From Symbionts to Societies: How Wood Resources Have Shaped Insect Sociality

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Sociality has independently arisen in several wood-dwelling insect lineages, yet little is understood about how the properties of decaying logs have favored the evolution of cooperative social groups. Here we evaluate the current literature on wood-dwelling social insects to identify the structural, nutritional, and microbial properties of decaying logs that have led to the repeated evolution of social behavior. Wood-tissue is structural resilient, and thus provided an enclosed, defensible nest site for early wood-feeding insect groups. This structural stability enabled the long-term persistence of family groups, and was likely a key feature in the transition toward more complex eusocial societies. The resilient structure and relatively poor nutritional quality of wood also likely provided a stable environment for the evolution of complex mutualisms with prokaryote and fungal symbionts to digest this resource. Parental care likely evolved as a means to protect the valuable nest site and ensure adequate nutrition for offspring in this environment by allowing parents to both provision and transfer microbial symbionts to offspring. Pathogenic microbes are also abundant in nests constructed in wood-tissue, and social adaptations such as allogrooming and nest maintenance may have evolved in response to microbial invaders. In general, the dynamic relationships between insects, microbes, and the wood-tissue that they inhabit was a critical component in the evolution of sociality in this habitat.

Keywords: social evolution, social insects, log decomposition, saproxylic, microbial community, symbionts

INTRODUCTION

Of William D. Hamilton's many notable contributions to evolutionary biology, his most significant work was his formalized theory of kin selection (Hamilton, 1964). This theory provided an explanation for the evolution of altruism that was consistent with individual selection by demonstrating that helpers could produce copies of their own alleles by assisting non-descendent

kin (Hamilton, 1964). In addition to investigating the genetic processes of altruistic evolution, William D. Hamilton was also fascinated by the ecological conditions that facilitated the evolution of complex insect societies. In his lesser known 1978 paper, "Funeral Feasts: Evolution and Diversity Under Bark," Hamilton noted the peculiar diversity of social insects inhabiting decaying logs (Hamilton, 1978). He recognized that while close relatedness was essential to the evolution of worker altruism, these early social groups were more likely to arise in certain habitats. He suggested that decaying logs, due to their protective, long lasting properties, provided the ideal environment for the early evolution of highly altruistic eusocial societies, such as those of ants and termites.

Since Hamilton's observations nearly 40 years ago, much has been revealed about the intricacies of insect sociality under bark. New social wood-dwelling insects have been discovered (Kent and Simpson, 1992), fascinating details of different insect societies have been described (Biedermann and Taborsky, 2011; Smith et al., 2018), and the mechanisms driving the evolution of sociality in these environments are continuing to be explored (Thorne and Traniello, 2003; Inward et al., 2007; Korb et al., 2012; Nuotclà et al., 2019). We draw upon this growing literature to investigate the factors that have contributed to the diversity of insect societies inhabiting decaying logs within the context of William D. Hamilton's pioneering work.

FAMILY AND GROUP FORMATION IN DECAYING LOGS

The evolution of complex sociality can be broken into three major phases: the onset of group formation (initially through extended parental care), maintenance of social groups, and the subsequent transition to complex, obligate social-living (Bourke, 2011; Korb and Heinze, 2016). Family groups consisting of parents and offspring are considered a critical prerequisite for the transition to more complex eusocial societies, and are generally more common in social log-dwelling lineages than aggregations of unrelated individuals (**Table 1**; Kent and Simpson, 1992; Inward et al., 2007; Nalepa et al., 2008; Biedermann and Taborsky, 2011; Suzuki, 2013; but see Zorapterans, Mashimo et al., 2014). Indeed, the two instances of eusociality that have arisen in wood-dwelling insect lineages evolved from ancestral family groups (ambrosia beetles, Smith et al., 2018; termites, Klass et al., 2008). Identifying the properties of the decaying log habitat that favored the evolution and maintenance of parent-offspring groups is thus key to understanding the prevalence of sociality in log-dwelling insects.

