associated with frass, as well as with the finely chewed wood paste that is used to line the walls of the galleries (Castillo and Reyes-Castillo 2009), continue the process of digestion outside the body, ultimately producing a more nutritious resource than the wood itself (Schuster and Schuster 1997; Rodriguez and Zorrilla 1986; Larroche and Grimaud 1988). Coprophagy is not uncommon among invertebrates that feed on decomposing plant matter (Szlávecz and Pobozsny 1995) and appears to be particularly important to passalids. It has been shown that *O. disjunctus* individuals quickly lose weight or even die in the absence of frass, for example (Pearse et al. 1936; Mason and Odum 1969; Mishima et al. 2016). The parents of at least one species of passalid, *Cylindrocaulus patalis* (Lewis) of Japan, go so far as to provision their larvae with trophic eggs, i.e., nonviable eggs which are consumed by the larvae (Ento et al. 2008).

The parents and their teneral and mature adult offspring assist larvae in the creation of a pupal case, constructed out of frass and providing protection for the vulnerable pupal stage (Schuster and Schuster 1997). Weeks or months are needed for teneral adults to change from reddish brown to black and to become sexually mature (Schuster and Schuster 1997). At that point [and sometimes before, see Jackson et al. (2009)], they either migrate to initiate a new colony [usually nearby, see Galindo-Cardona et al. (2007)] or excavate galleries off those created by their parents (Schuster and Schuster 1997). Migration typically takes place during particular parts of the year (e.g., at the beginning of the wet season in tropical areas) and, depending on the species, can involve flying and/or walking (Schuster and Schuster 1997). Passalids are known to communicate through tactile, chemical, and acoustic cues (Castillo and Reyes-Castillo 2009). Both larvae and adults produce a variety of sounds through stridulation, but the sounds produced by adults are louder and known to vary depending on the behavioral context. Schuster (1983) reported that the sounds produced by adult passalids can be separated into seven basic structural types and exist in 13 different behavioral contexts. The same study showed *O. disjunctus* to produce 14 different sound signals depending on the situation, representing perhaps the most complex repertoire of acoustic signals produced by any arthropod.

Social behavior is not uncommon among saproxylic insects, as evidenced by the high number of eusocial (e.g., termites) and subsocial (e.g., *Cryptocercus*) wood-feeding cockroaches, the eusocial ambrosia beetle *Austroplatypus incompertus* (Schedl) (Kent and Simpson 1992), subsocial stag beetles (Mori and Chiba 2009),

