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Synergies Between Division of Labor and Gut Microbiomes of Social Insects

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Social insects maximize resource acquisition and allocation through division of labor and associations with microbial symbionts. Colonies divide labor among castes and subcastes, where the plasticity of caste roles decreases in clades with higher social grades. Recent studies indicate that specific castes may also foster distinct gut microbiomes, suggesting synergies between division of labor and symbiosis. The social organization of a colony potentially partitions evolutionary persistent microbial partners to optimize symbioses and complement division of labor. However, research in this area has received limited attention. To elucidate if a structured microbiota is adaptive, we present three testable predictions to address consistent community structure, beneficial functions, and selection for microbiota that support caste roles. First, we posit that social insect groups spanning lower to higher social grades exhibit increasingly distinct caste microbiomes, suggesting that structured microbiomes may have evolved in parallel to social complexity. Second, we contend that the development of these microbiomes during colony maturation may clarify the extent to which they support division of labor. Third, we predict that mature social insect colonies with the most extreme division of labor demonstrate the strongest distinctions between caste microbiomes, carrying the greatest promise of insight into microbiome composition and function. Ultimately, we hypothesize that caste-specific microbiomes may enhance symbiotic benefits and the efficiency of division of labor, consequently maximizing fitness.

Keywords: symbiosis, division of labor, gut microbiome, major evolutionary transition, superorganism

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INTRODUCTION

Organisms are selected to optimize resource use through their own actions and interactions, in turn maximizing reproductive success. Ants, termites, and the social bees and wasps compose more than half of the biomass of land-dwelling insects (Hölldobler and Wilson, 2009) and have comprehensive ecological impacts as pollinators, predators, herbivores, and decomposers (Bignell and Eggleton, 2000; Richter, 2000; Aizen et al., 2008; Del Toro et al., 2012). Their success has, in

part, been attributed to their division of labor (Oster and Wilson, 1978), where castes within the colony optimally divide tasks and thus improve the efficiency by which resources are amassed, distributed, and utilized (Anderson and Ratnieks, 1999; Duarte et al., 2011).

Microbial gut symbionts augment social insect metabolism and defense, further allowing the colonies to monopolize various resources. Termites digest recalcitrant plant substrates with obligate gut symbionts that degrade lignocellulose and upgrade dietary nitrogen (Cleveland, 1923; Brune, 2014). Social corbiculate bees host bacterial communities that aid in nutrient acquisition from pollen (Kwong and Moran, 2016; Kesnerova et al., 2017; Zheng et al., 2017). Herbivorous ants maintain gut bacteria that offset host dietary and metabolic limitations through amino acid supplementation, nitrogen recycling, and catabolism of glucose and citrate (Russell et al., 2009; Hu et al., 2018; Sapountzis et al., 2018). Gut microbes also contribute to disease defense in bees and termites by imparting pathogen colonization resistance (Koch and Schmid-Hempel, 2011; Peterson and Scharf, 2016; Raymann et al., 2017; Inagaki and Matsuura, 2018), further enabling host persistence and resource acquisition across environments.

The colony gut microbiota may be organized and optimized to complement division of labor, with castes partitioning the gut microbiota to support specialized roles. This could potentially enhance symbiont productivity to meet host needs and increase the efficiency of division of labor. A partitioned microbiota may incur a selective benefit if it improves resource acquisition and allocation. To begin to assess this hypothesis, we review division of labor in the social insects, known gut microbiota compositional differences between castes and subcastes, and the role of social interactions in influencing persistent gut microbiota. We then discuss three future avenues of research that may allow insights into putative interfaces between social organization and microbiomes: (1) structure and function of colony microbiomes across social insects that vary in social complexity, (2) development of caste microbiomes during colony maturation, and (3) caste-specific gut microbiomes within colonies with the most extreme division of labor.