The selective pressures that favor the transition to cooperative societies from simple family groups in any environment can generally be classified as either benefits associated with staying in the natal nest or costs associated with dispersal (Koenig et al., 1992; Emlen, 1994). The benefits of remaining in family groups in log-dwelling lineages can generally be classified as structural, nutritional, or microbial benefits that the log resource provides to offspring that delay dispersal from the nest (**Table 2** and **Figure 1**). Logs provide a safe, sheltered, food-abundant

nesting resource for retained offspring, allowing for prolonged parent-offspring interactions that set the stage for the subsequent evolution of more complex social behaviors. Dispersal costs can also be extremely high in wood-dwelling insects, drastically reducing the likelihood of independent establishment for those that disperse from the natal nest. Competition for log resources is fierce and some termite species experience a <1% success rate in establishing a new nest site following dispersal (Chouvenc, 2019). Below we discuss these specific attributes of wood environments that have shaped sociality in log-dwelling lineages in more detail.

STRUCTURAL RESILIENCE OF NEST SITES CONSTRUCTED IN WOOD TISSUE

Wood tissue is a stable, long-lasting resource that provides both food and protection for nests constructed within. When used as a food source, decaying logs serve as plentiful bonanza resources, reducing competition among group members and favoring family group formation by limiting within-group conflict (Korb and Heinze, 2016). Wood-tissue, particularly large tree trunks, degrades slowly and is structurally resilient, allowing insect families to persist for several generations before the resource is depleted (Nalepa and Bell, 1997; Thorne, 1997; Korb et al., 2012). Both wood-dwelling passalid beetles and ambrosia beetles form families in which the social group and the nest persist well after offspring mature into adults (Schuster and Schuster, 1997; Biedermann and Taborsky, 2011). In both systems, young adults have been observed helping to care for younger siblings, highlighting the importance of prolonged family cohesion in the evolution of cooperation (Schuster and Schuster, 1985; Biedermann and Taborsky, 2011).

Structural stability also ensures that the nest site remains intact even after the death of a parent, providing offspring that remain in the nest the opportunity to inherit the breeding resource. For instance, competition between colonies for nesting resources in *Microcerotermes papuanas*, an extant termite species that forms colonies in a single log resource ("one-piece" nesting; Abe, 1987), often results in the death of one or more primary reproductive individuals in the colony (Thorne and Traniello, 2003). Young workers in these colonies can molt into reproductive adults and begin to reproduce in the nest via parthenogenesis to fill this breeding vacancy (Roisin, 1990; Fougeyrollas et al., 2017). Indeed, the likelihood of inheriting a breeding position within the natal colony is actually higher than that of successfully dispersing and establishing a nest in a new log for some lower termite species (Korb and Schneider, 2007; Korb and Heinze, 2016).

Nesting in log resources also provided early social lineages with valuable, defensible nest sites, facilitating the evolution of eusociality via a "fortress defender" route (Queller and Strassmann, 1998). In contrast to eusocial "life insurers" in which workers specialized into a foraging caste, fortress defenders, such as deadwood termites, favored soldier castes to defend the nest site against competitors (Queller and Strassmann, 1998). Low establishment success, high competition, and high value of the log resource resulting from its function as both food and shelter

TABLE 1 | Summary of the ecology and life history of the social and gregarious wood-dwelling insects.