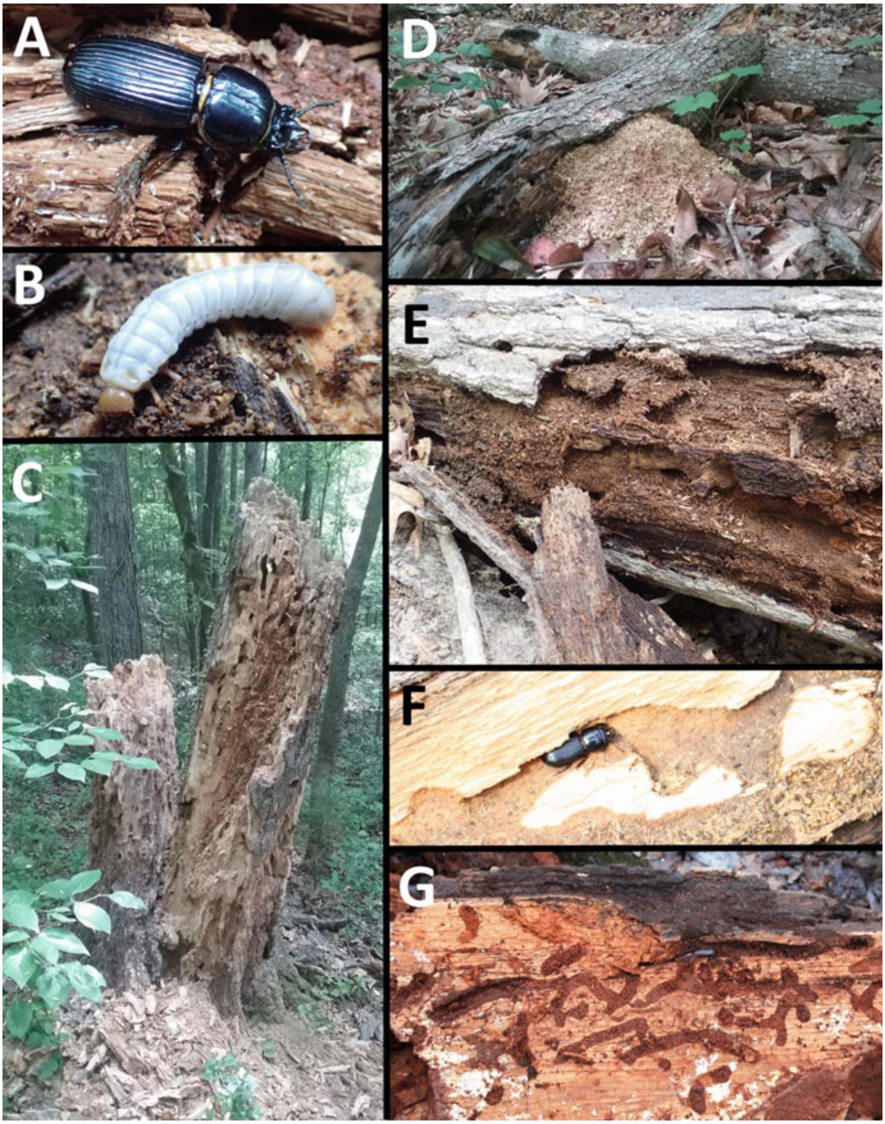

Fig. 3.2 *Odontotaenius disjunctus* in the southeastern United States: adult (**a**); third instar larvae (**b**); damage to standing trunk (**c**); pile of wood fragments near tunnel entrance (**d**); and galleries (**e–g**)

and a particularly interesting group of subsocial tenebrionids (*Phrenapates* spp.) which, as briefly discussed below, are in many ways similar to passalids (Nguyen et al. 2006). It is perhaps not surprising that a substrate as recalcitrant and nutritionally poor as wood would give rise to intraspecific cooperation in addition to the many examples of interspecific cooperation (e.g., endo- and ectosymbioses) documented among these insects. Just as N-fixing gut symbionts can greatly accelerate the development rates of their wood-feeding host insects (Ulyshen 2015), the parental care exhibited by passalids probably has similar benefits to the development of their offspring. Support for this comes from a study by Mori and Chiba (2009) who showed that a species of Asian lucanid, *Figulus binodulus* Waterhouse, develops more quickly when parents are present than when absent. The researchers concluded that improving food quality, e.g., by pulverizing wood, is the most likely mechanism by which *F. binodulus* parents improved juvenile growth. Moreover, passalids are known to develop more quickly than less social wood-feeding taxa. Whereas many lucanid species require one or more years to complete development, the larval period for passalids lasts for several months at the most (Mishima et al. 2016; Gray 1946; Castillo and Reyes-Castillo 2009). The passalid species with the shortest known larval period (approximately one month) is *Cylindrocaulus patalis* in Japan, a species that exhibits unusually high levels of parental care due to a parent/offspring ratio of 1:1 (Mishima et al. 2016).

The fact that passalids continue to feed on decomposing wood as adults, unlike most saproxylic scarabaeoids, may have set the stage for the development of subsocial behaviors by bringing adults and larvae into close contact (Schuster and Schuster 1997). Indeed, the wood-digesting gut symbionts passalid parents provide to their offspring in the form of frass appear to be of huge benefit to larval growth, and this may have selected for sociality. Evidence for the selective value of symbionts to larval wood-borer development comes from the existence of mycangia in female lucanids. These structures, which are absent in passalids and related groups, are thought to provide a mechanism (i.e., in the absence of gut symbionts since adult lucanids do not feed on wood) by which female lucanids can provide assistance to their larvae by inoculating oviposition sites with beneficial xylose-fermenting yeasts stored within their mycangia (Tanahashi et al. 2010). The subsocial behavior of another group of wood-boring beetles, Central and South American tenebrionids of the genus *Phrenapates*, is particularly informative given their similarity, in a number of respects, to passalids. *Phrenapates* not only look like passalids (so much so that they are often confused with them) but also live in subsocial groups within decomposing wood and have similar symbiotic relationships with xylose-fermenting yeasts (Nguyen et al. 2006). These similarities appear to reflect convergent solutions to the challenges facing wood-feeding insects, although it should be noted that sociality in *Phrenapates* remains poorly studied.