DIVISION OF LABOR IS A CORNERSTONE IN SOCIAL INSECT BIOLOGY

Colony-level social complexity of social insect species is dictated by division of labor between worker and reproductive castes. Workers perform non-reproductive tasks such as brood care, defense, and foraging while the reproductive caste comprises one or a few individuals that secure colony fecundity. Variation in the degree of this division of labor can be interpreted along an evolutionary gradient of increasing social complexity and decreasing individual-level reproductive plasticity (Taylor et al., 2019) (**Figure 1**). In the most derived social insects, workers are morphologically precluded from attaining a reproductive role, resulting in strong suppression of inter-caste reproductive conflict (Boomsma and Gawne, 2018).

Morphological reproductive-worker differentiation and repression of conflict between interdependent castes represent a major evolutionary transition to higher complexity (Maynard Smith and Szathmáry, 1995; West et al., 2015). This transition aligns the fitness interests of all colony members, with selection acting more on the colony than on individual colony members. The developmentally irreversible distinction between worker and reproductive castes makes their division of labor comparable to that of the germline and soma, and they consequently have come to be regarded as superorganisms (Wheeler, 1911; Boomsma and Gawne, 2018).

The division of non-reproductive labor among workers also becomes more specialized along the sociality gradient (**Figure 1**). A variety of temporal, physical, and spatial factors may direct division of non-reproductive labor (Duarte et al., 2011). Temporal subcastes, with workers transitioning from tasks within to outside the nest as they age (e.g., nurse bees transitioning to foragers), and physical subcastes with morphological distinctions exhibiting task specialization (e.g., minor and major workers and soldiers), are commonly identified across social insects (Oster and Wilson, 1978) (**Figure 1**). Superorganismal clades exhibit the highest degree of specialization among workers, where their cohesive actions constitute colony-level adaptations for resource acquisition, comparable to the specialized functions of somatic tissues in a multicellular organism (Wheeler, 1911; Boomsma and Gawne, 2018).

CURRENT KNOWLEDGE ON CASTE-DISTINCT GUT MICROBIOMES

Microbial symbioses and division of labor are well-known to enhance resource acquisition, but few studies have compared gut microbiomes of castes and subcastes (**Figure 1**). In some social insect clades, the reproductive caste microbiome is distinct and drastically simplified compared to that of the worker caste. Foraging lower termite reproductives generally lack symbiotic protists that dominate the worker guts (Shimada et al., 2013; Inagaki and Matsuura, 2016), and the reproductive caste of Termitidae termites shows reduced diversity and disparate bacterial community composition (Otani et al., 2019) compared to the worker caste (Dietrich et al., 2014; Otani et al., 2014, 2016, 2019). Honey bee queens also host a simplified bacterial community that is significantly reduced compared to workers (Kapheim et al., 2015; Tarpy et al., 2015; Anderson et al., 2018). Albeit limited, data on the gut microbiomes of ants suggest some differences between reproductive and workers (Johansson et al., 2013; Brown and Wernegreen, 2016). The gut microbiomes of social wasps remain understudied, although some clades appear to retain consistent gut microbes (Stefanini et al., 2012, 2016; Gruber et al., 2019; Suenami et al., 2019).

Differences between worker subcastes have almost exclusively been explored in termites and bees. Studies suggest that the gut microbiome composition of worker bees varies with age and could be task-dependent, although patterns inferred are