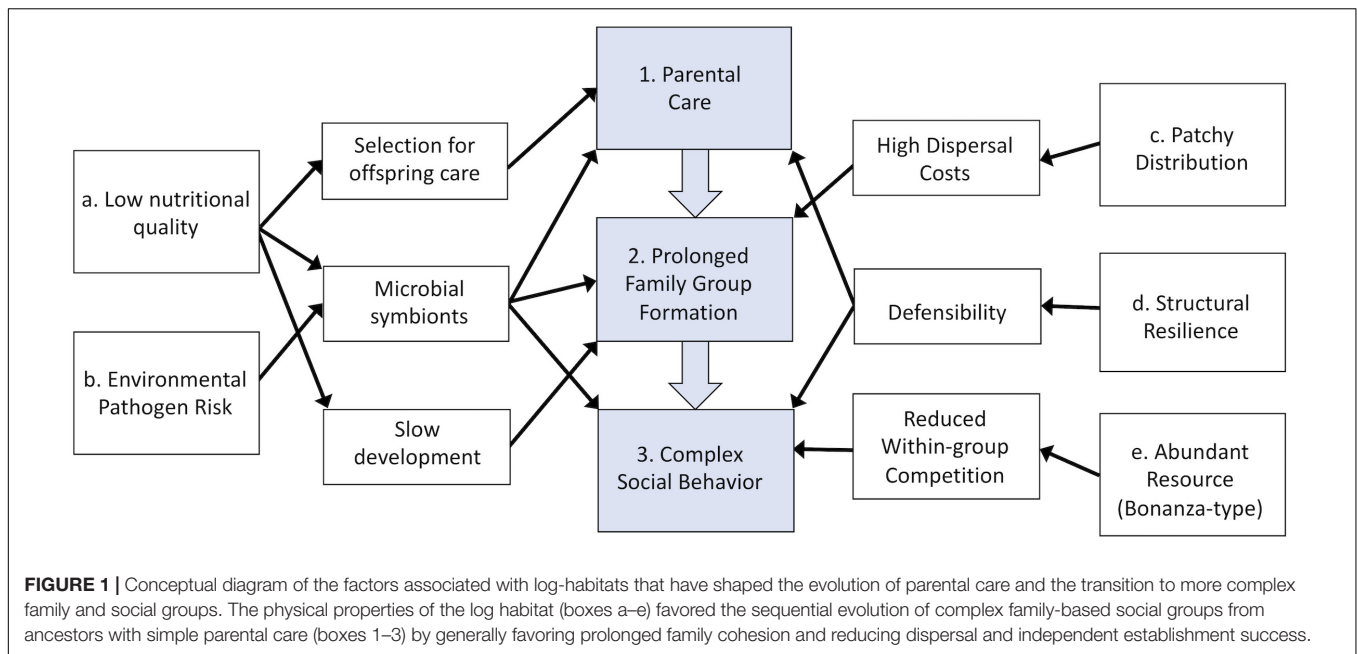| Group	Social system(s)	General ecology	References
Blattodea: Cryptocercidae and Blaberidae	Subsociality with biparental care.	Live and feed on wood in decaying logs and both parents provision dependent offspring, often for several years in some species.	Nalepa and Bell, 1997; Nalepa et al., 2008; Nalepa and Arellano, 2016
Isoptera	Eusociality with biparental care in initial stages, then cooperative care.	Derived from social wood-feeding cockroach ancestors likely similar to *Cryptocercus*. All contemporary lineages are eusocial and many still primarily live in wood-tissue. Colonies are founded by a breeding pair and are assisted by both male and female workers, and have a highly diverse hindgut microbiome that aids in wood digestion.	Abe, 1987; Thorne, 1997; Klass et al., 2008; Korb et al., 2012
Coleoptera: Passalidae	Subsociality with biparental care; Cooperative brood care.	Nest sites initiated in decaying logs by both parents who provision, defend, and construct pupal cases for offspring. Adult offspring and parents remain in contact for weeks or months, and may cooperate in brood care during this time.	Schuster and Schuster, 1985, 1997; Ento et al., 2008; Dillard, 2017
Coleoptera: Curculionidae	Eusociality, Subsociality with either maternal or biparental care, Cooperative brood care.	Highly variable life history, but in general nests are constructed in living or recently dead tree trunks by a single female or a female joined by a male. Adult female offspring may remain in the colony to provide care for younger siblings in cooperatively breeding *Xyleborus* species and the eusocial *Austroplatupus incompertus*.	Kent and Simpson, 1992; Biedermann and Taborsky, 2011; Biedermann et al., 2011; Baruch et al., 2017; Smith et al., 2018
Coleoptera: Tenebrionidae (*Phrenapates bennetti*)	Subsociality with biparental care	Subsocial behavior and ecology appears similar to that of passalids and involves prolonged parent-offspring interactions in heavily decayed log habitats.	Nguyen et al., 2006

TABLE 2 | Properties of wood tissue that may have facilitated the evolution of parental care and cooperative societies in wood-dwelling insects.

