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Nutritional Symbiosis Between Ants and Their Symbiotic Microbes

Yi Hu[1] and Corrie S. Moreau[2,*]

[1]Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing, China

[2]Department of Entomology and Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, USA; email: corrie.moreau@cornell.edu

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*Corresponding author

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Keywords

Formicidae, social insects, nutrition, microorganisms, microbiota, gut microbes, microbiome

Abstract

Nutritional symbioses with microorganisms have profoundly shaped the evolutionary success of ants, enabling them to overcome dietary limitations and thrive across diverse ecological niches and trophic levels. These interactions are particularly crucial for ants with specialized diets, where microbial symbionts compensate for dietary imbalances by contributing to nitrogen metabolism, vitamin supplementation, and the catabolism of plant fibers and proteins. This review synthesizes recent advances in our understanding of ant–microbe symbioses, focusing on diversity, functional roles in host nutrition, and mechanisms of transmission of symbiotic microorganisms. Despite progress, most research has concentrated on a few ant genera, and further exploration of microbial roles in different ant morphs and life stages and across various ant species is needed. Expanding research to include a broader array of ant lineages and integrating genomic data with additional experimental data will provide deeper insights into the metabolic strategies that facilitate ant success across diverse ecological habitats.

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1. INTRODUCTION

Ants are among the most diverse and evolutionarily successful animal groups on Earth (50). They play a crucial role in terrestrial ecosystems due to their significant biomass and abundance. They are involved in essential ecological processes such as soil turnover, nutrient cycling, and the creation of microhabitats that support diverse organisms (13, 20, 59). Over their nearly 140-million-year evolutionary history of expanding into global terrestrial ecosystems, many ant species have leveraged symbiotic partnerships with organisms such as hemipterans and plants to colonize previously uninhabitable ecological niches (40, 43, 54). In recent years, with the rapid advancement of sequencing technologies, it has become clear that symbiotic microorganisms also play a crucial role in many vital activities of ants, including nutrient assimilation, chemical defenses, and cuticle formation (3, 4, 18, 25, 45). These microorganisms are integral to understanding the ecological and evolutionary processes of ants. Therefore, studying ant symbiotic microorganisms provides valuable insights into the mechanisms and patterns underlying ant species diversity and success.

Previous reviews on ant-associated microbes have summarized the diversity and distribution of microorganisms across the ants (36, 46). Since then, with the widespread application of high-throughput sequencing, there has been a notable surge in research focused on ant-associated microbiomes, enhancing our understanding of the diversity and, more importantly, the functional roles of ant-associated bacterial communities. Scientists have uncovered a hidden diversity of microbial symbionts in these nonmodel organisms by deeply sequencing these communities (4, 8, 17, 21, 25, 28, 32, 41, 42, 45, 47, 52). Beyond the utilization of culture-independent techniques, advances in culturing ant-associated bacteria strains have facilitated complete genome sequencing to capture their genomic architecture and functional assays to validate the roles of specific microbes experimentally (2, 3, 25). It has become evident that a few ant lineages, particularly those with specialized diets, depend more on persistent and vertically transmitted bacterial communities, while other lineages lack consistent or functional bacterial associations (1, 36, 46, 47). This difference suggests a possible role of symbiotic bacteria in helping ant hosts manage nutritionally imbalanced diets. This review delves into the nutritional symbiosis between ants and their microbes, exploring how ants at various trophic levels depend on nutritional supplementation from these host-associated microbiomes. It covers the types of symbiotic microorganisms involved, their roles in nutrient acquisition, and the mechanisms by which these nutritional symbionts are transmitted.

2. NUTRITIONAL INTERACTIONS ARE FREQUENTLY OBSERVED IN ANTS WITH SPECIALIZED DIETARY NICHES

2.1. Nutritional Supplementation in Herbivorous Ants at Low Trophic Levels

Across the tree of life, microbial symbionts play a crucial role in enabling organisms to exploit new energy sources and access otherwise unattainable nutrients (34). Insects, being the most diverse and abundant group among animals, have particularly benefited from these symbiotic relationships (57). Nutritional symbioses have been increasingly recognized as a key factor that allowed insects to thrive on specialized diets deficient in essential nutrients, such as plant sap, blood, and wood. These symbiotic partnerships have also opened up new nutritional niches, significantly contributing to the remarkable diversification of insects (10, 14).