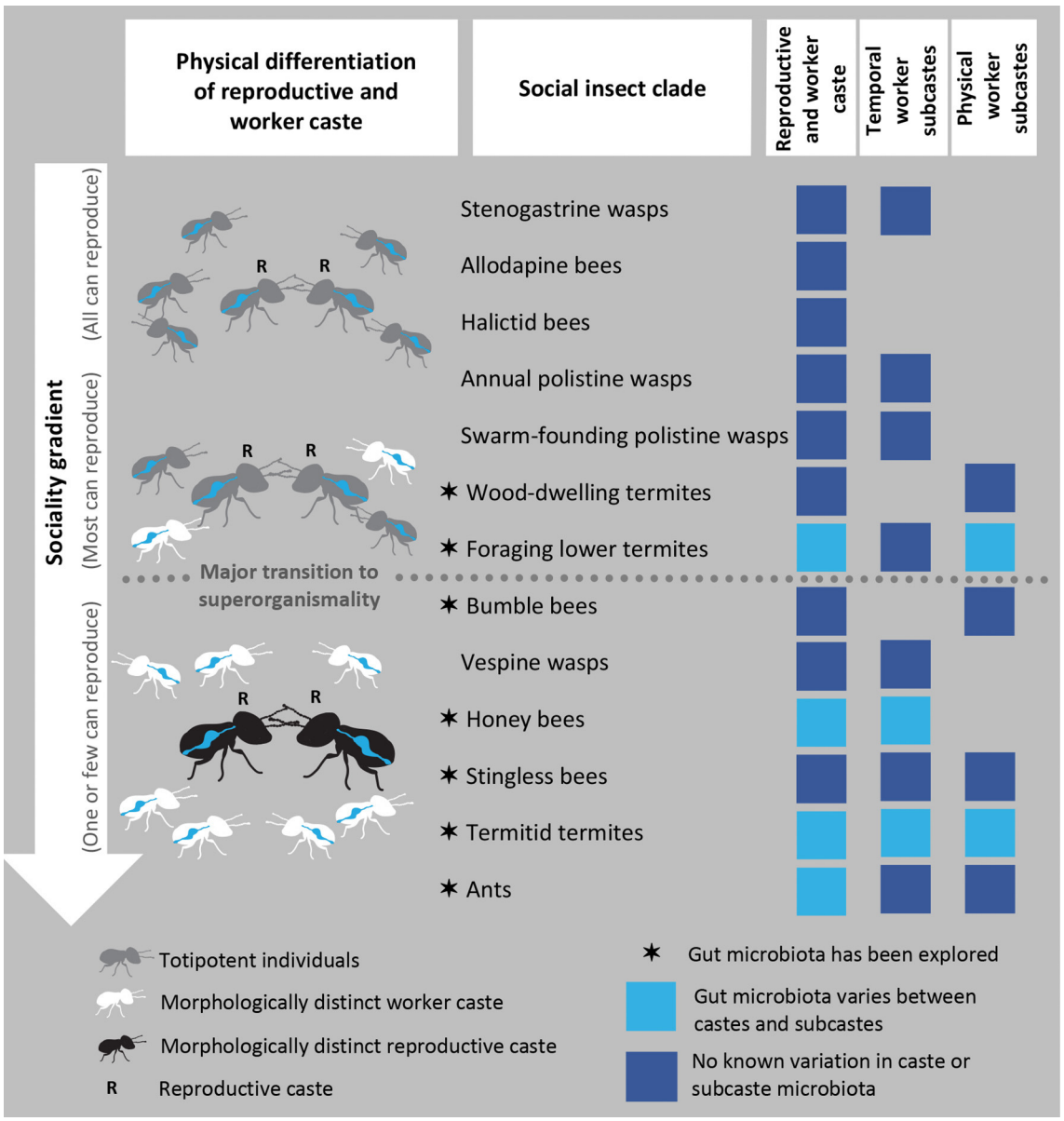


FIGURE 1 | The sociality gradient and gut microbial symbionts of social insects. The sociality gradient is illustrated by the greyscale changes in the insects, indicative of reductions in individual reproductive plasticity. The gradient begins with colonies where totipotent workers help reproductives through adulthood, to which subsocial family life is a critical evolutionary precursor and culminates in superorganismal colonies with morphologically distinct castes. The position of clades along the gradient is adapted from Boomsma and Gawne (2018). Clades for which the gut microbiota has been explored are marked with a star, while evidence or lack thereof on distinct (sub)caste microbiomes is represented by light and dark blue squares, respectively. The first column of boxes illustrates that all clades divide reproductive labor between the reproductive and worker caste. The second and third columns signify if members of the clade have specialized division of non-reproductive labor among temporal and physical worker subcastes (temporal: bees, Seeley, 1982; Wille, 1983; termites, Watson and Sewell, 1985; ants, Hölldobler and Wilson, 1990; physical: bees, Goulson et al., 2002; Spaethe and Weidenmüller, 2002; Evans, 2006; wasps, Jandt and Toth, 2015; Li et al., 2015; Du et al., 2017; Grüter et al., 2017; termites, Korb and Thorne, 2017).