Property	Relevance to the evolution of insect sociality
Structural resilience	Wood tissue is structurally stable, allowing for prolonged cohesion of family groups and overlapping generations.
Defensibility	Nests constructed in wood tissue are generally high value due to the processing investment, and may promote the evolution of social defense behaviors.
Dispersal costs	Leaving the safety of a log in search of new nesting resource is risky, and the probability of surviving dispersal and finding a suitable log to colonize are very low for many insects.
Poor nutritional quality	Wood tissue is nutritionally poor, providing selection for parental provisioning or resource processing for young.
Microbial symbionts	Microbial symbionts are required to digest nutrient poor wood, and the need to transmit these microbes to subsequent generations may favor prolonged family interactions.
Microbial defense	Nests in wood tissue are sensitive to growth of pathogenic microbes, providing selection for social microbial defenses such as allogrooming or egg grooming.
Resource modification	The physical and chemical properties of wood allow social insects that nest in this resource to drastically alter their chemical, microbial, and physical environment to meet the needs of the colony.

makes this habitat particularly amenable to the evolution of fortress defense eusociality.

SOCIALITY AND SYMBIONTS: ADAPTATIONS TO POOR NUTRITIVE QUALITY OF WOOD

Although wood is abundant and long-lasting in large tree trunks, most of the nutrients contained in wood tissue are not accessible to the digestive systems of animals (but see Tokuda et al., 2004), and feeding on this resource could select for a variety of social adaptations to overcome this limitation. Wood is generally nitrogen-poor and difficult to digest due to its high cellulose and lignin content (Tallamy and Wood, 1986). Generally, feeding on resources that are low quality can result in slower development of young, ultimately increasing the amount of time during which offspring are dependent on parental care (Beehler, 1985; Strahl, 1988; Nalepa and Bell, 1997; Nalepa and Arellano, 2016). In some wood-feeding taxa, juveniles that do not possess the enzymes or symbionts necessary to digest wood depend on parents to process the wood resource for them (King and Fashing, 2007; Mishima et al., 2016). Parental care in these systems may thus primarily function as a means to provide offspring with adequate nutrition. The evolution of both parents assisting in brood care (which has occurred in passalids, cockroaches, and termites) may have arisen to meet the high nutritional needs of the brood, with

FIGURE 1 | Conceptual diagram of the factors associated with log-habitats that have shaped the evolution of parental care and the transition to more complex family and social groups. The physical properties of the log habitat (boxes a–e) favored the sequential evolution of complex family-based social groups from ancestors with simple parental care (boxes 1–3) by generally favoring prolonged family cohesion and reducing dispersal and independent establishment success.

increasing parental care setting the stage for the co-evolution of even more dependent (altricial) young (Nalepa et al., 2008). The nutritional deficiencies of wood may therefore have been a major determinant of the subsequent evolution of complex cooperation by initiating the evolution of extreme offspring dependency through parent-offspring feedback selection (Nalepa et al., 2001, 2008). Increased offspring altriciality likely then increased the benefits of offspring care, providing selection for the evolution of even more complex social traits, including cooperative breeding and eventually eusociality.

SYMBIONT TRANSMISSION BETWEEN PARENTS AND OFFSPRING

To subsist on the generally nutrient-poor wood tissue, wood-feeding insects have evolved complex symbiotic relationships with bacteria and fungi that allow them to extract nutrients from these largely indigestible resources (Nalepa et al., 2001; Suh et al., 2003; Biedermann et al., 2009; Mishima et al., 2016). Although these microbial symbionts allow their insect partners to thrive in the nutrient-poor wood tissue environment, maintaining the integrity of the microbial communities and transmitting them to subsequent generations can be challenging.

Intraspecific coprophagy (feces ingestion) and anal trophallaxis were key adaptations allowing for the transfer of beneficial microbial communities from parents to offspring. In the *Cryptocercus* cockroaches and termites, the need to share symbionts between parents and offspring was likely a major driver of prolonged parental care (Nalepa et al., 2001). Juveniles are fed microbe-rich secretions produced by their parents via anal trophallaxis to initiate and maintain their own hindgut community of wood-digesting microbial symbionts (Thorne, 1997; Klass et al., 2008). This mode of direct

transfer rendered these microbes dependent on their hosts, and contributed to the strong mutualism observed between host and symbiont observed in both cockroaches and termites (Nalepa et al., 2001; Nalepa, 2017). Passalids, in contrast, share symbionts with offspring via ingestion of feces (coprophagy) and processed wood in the nest (Suh et al., 2003; Mishima et al., 2016). *Phrenapates bennetti*, a tenebrionid that strongly resembles passalids in morphology, life history, and subsocial behavior, also uses similar xylose fermenting yeasts (Nguyen et al., 2006). Although little is known about the social behavior of *Phrenapates*, given their convergent evolution with the passalids it is possible that they transfer symbiotic yeasts from parents to young via coprophagy as well, with subsociality potentially arising as a consequence.