As a remarkably ecologically successful insect group, ants have a history that dates back approximately 140 million years (37, 38). Recent research suggests that ants likely codiversified with angiosperms, which offered new ecological niches, such as forest litter and arboreal nesting sites, as well as additional plant-based resources (38–40). This codiversification led to a significant evolutionary shift in ants, with many lineages transitioning from their carnivorous ancestors to

herbivorous diets at least 11 times independently (40). They feed mainly on different plant-based resources, such as the extrafloral nectaries of plants, the honeydew of hemipterans, pollen, and fungi.

Like other herbivores, herbivorous ants face a significant nutritional challenge due to the limited availability of nitrogen in their diet (9, 11). Recent studies using high-throughput sequencing and functional assays have shown that, in addition to some herbivorous ant lineages from the ant tribe Camponotini (18, 64), the ant genera *Cardiocondyla*, *Plagiolepis*, and *Formica* all harbor endosymbiotic bacteria (26, 28) while other species from the ant genera *Cephalotes*, *Dolichoderus*, and *Tetraponera* maintain a complex community of gut bacteria (4, 24, 25, 56), all of which exhibit functional convergence. In all cases, whether through a single endosymbiotic bacterium or a consortium of gut bacteria, these symbionts improve the nitrogen economies of herbivorous ants by recycling nitrogen and utilizing the recycled nitrogen to synthesize essential amino acids.

In addition, there is a unique group of ants known as fungus-growing ants, which, like other herbivores, rely on symbiotic microbes but in this case within the fungal gardens to fix atmospheric nitrogen into a usable form (42). These ants are dependent on cultivating fungi for their survival. They gather plant material mainly to provide a substrate for the fungi, which they carefully tend. In return, the fungi help the ants degrade complex plant carbohydrates and produce a nutrient-rich food source, abundant in lipids, sugars, and essential amino acids, serving as the primary diet of the fungus-growing ants (58). Notably, fungus-growing ants also harbor specialized gut bacterial communities, though their functional roles remain uncharacterized. This finding suggests that the fungal garden symbionts have not entirely supplanted the ants' interactions with endogenous bacterial symbionts (42).

2.2. Putative Role of Improving Nutrient Uptake in Ants at High Trophic Levels

As expected, nitrogen-provisioning symbioses were identified in some herbivorous ants, given their reliance on nitrogen-poor diets. However, specialized symbioses in predatory ants were an unforeseen discovery. In a broad sampling of symbiotic bacteria associated with ants, several predatory ant groups belonging to the subfamilies Dorylinae and Ponerinae harbor relatively abundant but low-diversity microbial communities (12, 21, 32, 35). Specifically, gut microbiomes of those predatory ants are dominated by a few host-specific bacterial taxa, mainly from *Entomoplasmatales* and *Firmicutes*. Functional characterization within carnivorous ants has been performed so far in only one study of *Harpegnathos saltator*. Genomic sequencing of its gut symbiotic bacteria "*Candidatus* Tokpelaia hoelldobleri" revealed a capacity to import and degrade protein and synthesize riboflavin, suggesting roles in nitrogen metabolism and perhaps some aspects of vitamin supplementation (41). To further elucidate the roles of these specialized bacteria, future metagenomic analyses and, where feasible, experimental studies will be essential. Similarly, other carnivorous insects, such as carrion beetles (27) and necrophagous bees (33), also harbor specialized gut symbionts. This finding suggests that symbiotic relationships involving specialized nutritional symbioses may be more widespread, extending beyond herbivorous and fungus-growing insects.

3. TYPES OF NUTRITIONAL SYMBIONTS FOUND IN ANTS

3.1. Endosymbiotic Microbes Found in Ants

Bacteriocytes are a common feature of ancient nutritional symbioses, where endosymbiotic microorganisms inhabit cells and tissues of hosts and are primarily vertically transmitted through the egg. These highly specialized, maternally transmitted microorganisms produce nutrients lacking in imbalanced diets, such as vertebrate blood and plant sap, and have been critical to the evolution