subtle (Guo et al., 2015; Anderson et al., 2018; Jones et al., 2018). Similarly, the fungus-farming subfamily of the Termitidae exhibits differences in gut bacterial composition related to food-processing by temporal subcastes (Hinze et al., 2002; Hongoh et al., 2006; Li et al., 2015, 2016). Termites also present differences among physical subcastes, where soldier microbiomes can be distinct from other subcastes (Hongoh et al., 2006; Shimada et al., 2013; Inagaki and Matsuura, 2016; Otani et al., 2019, but see Berlanga et al., 2011), and in highly polymorphic termites, such as the genus *Macrotermes*, minor and major workers and soldiers display variable microbiomes (Hongoh et al., 2006; Schnorr et al., 2019).

SOCIALITY SUPPORTS PERSISTENT SYMBIOTIC GUT MICROBIOTA

For an individual insect, the repeated remodeling of the gut and shedding of the microbiota throughout development can impede extracellular gut symbionts from persisting within individuals and over generations (Engel and Moran, 2013). Group living overcomes this challenge by providing access to microbiota through social interactions (Troyer, 1984; Nalepa et al., 2001; Lombardo, 2008; Engel and Moran, 2013).

Microbiota characteristic of natal social insect colonies have been suggested to be transmitted by reproductives in colonies founded independently (Benjamino and Graf, 2016; Meirelles et al., 2016; Stefanini et al., 2016; Diouf et al., 2018), or by workers and reproductives (Kwong et al., 2014) in colonies that are founded dependently, such as honey bees and army ants. Workers within colonies then stabilize the gut microbiota through intracolonial transfer of symbionts; newly-eclosed microbe-free workers typically receive inocula from mature workers through fecal-oral transmission (Wheeler, 1984; Ohkuma and Brune, 2010; Powell et al., 2014; Lanan et al., 2016). Additional oral exchanges, interactions, and the shared nest environment and resources facilitate continuous microbiota transmission and homogenization between colony members (Martinson et al., 2012; Stefanini et al., 2012; Powell et al., 2014; Zhukova et al., 2017). The reliable transmission of gut microbes between and within colonies thus allows transgenerational persistence of microbial communities.

Host transmission of heritable extracellular symbionts has been hypothesized to result in long-term associations between some social insects and specialized microbiota. Termites, social corbiculate bees, and clades of ants consistently host microbial phylotypes over evolutionary timescales, as indicated by patterns of phylogenetic congruence of microbial communities with hosts (Russell et al., 2009; Dietrich et al., 2014; Sanders et al., 2014; Kwong et al., 2017; Lukasik et al., 2017; Bourguignon et al., 2018; Sapountzis et al., 2019). Although this indicates vertical transmission across generations, most symbioses are characterized by the presence of at least some degree of host switching, suggesting that horizontal transmission persists across host clades (Koch et al., 2013; Sanders et al., 2014; Kwong et al., 2017; Bourguignon et al., 2018). Nevertheless, the extensive evolutionary histories of hosts and symbionts are presumably facilitated by social interactions and insect physiological or morphological characteristics that promote specific microbial partners (c.f. Kwong and Moran, 2015; Lanan et al., 2016; Sapountzis et al., 2019).

DISCUSSION

Is the Colony Gut Microbiota Optimized Through Social Organization?

We hypothesize that hosts may organize and optimize the gut microbiota among colony members to increase the benefits of symbioses and social organization. Consistent caste-specific differences in honey bee and termite microbiomes suggest that microbial community compositions have been selected over evolutionary time to align with caste roles. If these caste-specific microbiomes enhance productivity of symbioses and efficacy of division of labor, they may be selected for as an emergent property of the combined effects of division of caste and microbiome labor.