Other possible factors contributing to the emergence of sociality in passalids have received less attention, including the role adult passalids may play in protecting their offspring from predators as well as other passalids [i.e., adult passalids are known to cannibalize immature stages (Gray 1946)]. Alternative explanations for social behavior are worth further consideration given that some previous researchers have cast doubt on the idea that passalid larvae are closely attended to by their parents and adult siblings. Based on his observations in South America, for example, Heymons (1929) noted that parents and larvae are often widely separated within a gallery system, and the space between them is often clogged with wood fragments. The possibility that these piles of fragments may serve as fortifications against predators, similar to the fortifications termites construct using soil carried into logs, is deserving of investigation, as are the potential benefits parents provide in driving away predators. In North America, the tachinid *Zelia vertebrata* (Say), a generalist parasitoid of saproxylic beetle larvae, is one of the most important predators of *O. disjunctus*. It seems possible that walls of wood fragments, as well as the adults themselves, may provide a protective function against these and other natural enemies.

3.2.2 Endosymbionts

It has long been known that wood-feeding insects rely on a variety of symbiotic gut-dwelling microbes to aid in the digestion of wood and that many of them may gain more nourishment from these microbes than from the wood itself (Uvarov 1928). Although the gut-dwelling microbes of passalids have been studied for well over a century (Pearse et al. 1936; Leidy 1852; Lichtwardt et al. 1999), the biggest advances in understanding have been made in the past 10–20 years, and the findings from these more recent studies are briefly summarized here. It is clear that passalid guts house complex assemblages of microorganisms (including bacteria, Archaea, protists, nematodes, and various fungi) and that the composition of microbial communities varies among gut regions (Nardi et al. 2006). Ceja-Navarro et al. (2014), for example, reported significant compositional differences in bacteria and archaea communities among the four main gut regions (foregut, midgut, anterior hindgut, and posterior hindgut) of *O. disjunctus*, although the midgut and posterior hindgut communities did not differ from one another. Higher taxon richness was observed in the foregut and posterior hindgut than in the midgut or anterior hindgut. Moreover, aerobic bacteria were more abundant in the foregut and posterior hindguts, while anaerobic bacteria dominated the anterior hindgut and midgut. All gut regions contained an anaerobic core but also possessed radial gradients in oxygen concentration, indicating that aerobic and anaerobic metabolism occur within close proximity. Ceja-Navarro et al. (2014) also confirmed the presence of N-fixing prokaryotes (mainly *Bacteroidetes* spp., rather than the N-fixing spirochetes common in termites) in various gut regions of *O. disjunctus*, and these organisms are likely to contribute to the N economy of their hosts, as they do in so many other wood-feeding insects (Ulyshen 2015).

The first suspected endosymbionts reported from passalid guts were yeasts that Suh et al. (2003) found in consistent association with their hosts over a broad geographical area. Because some of the yeasts are known to ferment and assimilate xylose or hydrolyze xylan (major components of hemicellulose), they are suspected to play an important role in the digestion of wood within the passalid gut. More recently, Nguyen et al. (2006) showed that similar yeasts to those found in the guts of passalids can also be found in the guts of distantly related wood-boring beetles, such as *Phrenapates bennetti* Kirby, a tropical wood-feeding tenebrionid. Urbina et al. (2013) documented approximately 78 yeast species from 16 Guatemalan passalid species. Xylose- and cellobiose-fermenting yeasts belonging to *Scheffersomyces* and *Spathaspora* were the most abundant and consistently present clades reported in that study. In addition to their role in digesting wood, these yeasts have the potential to also benefit their hosts by providing certain essential amino acids, vitamins, and sterols or by detoxifying plant metabolites (Urbina et al. 2013). The importance of these and other gut-dwelling microbes to their hosts remains poorly understood, and the extent to which the growth of passalids is fueled by wood vs. microbial biomass remains an unanswered question. Mishima et al. (2016) recently argued that the Japanese passalid, *Cylindrocaulus patalis*, is primarily fungivorous because the activities of enzymes required to digest β-1,3-glucan (present in fungal cell walls) were much higher than those required to digest β-1,4-xylan (present in wood). Moreover, the researchers found much lower enzymatic activity in *C. patalis* larvae compared to adults.