Other wood-dwelling lineages, including the Xyleborine and Platypodine ambrosia beetles, feed on fungus that they cultivate in tree trunks rather than on the wood tissue itself (Kent and Simpson, 1992; Biedermann and Taborsky, 2011). Xyleborine ambrosia beetle females disperse as young adults to initiate their own colonies, and solve the transmission problem by carrying "starter" cultures from their natal nest that they store in either the gut or fungal storage organs called mycangia prior to dispersal (Batra, 1963; Biedermann et al., 2009; Seibold et al., 2019). As with the other microbial-dependent, wood-feeding insects, this form of symbiont transmission requires prolonged interaction between parents and offspring in the natal nest.

Interestingly, not all insects that breed in wood that rely on symbionts to aid in digestion live socially. Females of many stag beetle species, for instance, do not remain with their offspring after oviposition, although they appear to inoculate the oviposition site with xylose-fermenting yeasts from a fungal storage structure (mycangium) before departing to transmit the symbionts to their young (Tanahashi et al., 2009, 2010). Stag beetles only consume decaying wood as

larvae, however, and this difference in feeding modes between adult and neonates may partly explain how they have adapted to transmit endosymbionts to young without prolonged parent-offspring associations (Tanahashi et al., 2009, 2010). In contrast, all of the social wood-dwelling insects that feed on wood or microbes cultivated in wood do so as both adults and larvae (Nalepa and Bell, 1997; Schuster and Schuster, 1997; Thorne, 1997; Biedermann et al., 2011). Remaining in the log nest to feed as adults may have been an important pre-requisite in the evolution of parental care as well as more complex social behaviors. Further research comparing the ecological, physiological, and microbial differences between wood-feeding insects that transmit symbionts to offspring socially to those that can do so without prolonged parent-offspring contact may reveal valuable insight into the predisposing factors that have promoted sociality in certain wood-feeding insect groups.

MICROBIAL DEFENSE AGAINST PATHOGENS IN SOCIAL GROUPS

Although wood tissue is amenable to the growth and maintenance of beneficial microbes, these environments also provide suitable habitat for growth of harmful or pathogenic microbes. These challenges might be exacerbated for lineages that facilitate the growth of beneficial microbes in the nest site (Nuotclà et al., 2019). Many wood-feeding insects have evolved social defenses against these deleterious microbes such as corpse management (López-Riquelme and Fanjul-Moles, 2013; Sun and Zhou, 2013; Sun et al., 2018), allogrooming (Rosengaus et al., 1998; Wilson-Rich et al., 2009; Meunier, 2015), and chemical defenses (Biedermann and Rohlfs, 2017). While many of these social adaptations most likely arose after the onset of group-living, they suggest ways that living in resources like wood could provide feedback selection on incipient social groups, reinforcing and elaborating social traits. Female ambrosia beetles of the species *Xyleborinus saxesenii*, for instance, delay dispersal for longer periods of time when their nests have been infected with *Aspergillus* spores (Nuotclà et al., 2019). Infection of ambrosia beetle nests with *Aspergillus* also leads to greater expression of allogrooming and corpse maintenance behavior, providing evidence that social behavior can be enhanced when microbial defense is needed. The gut symbionts of dampwood termites (*Zootermopsis nevadensis*) also have been shown to have anti-pathogen properties. In addition to their digestive function, the intestinal microorganisms of these dampwood termites increase intestinal acetate which has inhibitory effects on the opportunistic pathogen *Serratia marcescens* (Inagaki and Matsuura, 2018).