Hosts are under strong selection to promote a beneficial microbiota; particularly in semi-closed systems like the gut (Foster et al., 2017). While microbes may compete within the gut ecosystem, potentially reducing symbiont expression of cooperative traits, hosts wrangle microbiota into stable and productive communities (Frank, 1996; Coyte et al., 2015). Hosts may shape microbiomes through mechanisms that regulate the immigration of microbes, support specific microbial community members through immune, physiological or dietary responses, and compartmentalize microbial communities (Frank, 1996; Foster et al., 2017), which in the social insects can occur both at the level of individuals and the colony. This could increase the net benefit of symbioses because optimization of microbiomes within specific castes may promote a simplified microbiota to meet distinct needs, enhancing the productivity of individual communities, while the colony-level conglomerate remains diverse.

Conclusions about optimization of symbiotic communities require elucidation of their compositions, functions, and impacts on host reproductive success. Since some microbes within a community could be driven by diet, gut morphology and physiochemistry, social interactions, or environmental exposure without further implications to the host, we propose three necessary levels of evidence to elucidate symbiotic benefit: (a) identification of consistent microbial communities within clades and castes, (b) characterization of conserved functions and benefits to hosts, and (c) determination of how hosts select for microbial community compositions and functions. With these needs in mind, we propose three focal areas that we believe can provide insight into the implications of structured colony microbiomes.

Caste Microbiomes Along the Sociality Gradient

The distinctiveness of caste microbiomes should predictably increase along the sociality gradient. In lower social grades, all colony members remain totipotent and typically undergo physical remodeling when transitioning to a different caste (Roisin, 1990; Sumner et al., 2010), which may prevent strong specialization of their gut microbiota. In contrast, early developmental determination of committed castes may fine-tune the composition of microbial communities over their lifetime to meet divergent needs, resulting in distinct microbiota structure, and function. Termites and wasps are promising models to test this prediction as they have representative clades across the sociality gradient (**Figure 1**).

Social structure constrains the level of adaptation and thus the potential disparity in caste and subcaste microbiota. In social grades that have not undergone the major transition to superorganismality, the distinct microbiomes may represent

individual-level adaptations, and host interests in direct fitness benefits may limit specialization (Boomsma and Gawne, 2018; Cooper and West, 2018). After the major transition, however, workers can only improve their reproductive success through indirect fitness benefits gained at the colony level; thus, the colony acts as a fitness maximizing agent that can develop group-level adaptations (Gardner and Grafen, 2009), such as distinct caste and subcaste microbiota that optimize resource use and maximize colony fitness.

Colony and Microbiota Development

The microbiomes of organisms are characterized by shifts associated with changing physiology and needs over the lifetime of the individual, and social insect colonies likely undergo comparable processes, from founding (possibly excluding taxa with dependent founding) through growth and development to maturity (left part of **Figure 2**). If caste specificities in microbiomes play important roles for colony reproductive success, the characterization of their development over colony maturation, during which caste roles are established and maintained, may allow us to corroborate functional predictions aligned with the division of labor.

As colonies grow, workers liberate reproductives from non-reproductive tasks, and both worker and reproductive castes become increasingly specialized (Wheeler, 1911; Oster and Wilson, 1978). Similarly, we predict that the structure and function of worker and reproductive gut microbiomes diverge during colony growth (**Figure 2**). The gut microbiomes of termite reproductives indicate a transition from diverse to simplified communities from founding to maturity (Shimada et al., 2013; Benjamino and Graf, 2016; Inagaki and Matsuura, 2016; Diouf et al., 2018; Otani et al., 2019) (**Figure 2**), which has been suggested to be a consequence of specialization on reproduction and dependence on workers (Chouvenc and Su, 2017). Similarly, the gut microbiome of honey bee queens exhibits slight changes with age (Tarpy et al., 2015; Anderson et al., 2018), suggesting that physiological and dietary changes related to reproductive specialization and duration may influence gradual shifts the reproductive microbiota. Additionally, as the number of workers increases, temporal and physical subcastes may develop unique microbiota, where age-dependent tasks, environments, and diets could influence microbial community composition. Exploration of changes in host characteristics and microbiota during colony development could thus clarify mechanisms of selection and caste complementarity, while examining changes in the functional microbiome and its influence on colony growth may elucidate how a divided microbiome supports colony maturation and the accretion of fitness benefits. Secondarily, the significance of independent or dependent colony founding should explored, as it independent founding may cause a microbial bottleneck that reduces both the stability and diversity