3.2.3 Substrate Selection

Like many insects associated with wood at intermediate or late stages of decomposition, passalids are not very discriminating with respect to which wood species they utilize. The activities of most species are limited to angiosperms, however, with just a few known from pines or other conifers (Schuster 2008). In Puerto Rico, Galindo-Cardona et al. (2007) found *Spasalus crenatus* (MacLeay) in logs belonging to 18 (64%) of the 28 wood species sampled. Some wood species were less readily colonized than others, however, with the relatively soft wood of pioneer species being less preferred. Gray (1946) reported that *O. disjunctus* can be found using the logs or stumps of nearly all species of tree in North Carolina although only rarely pine and never cedar. Jackson et al. (2012) found the probability of *O. disjunctus* being present in logs to be higher for large logs compared to small logs as well as logs belonging to intermediate stages of decomposition and logs without heart rot. Moreover, *O. disjunctus* appears to strongly prefer white rot (Jackson et al. 2013). The extent to which these substrate associations hold true for other passalid species is not clear although many species exhibit preferences for particular microhabitats. For example, some species focus their activities beneath the bark, within the sapwood/heartwood or at the wood-soil interface (Kon and Johki 1987; Moreno-Fonseca and Amat-García 2016). Although the width/length ratio of passalid bodies is remarkably consistent across taxa (Fig. 3.1), species found primarily under bark tend to more dorsoventrally flattened than sapwood/heartwood feeders (Johki 1987; Lobo and Castillo 1997). Moreno-Fonseca and Amat-García (2016) also found differences in tibia morphology among different passalid guilds. Passalids are not limited to fallen logs but can also be found tunneling into standing deadwood (Fig. 3.2c). Working in Brazil at the end of the nineteenth century, Ohaus (1909) described the experience of witnessing a 20 m tall tree fall nearby. As it came crashing to the ground, it broke apart, revealing galleries extending along the entire length of the trunk and containing hundreds of passalids. Similarly, Schuster (1978) reported collecting a species of *Spasalus* at a height of 7 m in a standing trunk in Peru. *Odontotaenius disjunctus* has also been collected many meters above the ground (Schuster 1978) although Jackson et al. (2012) showed that the probability of standing deadwood being colonized by that species to be lower than that of downed wood.

Jackson et al. (2013) showed that the positive relationship observed between *O. disjunctus* density and log size (Jackson et al. 2012) is better explained by a preference for larger logs than by differences in habitat quality between large and small resources (i.e., beetle preference did not correspond with greater reproductive success). The possibility that large logs may result in higher lifetime fitness or allow for multiple generations by providing more stable habitats was not tested, however, and the researchers stopped short of suggesting that large-diameter logs have no special value to passalid conservation. Although little information has been published about the importance of large logs in providing long-term resources, Gray (1946) reported that an oak log approximately 1 m in diameter supported *O. disjunctus* for more than a decade in North Carolina. Jackson et al. (2013) also found that *O. disjunctus* preferred to colonize logs that already contained conspecifics (something they can detect from outside a log) even though this had short-term negative effects on reproductive success. Selecting logs that are already colonized may have benefits not measured in that study, however, including reduced search costs, increased mating opportunities, and reduced predation risk (Jackson et al. 2013). Although *O. disjunctus* is the only passalid species present throughout most of its range, it is not uncommon for multiple species to coexist within many tropical forests (Kattan et al. 2010) and as many as 5–10 species can be found residing within the same log (Castillo and Reyes-Castillo 2009; Luederwaldt 1931).