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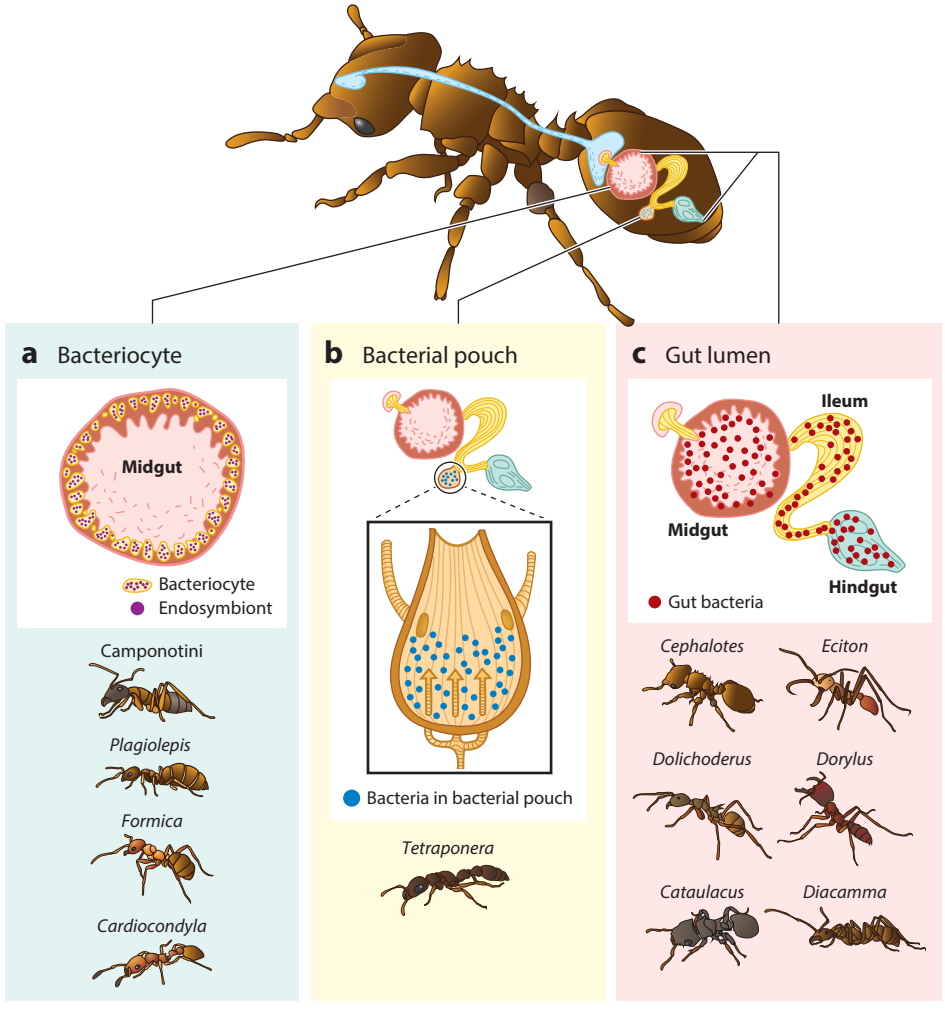

Figure 1

The localization of nutritional microbes in ants. (*a*) Endosymbiotic bacteria are localized in bacteriocytes surrounding the midgut in ants. These microorganisms are primarily vertically transmitted through the egg. Four ant lineages—Camponotini, *Plagiolepis*, *Formica*, and *Cardiocondyla*—have been found to harbor these endosymbiotic bacteria in bacteriocytes. (*b*) In *Tetraponera* ants, symbiotic microbes are localized in a specialized pouch located at the junction between the midgut and hindgut, connected to multiple Malpighian tubules and tracheae. This unique structure suggests an evolved organ for symbiotic bacteria. (*c*) Nutritional microbes are also found in the gut lumen of the digestive tract of several other ant species, including *Cephalotes*, *Dolichoderus*, *Cataulacus*, *Eciton*, *Dorylus*, and *Diacamma*. Ant images adapted with permission from original photographs by Alex Wild.

of insect groups that consume these foods exclusively (15). So far, four ant lineages have been found to harbor endosymbiotic bacteria in bacteriocytes surrounding the midgut (**Figure 1**). A recent study based on core gammaproteobacterial genes revealed that all four bacteriocyte-associated symbionts originate from a *Sodalis*-allied bacterial clade (26).

3.1.1. *Blochmannia* in Camponotini. The best-known bacteriocyte-associated symbiont in ants is *Blochmannia*, an obligate symbiont of the ant tribe Camponotini. The first discovery of

Blochmannia dates back to 1882, when Friedrich Blochmann identified this endosymbiont within the carpenter ant *Camponotus ligniperdus*, naming it "*Candidatus* Blochmannia" (5). Since then, *Blochmannia* has been found in nearly all species within the Camponotini tribe, encompassing over 1,950 species (49). These bacteria reside in bacteriocytes between the epithelial cells of the ant host midgut and within the ovaries of female hosts. They are vertically transmitted from one generation to the next through migration from follicle cells to oocytes (44, 48). Phylogenetic analyses indicate that the *Blochmannia* bacteria and its ant hosts have coevolved for at least 40 million years (64). This genus is closely related to the endosymbionts of hemipterans, such as aphids and whiteflies, and the endosymbionts of tsetse flies (Diptera). It is hypothesized that the ancestors of Camponotini ants acquired *Blochmannia* from these insects, likely through the consumption of honeydew produced by hemipterans (62).