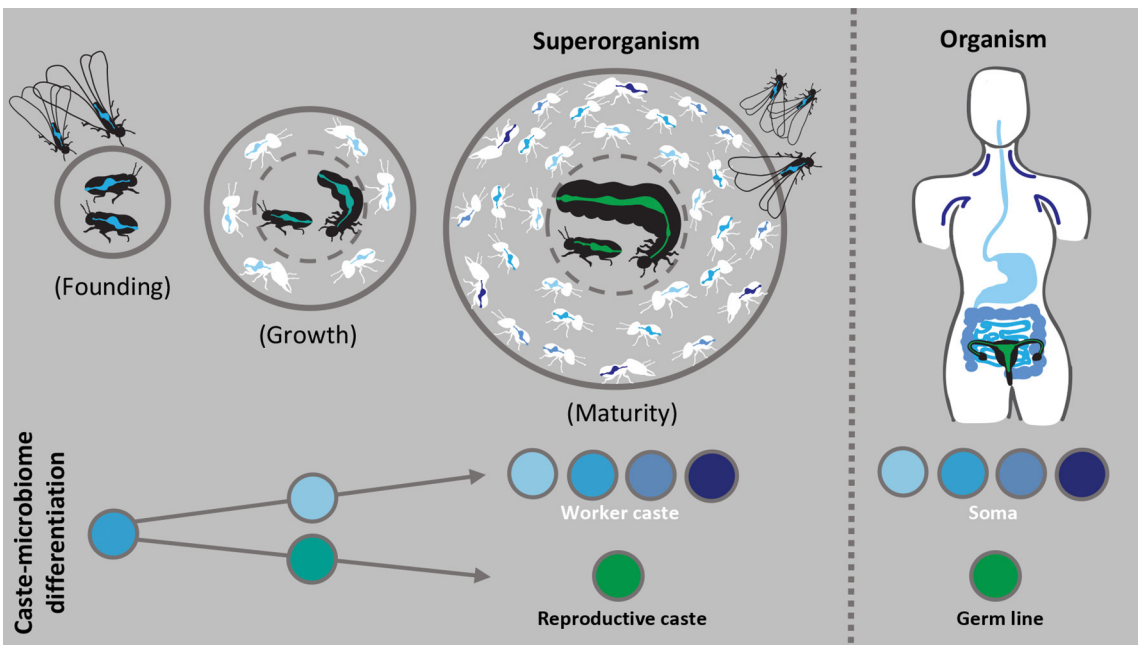


FIGURE 2 | Caste-specific microbiomes during growth and maturity of the superorganism. The left panel illustrates how gut microbiomes (spectrum of blue to green) of the reproductive (black) and worker caste (white) may structurally and functionally differentiate during the development of an independently founded colony. Such colonies undergo ergonomic growth before reaching maturity, during which caste roles establish and gut microbiota may similarly diverge. Reproductive gut microbiota (green) likely simplifies in structure and function while worker microbiota (blue) remains relatively diverse and may be partitioned among subcastes. The right panel proposes that the general structure and function of the superorganism microbiota could be analogous to that of multicellular organisms, in this case microbiota of human tissues. The major transition to superorganismality causes selection to act on the colony as a unit, similar to an individual organism, and the binary distinction between the worker and reproductive caste is comparable to the soma and germ line. Greater understanding of the cohesive actions carried out by the divisible units of superorganisms and their microbial partners may allow us to derive novel insights into higher-level emergent characteristics typically associated with and observed in organisms.

of the colony gut microbiome (Kwong et al., 2017; Lukasik et al., 2017). Consistent with our previous inferences, we expect that insights into these processes can be achieved through comparative analyses of social insects across the spectrum of social organization.