3.2.4 Succession

While relatively few studies have explored the succession of passalid species throughout the decomposition process, it is well established that species feeding beneath the bark are typically the first to colonize a dead log (often before the wood has begun to decompose). These species are characterized by rapid feeding and reproductive rates as well as strong dispersal abilities relative to those that feed on decomposing sapwood/heartwood (Castillo and Reyes-Castillo 2009). Castillo and Reyes-Castillo (2003) provide a table showing which species of passalids were present in logs belonging to four stages of decomposition in Mexico. While some species were found in all four decay classes, others showed a preference for those at early or late stages of decomposition.

3.2.5 Occupancy Rates

Early naturalists working in South America noted that dead tree trunks and branches are almost always occupied by passalids (Ohaus 1909). Only a few efforts have been made to carefully quantify this, however. In Chiapas, Mexico, passalids were found in 91% of logs examined by Morón et al. (1988). Galindo-Cardona et al. (2007) reported finding *Spasalus crenatus* (MacLeay) in 42% of sampled logs in Puerto Rico, with some wood species more likely to be occupied than others. Out of 248 decomposing logs examined in a primary Mexican rain forest, 64% were inhabited by one or more passalid species, with 13 species collected overall (Castillo and Reyes-Castillo 2009). A similar study carried out in a less pristine forest and pastureland in Brazil found 21.5% of all logs examined to have one or more passalid species, with a total of nine species detected overall (Castillo and Reyes-Castillo 2009). Castillo and Reyes-Castillo (2009) suggested that the differences in occupancy rates between these Mexican and Brazilian sites may indicate the negative effects of disturbance on passalid communities. In Colombia, Kattan et al. (2010) found passalids present within 36% of logs sampled in three forest types, but old-growth remnants appeared to have higher occupancy rates than Andean alder plantations or naturally regenerating forests. In Louisiana, Jackson et al. (2012) found 26% of hardwood logs ($\geq$5 cm in diameter and showing evidence of decay) were colonized by *O. disjunctus* and found the species in 73% and 95% of their 314 m^2 subplots and 1256 m^2 plots, respectively. In order of importance, Jackson et al. (2012) found the probability of occupancy in sampled log sections was higher when (1) logs were moderately decomposed, (2) logs were large, (3) the area did not experience flooding, (4) the surrounding 225 ha was more forested, (5) heartrot was absent, (6) ants were absent, (7) other wood borers were present, (8) there was less canopy cover, and (9) the piece of wood was downed and not standing.

3.2.6 Importance as Decomposers

Although passalids obviously play an important role in the physical degradation of wood (Morón 1985; Castillo and Reyes-Castillo 2003; Rodriguez and Zorrilla 1986) and are perhaps rivaled only by termites in their importance to wood decomposition in many tropical forests, their contributions to this process remain poorly quantified. With respect to insect-mediated decomposition, it is important to distinguish between the physical destruction (i.e., fragmentation or comminution) and chemical digestion of wood as these are two completely different processes. Only the latter qualifies as decomposition although comminution can indirectly accelerate decomposition by improving gas exchange and increasing the surface area of wood exposed to microbes (Ulyshen 2016). The extent to which wood-boring insects consume the wood they fragment varies greatly among species. Ambrosia beetles, for example, only fragment wood during the creation of the galleries within which they cultivate their symbiotic fungi. On the other end of the spectrum are wood-feeding termites which consume virtually all of the wood that they process and assimilate much of it with the help of endosymbionts. Passalids fall somewhere in between, fragmenting large amounts of wood and consuming some of it. Compared to the high assimilation efficiency exhibited by termites, wood passing through the gut of a passalid is not well digested. In fact, most of the chemical degradation of wood consumed by passalids occurs on the frass deposited by the beetles in their galleries [i.e., the external rumen as described by Mason and Odum (1969)]. The frass gets re-ingested multiple times and gets more digested and nutrient-enriched (Larroche and Grimaud 1988; Rodriguez and Zorrilla 1986) with each cycle. A full understanding of the role passalids play in wood decomposition will thus require information on how much wood is fragmented, how much of the fragmented wood is consumed, how thoroughly the consumed wood gets digested after multiple gut transits, etc. Another important question concerns how much faster (or slower) wood fragments created but not consumed by passalids decompose relative to intact wood.