3.1.2. "*Candidatus* Westeberhardia cardiocondylae" in *Cardiocondyla obscurior*. Klein et al. (28) identified another obligate endosymbiont in the ant genus *Cardiocondyla*, named "*Candidatus* Westeberhardia cardiocondylae" (termed *Westeberhardia* hereafter). *Westeberhardia* colonizes the bacteriocytes in the midgut of the host and the nurse cells in the queen's ovaries, where it is vertically transmitted to the next generation by migrating from nurse cells to follicle cells. The genome of *Westeberhardia* is highly reduced—a feature common to many vertically transmitted, coevolved endosymbionts—lacking the genes necessary for synthesizing all essential amino acids and vitamins while retaining a complete shikimate pathway. This pathway provides the metabolic precursors needed for synthesizing aromatic amino acids, which are crucial for the host's cuticle formation during eclosion. The number of *Westeberhardia* bacteria within the host increases during the pupal stage and gradually declines with the age of the worker ants, suggesting that the symbiont plays a key role in supporting normal host development during eclosion (28).

3.1.3. *Gammaproteobacteria* in *Plagiolepis* and *Formica*. The *Sodalis*-allied endosymbionts were also found to be associated with *Formica* and *Plagiolepis* ants (26). While those symbionts have not been extensively studied, they have been observed within bacteriocytes flanking the midgut epithelium (31). In *Formica*, these symbionts are also present in the queen's ovarioles and in developing brood (26, 31). While these bacteria are believed to be maternally transmitted, their presence is inconsistent across different *Formica* species (26). Depending on nutritional conditions, their presence can fluctuate within the same species, leaving their role in host nutrition unclear.

3.2. Ectocellular Symbiotic Microbes Found in Ants

Ant digestive tracts, specifically the lumen, represent the ectocellular environment—spaces external to host cells where nutritional symbionts colonize (**Figure 1**) with substantial variation in microbial abundance and diversity across species. Several recent large-scale microbial surveys of gut microbiota across Formicidae have shown that while most ant species harbor relatively few gut microbes, some species maintain dense microbial communities in their digestive tracts. These ants associate with diverse bacteria inhabiting different parts of the digestive tract. For instance, in *Tetraponera nigra* ants, a dominant bacterial strain from the order *Rhizobiales* resides in a specialized pouch located at the junction between the midgut and the hindgut and connected to multiple Malpighian tubules and tracheae, suggesting a highly adapted symbiotic organ (56, 61) (**Figure 1**). In addition, ants from the genera *Cephalotes*, *Cataulacus*, and *Dolichoderus* host large populations of ectocellular bacteria within the midgut, ileum, and hindgut (4, 6, 7, 19, 25, 45) (**Figure 1**). In the army ants *Labidus* and *Eciton*, small populations of bacteria are localized in the hindgut epithelia (32, 47). Recent studies indicate that ants with substantial amounts of bacteria tend to harbor ant-specialized bacterial lineages, which have evolved ancient and specific symbiotic relationships with their hosts, reflecting deep evolutionary integration (36).

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3.3. Symbiotic Microbes Found in Ant-Associated External Environments

A unique group of nutritional symbionts is present in the fungus garden of fungus-growing ants. All genera of fungus-growing ants (Myrmicinae: Attini) cultivate symbiotic fungi (Leucocoprineae and Pterulaceae) in their fungus garden as food for their young (51). In addition, the fungus garden serves as a specialized niche for nitrogen-fixing bacteria in the genera *Klebsiella* and *Pantoea*, which supply a substantial portion of the nitrogen required by both the ants and their cultivated fungi (42).