DYNAMIC STRUCTURE OF DECOMPOSING LOG RESOURCES

Feeding within decaying logs either on the wood tissue itself or on the microbes cultivated in the nest site results in complex, dynamic resource properties. First, by boring into the wood, insects increase both the surface area and physical heterogeneity of the resource, allowing wood-degrading microbes (i.e., bacteria, protists, and fungi) to more readily colonize the resource (Ulyshen, 2016). Many insects alter the wood via physical processing, chemical additives, and inoculation of beneficial microbes to either enhance the quality of the wood (external rumination; Suh et al., 2003) or to cultivate food resources (fungal farming; Batra, 1963; Biedermann et al., 2009). Insect tunneling also leads to better aeration and fragmentation of the wood, improving habitat quality for both the insects and microbes (Ulyshen, 2016). This fragmentation, however, may reduce the structural integrity of the resource over time, causing the wood to collapse or the bark to slough off. Log degradation from colonization, which can be rapid when colonized by large or efficient social insects such as the passalids or termites, respectively, may thus reduce the total lifespan of the colony resource. Each log likely has a carrying capacity that varies not only with the abiotic conditions of the surrounding habitat, but also the use and transformation by the inhabiting insects through activities such as tunneling, enhancing, and cultivating the resource. This eventual degradation of the log resource by wood-feeding insects is perhaps one reason why the most complex termite societies evolved following the transition from log-nesting to inhabiting more permanent, self-constructed nest sites (Korb et al., 2012).

SOCIAL INSECT AND MICROBIAL COMMUNITY ECOLOGY IN DECAYING LOGS

Microbial communities of logs and other large and recalcitrant wood debris are complex and not well understood (see review by Johnston et al., 2016). However, they are known to be mediated by organisms that have evolved to either consume the organic matter directly or use it as a relatively stable habitat (e.g., compared to carrion or leaf litter) for breeding or nest establishment (Ulyshen, 2016). Habitat stability has been proposed to provide the circumstances for positive evolutionary feedback between insect sociality and microbial community management (Biedermann and Rohlfs, 2017). However, as wood becomes more fragmented either through abiotic damage (e.g., wind, damage by falling, and rain) and insect tunneling activities (e.g., ambrosia beetles), the area available for microbial colonization increases (Ulyshen, 2016), suggesting that the importance of microbes to wood inhabiting insects becomes increasingly relevant during later decomposition. For many wood feeding insects, such as some Passalidae, those microbes likely make up a considerable portion of their nutritional needs (Castillo and Reyes-Castillo, 2009; Filipiak, 2018). Thus, the microbial communities and how they change during the long course of wood debris decomposition are thought to play at least a nutritional role in the ecology of wood feeding insects. There is also evidence of additional relationships between microbes and wood feeding insects, especially within the

context of co-evolution of endosymbionts (Suh and Blackwell, 2005; Nardi et al., 2006; Warnecke et al., 2007; Ulyshen, 2016) and fungal ectosymbiosis (Krivosheina, 1991; Mueller et al., 2005; Biedermann and Vega, 2020).

CONCLUSION AND FUTURE DIRECTIONS

Some of the most complex, cooperative insect societies have arisen from ancestors that lived and fed in the wood tissue of large trees (Kent and Simpson, 1992; Klass et al., 2008). William D. Hamilton largely attributed this occurrence to the structural longevity of wood tissue, and the defensibility of nest sites constructed within (Hamilton, 1978). Newer discoveries reveal a critical role of both symbiotic and pathogenic microbes in the evolution and maintenance of parental care and sociality in wood-dwelling lineages (Biedermann and Rohlfs, 2017; Nuotclà et al., 2019). Parental care and other forms of sociality afforded these insects the means to provide adequate nutrition of young through provisioning and symbiont transfer and to defend their nest sites from biological threats (microbial and otherwise). The structural longevity of large tree trunks likely allowed these small family groups to persist for multiple generations, facilitating the transition from subsociality to eusociality in some lineages.

Despite this developing framework, much still remains to be understood about the nuanced interactions between social insects and their microbial and physical environment. Not all wood-dwelling insects have evolved social behavior to better exploit wood-tissue, and identifying the fundamental similarities and differences between the non-social and social wood-dwelling species may provide insight into the factors critical to the evolution of sociality in wood (Tanahashi et al., 2009, 2010). For instance, the microbial communities employed by different species to aid in wood digestion may differ drastically between social and non-social species, and the properties of these microbial symbionts may have been a critical factor determining whether or not a lineage became social. Fundamental differences in life history may also distinguish social from solitary wood-feeding insects, including adult feeding behavior. Further investigations into the coevolution between microbes and the behavior of their insect hosts will likely yield tremendous insight into the ways that microbes have contributed to the evolution of insect societies.

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