The most straightforward way to assess the net effect of insects on wood decomposition is to compare differences in dry wood mass loss between logs from which the insects of interest have or have not been excluded [preferably under field conditions, as discussed below and described by Ulyshen et al. (2016)]. However, most past efforts to assess the role of passalids in wood decomposition have focused on measuring the amount of debris (including fragments and frass) produced per individual over a given unit of time. While such information provides a sense of how much wood is transformed by these insects, it is technically a measure of physical breakdown and should not be confused with decomposition. One of the earliest efforts to quantify the role of passalids as decomposers was a laboratory study by Preiss and Catts (1968). Although wood mass loss was not calculated in that study, the researchers found an oak log to be almost completely fragmented by seven adult *O. disjunctus* after a 30-week period. In another laboratory study, Rodriguez and Zorrilla (1986) similarly found *Passalus interstitialis* (Eschscholtz) fragmented 3–33% of wood weight within one month, with some wood species experiencing higher rates of fragmentation than others.

A study by Castillo and Morón (1992) yielded some of the best existing information about the importance of passalids to both the physical and chemical breakdown of wood. They investigated the rate at which ten species of passalids native to Mexico processed wood under laboratory conditions. Overall, the 110 beetles used in the study processed 43.6% of the dry wood weight provided. More than half (54.7%) of the processed wood (or 23.8% of the total wood provided) was converted to detritus. Although not explicitly stated in the article, the remaining 45.3% (or 19.8% of the total wood provided) was presumably respired or assimilated by the beetles (it is not possible to determine what fraction of this weight was due to decay fungi active in the wood vs. due to the passalids themselves, however). Overall, passalids in that study processed about 4.5 times their total body weight in wood although the relative rate of consumption (i.e., rate of immobilization/assimilation after correcting for differences in body mass) varied greatly among the ten passalid species studied. The relative rate of consumption decreased with increasing body weight and was highest for *P. interstitialis*, a species that feeds on the relatively nutritious (and perhaps more readily assimilated) wood just beneath the bark. Species that feed under the bark are also characterized by rapid population growth in order to make use of an ephemeral resource (Castillo and Reyes-Castillo 2009), and this might also explain their higher relative consumption rate. The researchers also observed strong differences in the amount of wood processed (fragmented) by the different passalid species and attributed these to differences in body size (i.e., large species create larger tunnel systems) as well as to uneven levels of acceptance among the species for the type of wood used in the experiment.

Most recently, Fonseca (2014) used similar methods to investigate the amount of wood processed by six species of Colombian passalids held under laboratory conditions. Closely matching the findings of Castillo and Morón (1992), detritus accounted for about 58%, on average (with a range of about 33–79% among the six species studied), of wood mass loss. As with the study by Castillo and Morón (1992), however, it is not possible to determine how much of the remaining wood loss was due to the activities of wood-rotting fungi vs. the beetles. Future studies addressing this question would benefit from the addition of a reference treatment as this would provide information on how much mass loss occurs in the absence of passalids. Inconsistent with the pattern reported by Castillo and Morón (1992), Fonseca (2014) found sapwood/heartwood feeders and generalists to exhibit higher relative consumption rates than species belonging to the under-bark feeding guild. It is clear from these and other studies that the degree to which passalids accelerate wood decomposition will ultimately depend on the species of passalid(s) present; wood characteristics such as density, nutritional content and other factors that vary among tree species; and abiotic conditions (Cano and Schuster 2012).

To my knowledge, no effort has been made to experimentally quantify the contributions of passalids to wood decomposition under natural conditions in the field. Such work would be of great value considering that laboratory studies are typically done under unnatural conditions including forced colonization by beetles (after removing them from active colonies located elsewhere), an absence of inter-specific interactions with other insects known to coexist with passalids in decomposing logs, and disturbed or unrealistic fungal communities. One of the biggest challenges to overcome in field-based insect exclusion studies is to avoid differences in microclimate (and therefore microbial activity) between treatments (Ulyshen and Wagner 2013; Kampichler and Bruckner 2009). Among several methods tested in Mississippi over a 10-year period, Ulyshen et al. (2016) found that pans with screened bottoms and open tops showed the most promise with respect to excluding termites without resulting in differences in microclimate between experimental logs protected or unprotected from termites. Although passalids were not included in that study, future studies could include holes along the sides of the pans to permit the natural colonization of “unprotected logs” by walking passalids. Pans without holes could serve as the “protected” treatment.