4. NUTRITIONAL ROLES OF ANT SYMBIOTIC MICROORGANISMS

4.1. Nitrogen Metabolism

Entomologists conducting rainforest canopy surveys discovered a biomass paradox (60). Ants, which were typically assumed to be predators or scavengers, were found to outweigh their potential prey in total biomass. This finding challenges the conventional expectations of a biomass pyramid. Stable isotope analysis has shown that many arboreal ants are functionally herbivorous ants, subsisting on nitrogen-poor or nitrogen-inaccessible diets (11). These diets include primarily sugar-rich resources such as extrafloral nectar and hemipteran exudates. Such dietary adaptations suggest that herbivorous ants may rely on symbiotic bacteria to supplement nitrogen and other essential nutrients (9, 11). This shift from nitrogen-rich carnivory and omnivory to nitrogen-limited herbivory has occurred at least 11 times in ant evolution (40), likely reflecting a convergent reliance on microbial symbionts to overcome dietary imbalances and support nutritional needs (45, 46). The major ways to compensate nitrogen limitations include recycling of nitrogenous wastes and fixation of N_2 gas (**Figure 2**).

4.1.1. Nitrogen recycling. Symbiotic bacteria contribute to their hosts' nitrogen economies through recycling nitrogen from nitrogenous wastes in several unrelated ant groups. The first identified nitrogen-recycling symbiosis involved ants in the tribe Camponotini and their *Blochmannia* symbionts. The genome sequencing of *Blochmannia* from *Camponotus floridanus* revealed a capability to convert urea to ammonia via urease enzymes and further synthesize most essential amino acids (22). Feldhaar et al. (18) highlighted the significant role of *Blochmannia* by demonstrating that in *C. floridanus* ants, nitrogen derived from ^{15}N-labeled urea is metabolized and subsequently utilized to synthesize both essential and nonessential amino acids found in the hemolymph of the ants. Further investigations into the camponotine system reveal the significance of *Blochmannia* in meeting the host's nitrogen demands. *Blochmannia* reaches its highest abundance during pupation and shortly after eclosion, with active nitrogen recycling evident through the high expression of urease, agmatinase, and glutamine synthetase genes during late larval and early adult stages (65). Additionally, aromatic amino acid biosynthesis genes peak mid-to-late pupation, indicating that *Blochmannia*'s nitrogen metabolism is vital for camponotine cuticle development (55, 66). Several strains of *Blochmannia* that encode urease but lack glutamine synthetase raise questions about their capability to assimilate ammonia from urea. The presence of carbamoyl phosphate synthase might provide a unique mechanism for ammonia processing in specific camponotine–*Blochmannia* symbiotic relationships (63, 64).

Another example of nitrogen-recycling symbiosis has been extensively studied in herbivorous ants of the turtle ant genus *Cephalotes*. Hu and colleagues (25) conducted dietary manipulation experiments on *Cephalotes varians*, revealing that their gut symbionts can convert nitrogen from ^{15}N-labeled urea into essential and nonessential amino acids by tracking ^{15}N incorporation into amino acid pools in the ants' hemolymph. Genomic and metagenomic analyses of the microbiomes of 17 *Cephalotes* species further elucidated the mechanisms behind this nitrogen recycling

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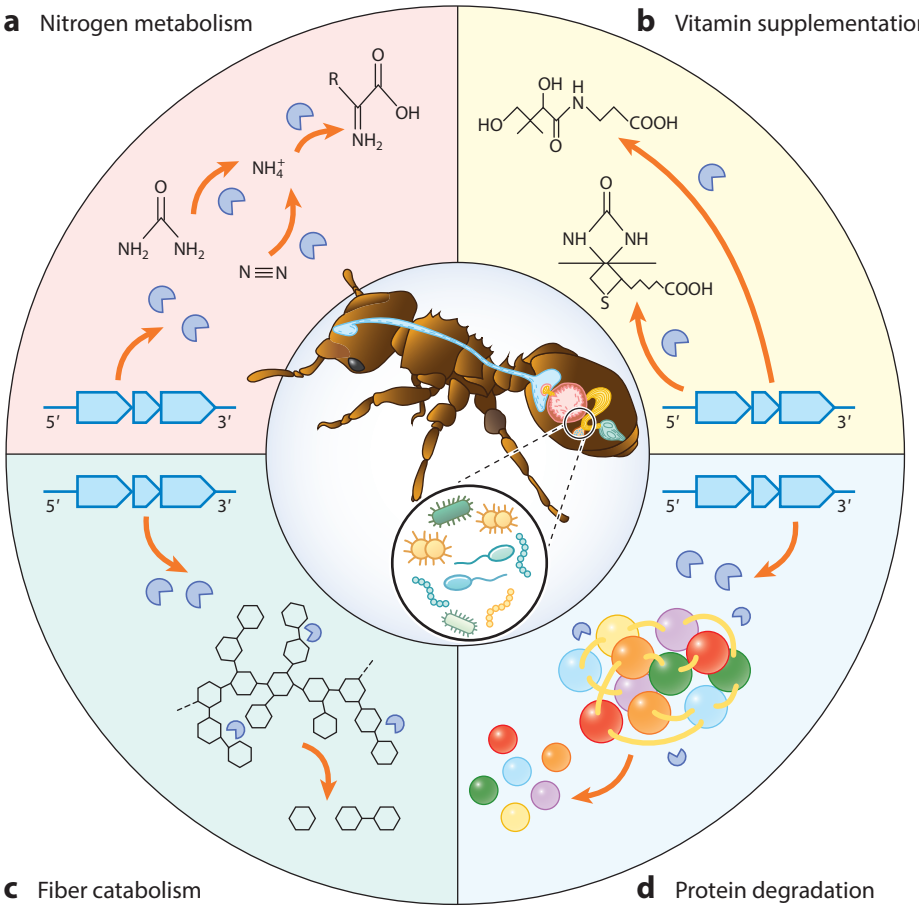