The Structured Gut Microbiota of the Superorganism

We contend that the tightest associations and most distinct caste-specific microbiomes will be in clades with extreme and irreversible division of labor, the superorganisms. In particular, social insects such as honey bees, certain ants and the Termitidae may provide the greatest insights because the complex division of non-reproductive labor supports remarkable fecundity of reproductives (Winston, 1991; Kaib et al., 2001; Hölldobler and Wilson, 2009). A simple reproductive gut microbiota may be influenced by traits of the individual, such as their unique diet, typically consisting of buccal secretions from workers (Noirot, 1969; Haydak, 1979), and limited exposure to environmental microbes (Cremer et al., 2018; Stroeymeyt et al., 2018), thus, reducing microbial immigration. The reproductive microbiome then likely supports specific metabolic demands, critical disease defense, or increased longevity, while most other colony functions are outsourced to workers and their microbiomes (**Figure 2**).

Complexity in the worker gut microbiota is likely driven by variable host tasks, diets, and interactions. Immigration of microbiota into the worker gut is controlled during post-eclosion microbial inoculation (Ohkuma and Brune, 2010; Powell et al., 2014; Lanan et al., 2016) and remodeling of gut morphology (Zhukova et al., 2017). Changes in host diet and physiology, such as the differential diet and gut enzyme expression of honey bee workers with age (Crailsheim et al., 1992), may influence the gut microbiota. Subcaste microbiota could additionally be influenced by interaction and transmission networks, resulting in compartmentalization. Notably, since the majority of microbiota studies utilize 16S rRNA profiling, it is likely that compositional differences at the bacterial strain level have been overlooked (Engel et al., 2014; Ellegaard and Engel, 2016), as indicated by compartmentalization of strains between individual honey bees and variable functional gene content across age groups (Ellegaard and Engel, 2019). Compartmentalization among subcastes would conceivably allow microbes to cater to specific host roles, create adaptive heterogeneity (Masuda et al., 2015; Kennedy et al., 2017), and reduce the potential for competition between symbionts (Frank, 1996). Consequently, the various roles and interactions of worker (sub)caste(s) should promote functionally diverse microbiomes that hosts optimally divide to complement tasks.

A superorganism's highly structured colony microbiome, shaped by distinct (sub)caste communities, may be adaptive to the colony as a unit, similar to the composite of different microbiomes observed in tissues or body regions of multicellular organisms such as humans (The Human Microbiome Consotrium, 2012) (**Figure 2**). The major evolutionary transition to superorganismal social complexity shifts selection to act more strongly at the colony-level, similar to selection on multicellular organisms, and the coherent actions of morphologically committed reproductive and non-reproductive (sub)castes is comparable to the division of cells into germ and soma (Wheeler, 1911; Boomsma and Gawne, 2018). The analogous organization of the two systems allows comparisons and insights into higher-level characteristics typically associated with and observed in organisms (Helanterä, 2016; Kennedy et al., 2017), which could include the structure and function of the microbiome (**Figure 2**). For example, the significance of microbial partners in the framework of social immunity, another emergent property enabled by social structure (Cremer et al., 2007, 2018), may be compared to the interplay between microbiota and the human immune system (Hooper et al., 2012). We believe that considering this analogy in future research will help improve our fundamental understanding of the impact of symbioses on individuals, (sub)castes and superorganismal division of labor.

CONCLUSION

Current research on social insect symbioses focuses on microbiome function and the importance of social life in maintaining a consistent microbiota. However, we have yet to fully integrate these paradigms. The division of labor, which directs social roles and interactions, may secondarily partition the microbiota, shaping caste-specific microbiomes that dually enhance productivity of symbioses and efficiency of castes. While individual and colony-level mechanisms may drive distinctions in gut microbiota, microbial interactions within these communities should be examined to fully understand structured microbiota as a potential adaptation. Overall, we contend that integration of gut symbionts into the framework of sociality defined by division of labor may elucidate its potential adaptive value to individual insects and the colony as a whole.

AUTHOR CONTRIBUTIONS

VS, JR-H, and MP conceived the ideas. VS drafted the first version of text and figures. VS, JR-H, BT, KE, PS, MV-C, and MP contributed with expertise, input, and edits throughout the remainder of the text.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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