3.2.7 Interspecific Interactions

Many animals have been shown to opportunistically use the galleries created by passalids. Gray (1946), for example, reported a long list of invertebrates (including nematodes and earthworms) as well as various reptiles and amphibians found within *O. disjunctus* tunnels in North America. Some species appear to be strongly, if not entirely, dependent on passalids for food, shelter, or transportation. Examples include cockroaches (e.g., *Panchlora* in Mexico) that feed on detritus within passalid galleries in Central and South America (Castillo and Reyes-Castillo 2009; Ohaus 1909), ceratocanthids associated with passalid galleries in Southeast Asia and the Americas (Ballerio and Maruyama 2010; Ohaus 1909; Woodruff 1973), a scarab in West Africa (*Paraphytus aphodioides* Boucomont) that forms brood balls from a mixture of passalid frass and wood fragments (Cambefort and Walter 1985), and many species of mostly phoretic mites and pseudoscorpions (Ohaus 1909). Hunter (1993) reported 21 families, 68 genera, and over 200 species of mites known from passalid beetles, including 6 families found only in association with these insects. Although a few mite species associated with passalids are believed to be parasitic, most are believed to be commensal and phoretic, using their hosts as transportation to new habitats. Different phoretic mite species attach to different parts of the passalid body. The 16 mite species associated with *O. disjunctus* in North America, for example, can be distinguished between those that ride on external surfaces (e.g., gular region, frons, near the front coxae) vs. those that ride in protected body niches (e.g., antennal and maxillary sulci, between the pro- and mesothorax, under the elytra) (Hunter 1993). By contrast to that of *O. disjunctus*, the phoretic arthropod community associated with most passalid species remain mostly, if not entirely, unknown. This includes even some of the largest mites, as evidenced by the recent description of a giant (>5 mm) mesostigmatan mite from an Australian passalid (Seeman 2017). Moreover, only a few studies have investigated the habits of mites within passalid galleries (e.g., Butler and Hunter 1968).

Passalids commonly share logs with termites and ants throughout the tropics. In the Brazilian Amazon, for example, Fonseca (1988, see Table 2) reported that ants and/or termites were present in 86% of the logs containing passalids, with 54% of the logs containing all three taxa. Morón (1985) suggested there is intense competition for decomposing logs among termites, ants, and passalids in Mexican forests below 1000 m elevation and that the social insects tend to displace the beetles. Ants, in particular, are major predators of insects within deadwood and no doubt pose a serious threat to larval passalids. In Chiapas, Mexico, Morón et al. (1988) observed that ants commonly (in about 50% of the logs examined) colonize galleries excavated by passalids and other wood-boring beetles. They further noted that any larval or adult beetles present within these galleries were either killed by the ants or forced to leave. Consistent with this, Jackson et al. (2012) found the probability of a log section being occupied by *O. disjunctus* to be lower when ant colonies were present. The presence of subterranean termites (*Reticulitermes* spp.) was not important, however, Gray (1946) reported that adult *O. disjunctus* sometimes bite into

Reticulitermes galleries and will sometimes even eat termites they encounter but that *Reticulitermes* are only occasional and accidental inhabitants of passalid galleries.

Documented insect predators of passalid larvae include opportunistic predatory families like Reduviidae and generalist parasitoids like certain members of the fly family Tachinidae (Castillo and Reyes-Castillo 2003). In North America, Gray (1946) found *O. disjunctus* larvae to sometimes be parasitized at very high rates (up to 60% of third instar larvae, for example) by the tachinid *Zelia vertebrata*. It is possible that adult passalids can drive many potential predators out of their tunnels given the aggressive behaviors (e.g., biting and pushing) they exhibit toward conspecific intruders (Castillo and Reyes-Castillo 2009). According to Castillo and Reyes-Castillo (2009), predation of passalids by vertebrates is rarely seen but can include lizards and woodpeckers. Documented vertebrate predators of *O. disjunctus* include lizards, opossums, and bears (Brown 2004; Reynolds 1945; Vitt and Cooper 1985).