Figure 2

Nutritional roles of symbiotic microbes in ants. (*a*) Nitrogen metabolism. Symbiotic microbes play a critical role in nitrogen metabolism within ants. Endosymbiotic bacteria, such as *Blochmannia* in *Camponotus* and *Cephalotes* gut lumen microbes, recycle nitrogen from waste products like urea and uric acid, converting them into essential amino acids. In leafcutting ants, nitrogen-fixing bacteria (*Klebsiella* and *Pantoea*) in the fungus gardens fix atmospheric nitrogen, supplementing the nitrogen requirements of both the ants and their fungal crops. This metabolic pathway supports the nitrogen economy of herbivorous ants and facilitates their adaptation to nitrogen-limited diets. (*b*) Vitamin supplementation. Symbiotic microbes in ants provide essential vitamins, particularly B vitamins. In *Cephalotes* ants, gut symbionts such as *Klebsiella* and *Ventosimonas* synthesize nearly all B vitamins, including riboflavin (B2), pantothenate (B5), and pyridoxine (B6). These symbiotic microbes help supplement the ants' diet, especially during times of resource scarcity, such as drought or food shortage. (*c*) Fiber catabolism. In herbivorous ants, symbiotic gut microbes assist in the breakdown of recalcitrant dietary fibers, including pectin, cellulose, and xylan. In *Cephalotes* larvae, *Enterobacterales* symbionts degrade pectin, while adult ants rely on symbionts like *Xanthomonadales* to degrade fiber components. This specialization in fiber degradation is critical for enabling ants to process plant materials that are otherwise difficult to digest. (*d*) Protein degradation. Symbiotic bacteria in predatory ants such as *Harpegnathos* facilitate protein degradation and amino acid transport. This function supports the nutritional needs of predatory ants, although the extent of these processes across species remains under investigation. Ant image adapted with permission from original photograph by Alex Wild.

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through a multipartite gut symbiosis. In this system, host nitrogen waste from uric acid is recycled into urea by a group of *Burkholderiales* symbionts. Subsequently, the urease gene, which is universally present in *Cephaloticoccus* symbionts and occasionally present in *Rhizobiales* bacteria in certain *Cephalotes* species, is responsible for breaking down urea into glutamate. The majority of gut symbionts then utilize glutamate to synthesize most of the essential amino acids. This work highlights the multipartite gut microbiome in *Cephalotes* as a highly efficient system for the nitrogen economy (25). Further research has identified *Ischyrobacter davidsoniae* (*Burkholderiales*) as a key cooperative player in nitrogen-recycling symbiosis within *Cephalotes* ants. The midgut symbiont *Cephaloticoccus* initiates the collaborative nitrogen-recycling process by expressing genes that convert sugars and amino acids into inosine, which is subsequently transported to the ileum and converted to hypoxanthine by ileum-resident symbionts. *Ischyrobacter davidsoniae*, located in the ileum, relies on hypoxanthine and allantoin synthesized by coresident gut bacteria to produce urea. This physical and metabolic arrangement allows *I. davidsoniae* to produce urea without relying solely on dietary nitrogen or host nitrogen waste inputs. Instead, *I. davidsoniae* can be supplemented through purine metabolism intermediates supplied by upstream gut symbionts, enhancing the efficiency and resilience of nitrogen recycling in *Cephalotes* ants (2). However, how nitrogen enrichment via symbiotic bacteria in nitrogen-recycling activities affects colony-level fitness remains relatively underexplored. A foundational study by Duplais et al. (17) demonstrated that in *Cephalotes* ants, gut symbionts not only utilize urea-derived nitrogen for their own metabolism but also allocate recycled nitrogen to support larval development—specifically cuticle synthesis during pupation and adult emergence. While comprehensive assessments of colony-level fitness (e.g., reproductive success, colony survival under nitrogen limitation) remain sparse, Duplais et al.'s findings exemplify how symbiont-mediated nitrogen economies can transcend individual-level benefits to sustain entire colonies (17). In addition, researchers have gradually found evidence of nitrogen-recycling symbioses in other herbivorous ant groups. The dominant *Rhizobiales* bacteria colonizing the midgut of the herbivorous *Dolichoderus* ants encode ureases as predicted by metagenomic data, though this has not been experimentally demonstrated (4).

These findings further support the hypothesized importance of nutritional symbionts in canopy-dwelling, herbivorous ants. The mutualistic relationships with phylogenetically distinct but functionally convergent symbiotic bacteria, originating independently in various herbivorous ant lineages (belonging to diverse subfamilies such as Formicinae, Myrmicinae, and Pseudomyrmecinae), serve as a mechanism contributing to the success of arboreal ants within a seemingly marginal dietary niche.

4.1.2. Nitrogen fixation. Nitrogen-fixing symbioses have been demonstrated only in the fungus garden of leafcutting ants (42). Using acetylene reduction assays and $^{15}N_2$ enrichment experiments, researchers demonstrated active nitrogen fixation mediated by bacterial symbionts, primarily *Klebsiella* and *Pantoea* species, isolated from the fungus gardens of multiple leafcutting ant colonies. These bacteria fix atmospheric nitrogen, supplementing the nitrogen requirements of both the ants and their fungal crops. The findings highlight the significance of nitrogen-fixing symbioses in supporting the ecological success of leafcutting ants, allowing them to thrive in nitrogen-poor environments and play a substantial role in nutrient cycling within American tropical ecosystems.

4.2. Vitamin Supplementation

B vitamins are essential for the sustained growth and survival of insects and other animals (16). In addition to obtaining B vitamins from their diet, insects can derive these nutrients from microbial symbionts. Studies have shown that the gut symbionts of both adult and larval *Cephalotes*

ants collectively possess the genetic capability to synthesize nearly all B vitamins (3) (**Figure 2**). Notably, *Klebsiella* sp. in the *Cephalotes* ant larval gut can synthesize all B vitamins except thiamine (B1) and cobalamin (B12). Meanwhile, the *Cephalotes* ant adult gut symbiont *Ventosimonas* (*Pseudomonadales*) encodes complete or near-complete pathways for B vitamin biosynthesis, especially for riboflavin (B2), pantothenate (B5), pyridoxine (B6), biotin (B7), and folate (B9), providing diverse nutritional support for the worker ants. However, there are limitations in the synthesis of vitamin B12. The *Rhizobiales* symbionts in adult ants and the *Klebsiella* species in larvae lack a complete cobalamin production pathway. Despite these missing steps, the *Rhizobiales* symbionts may synthesize cobalamin-like cofactors, such as adenosylcobyric acid, which may function in place of cobalamin to facilitate methionine synthesis.

Similarly, in the predatory ant *Harpegnathos saltator*, the symbiont "*Ca*. Tokpelaia hoelldobleri" possesses a complete pathway for synthesizing vitamin B2 (41). Since animals cannot synthesize vitamin B2 independently, this riboflavin biosynthesis pathway in "*Ca*. Tokpelaia hoelldobleri" may provide a vital source of this vitamin for the ant host. However, the ability of "*Ca*. Tokpelaia hoelldobleri" to synthesize other vitamins is limited. While retaining partial pathways for vitamin B7 and tetrahydrofolate synthesis, its genome lacks biosynthetic genes for vitamin B1 and vitamin B6. These metabolic gaps may be compensated by host-mediated complementation of missing steps, or metabolic cross-feeding facilitated by auxiliary bacterial partners in multisymbiont consortia, or direct acquisition from the ant diets (41). Despite not having a full suite of vitamin biosynthetic pathways, "*Ca*. Tokpelaia hoelldobleri" may still supply essential nutrients to its host, particularly when external resources are scarce. Under extreme environmental conditions, such as drought, food scarcity, or flooding, when nitrogen sources may become limited, "*Ca*. Tokpelaia hoelldobleri" could help support the ant's survival by supplying key nutrients like vitamin B2.