3.3 Conservation

3.3.1 Threatened Species

Many passalid species are inherently at risk due to small distributions, dependence on particular habitats, or an inability to fly, and this appears to be the case throughout the world, e.g., flightless species are known from all subfamilies (Hinks 1933). Restricted to the Americas and containing roughly 19 genera (Boucher 2005), the tribe Proculini (subfamily Passalinae) exhibits particularly high levels of endemism and flightlessness. This is especially true for species limited to cloud forests, including the genus *Proculus* which contain some of the largest passalid species in the world (Fig. 3.1). Schuster et al. (2003) concluded their revision of the genus with this warning: "In general *Proculus*, as well as other montane species of passalids, is probably in danger of extinction throughout its range due to the elimination of most of the forest where it occurs." *Odontotaenius* also exhibits high levels of endemism. For example, Schuster (1994) described a second species of North American *Odontotaenius*, *O. floridanus* Schuster, that is restricted to sandy ridges in Florida that were once islands separated from the mainland. The limited distribution of this species makes it potentially at risk from future landscape changes.

3.3.2 Sensitivity to Disturbance

Castillo and Lobo (2004) compared passalid diversity and community structure between primary and secondary (i.e., dominated by pioneer tree species) tropical forests in Mexico. There were no strong differences in the abundance or richness of passalids collected in the two forest types. Only one species, *Verres cavicollis* Bates, differed in abundance per log between forest types, being more abundant in the secondary forest. Two of the least common species were only captured in old-growth forests, however. Although these findings suggest that passalids are not very sensitive to forest disturbance, not enough information was provided about the secondary forest to fully interpret these results. It is not clear if the logs sampled in the secondary forest originated from that or the previous forest, for example. More recently, Kattan et al. (2010) compared passalid communities among native Andean alder (*Alnus acuminata* Kunth) plantations planted as part of a restoration effort, naturally regenerating forests and old-growth forests in the Colombian Andes. The two secondary forest types were planted approximately 40 years before sampling took place on land formerly used for cattle ranching. The old-growth and naturally regenerating forests had more than twice the wood volume as the alder plantations and old-growth forests had more passalid individuals overall and per cubic meter of wood sampled than the other two forest types. Of the six species collected, one was found only in the regenerating forest, and two were only found in the old-growth forest. In India, Sarasija et al. (2012) reported that passalids were more common in natural forests containing moist logs at advanced stages of decay than in teak plantations.

Jackson et al. (2009) found walking *O. disjunctus* to be reluctant to venture into open habitats in Louisiana, suggesting a low likelihood of movement among forest fragments. Because *O. disjunctus* is abundant throughout much of its range and is often present within isolated forest fragments, the researchers predicted that the species may fly, rather than walk, between patches of forests. Although *O. disjunctus* is typically observed walking (Jackson et al. 2009), so much so that Gray (1946) suggested the species was incapable of flight, the observation of 12–15 individuals flying approximately 30 m from the nearest forest edge at dusk in Mississippi (MacGown and MacGown 1996) supports the idea that occasional flight events may be important to the dispersal of the species. Other species of passalids are truly flightless, however, and may benefit from wooded corridors connecting separate patches of forest.

3.3.3 Utility as Indicator Taxa

Because they are relatively well described compared to many other tropical insect taxa, exhibit high levels of endemism, and can be sampled quickly at any time of the year, passalids have been used in prioritizing areas for conservation in some countries. In Guatemala, for example, passalids were used as indicator organisms to justify the creation of the Sierra de las Minas Biosphere Reserve (Schuster et al. 2000). Schuster et al. (2000) developed a method to identify Guatemalan cloud forests in the greatest need for protection based on data collected for 66 species of passalids (e.g., richness, endemism, similarity among guilds) and forest conditions. Support for the use of passalids as indicator taxa in Guatemala comes from the fact that their endemism patterns are similar to those of other animals, e.g., scarab beetles, salamanders, and small mammals (Cano and Schuster 2009).

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