While metagenomic evidence strongly suggests that gut symbionts contribute to B vitamin provisioning in *Cephalotes* and *Harpegnathos* ants, direct experimental validation of symbiont-derived vitamin contributions remains a critical gap. To date, no studies have quantified B vitamin levels in symbiont-depleted ants (e.g., via antibiotic treatment or axenic rearing) to test whether microbial partners are essential for maintaining host vitamin homeostasis. Future work integrating multi-omics approaches with symbiont manipulation will be pivotal to confirm the hypothesized vitamin-provisioning roles and to assess their ecological relevance under nutrient stress.

4.3. Catabolism of Plant Recalcitrant Dietary Fibers

In herbivorous *Cephalotes* ants, symbiont-encoded capacities to break down recalcitrant dietary fibers—primarily from wind-dispersed pollen and potentially cryptic plant–associated materials like lichens and fungi—are outsourced to multiple gut bacterial symbionts (3) (**Figure 2**). Pectin degradation in *Cephalotes* ants reveals distinct capacities between larval and adult gut microbiomes. In larvae, *Enterobacterales* symbionts encode genes for homogalacturonan depolymerization, including polygalacturonase, transporters for pectate and galacturonate, and metabolic pathways (e.g., the Uxa route) for further processing. While *Lactobacillales* could import unsaturated digalacturonate, their metabolic pathways remained incomplete. In contrast, adult gut symbionts largely lack the ability to degrade homogalacturonan, though some low-abundance *Verrucomicrobia* encodes polygalacturonase and rhamnogalacturonan endolyase, found in only a subset of *Cephalotes* species (3). These findings emphasize the significant role of larval gut symbionts in pectin breakdown, while adult microbiomes exhibit more limited specialization in pectin catabolism.

Similarly, the gut microbiota of *Cephalotes* ants exhibits distinct yet complementary capabilities for other fiber degradation, reflecting both life stage specialization and evolutionary conservation (3). In larvae, gut symbionts, particularly *Enterobacterales*, encode genes for the complete catabolism

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of fibers such as cellulose, xylan, resistant starch, chitins, and lignins, with functions validated through in vitro assays. In adults, while fiber-degrading capacities are less extensive, *Xanthomonadales* symbionts uniquely retain the ability to degrade xylan and chitins, and some *Cephaloticoccus* strains metabolize maltose. Across species, conserved microbial functions include the breakdown of rhamnogalacturonan-I, cellulose, and xylan, with *Xanthomonadales* playing a key role in adult guts. These findings underscore the ecological and evolutionary importance of gut microbiota in enabling *Cephalotes* ants to exploit diverse dietary fibers.

4.4. Protein Degradation and Amino Acid Transport

Recent studies have revealed consistent associations between microbial symbionts and various predatory ants. While the functional roles of symbionts in predatory ants remain poorly understood, metagenome-based analysis of *Tokpelaia* strains infecting the predatory genus *Harpegnathos* has provided preliminary insights (41). The *Harpegnathos* symbionts exhibit protein degradation and amino acid transport capabilities (**Figure 2**) involving 17 protein families, including hydrolases, peptidases, aminotransferases, dehydrogenases, and ABC transporters, though the subcellular localization and functional validation of these proteins remain to be experimentally confirmed. However, it remains unclear whether these patterns are universal. Thus, further investigation into the functional roles of symbionts in predatory ants is needed.

5. TRANSMISSION OF NUTRITIONAL SYMBIONTS

The perpetuation of the mutualistic association between ants and nutritional symbionts across host generations depends on reliable symbiont transmission. Despite growing evidence that nutritional symbioses are present in different ant lineages, our knowledge of the mode of transmission of nutritional symbionts is restricted to a few ant species. Three fundamentally different modes of transmission can be distinguished. The first mode is vertical transmission, where symbionts are inherited from the mother. This transmission mode has been extensively studied in *Camponotus* ants, where endosymbiotic bacteria within bacteriocytes are passed to the next generation through a strict vertical transmission mechanism (29, 44). During oogenesis in *Camponotus* ants, *Blochmannia floridanus* infection follows a highly regulated pattern. Initially absent in the germarium, including germ-line stem cells and early cystocytes, the bacteria first appear in the determined oocyte during its early growth in the infection zone. As the oocyte matures, *B. floridanus* proliferates within its cytoplasm, while nurse cells remain uninfected, creating a necklace-like pattern in the ovariole. In fully grown oocytes, the bacteria migrate and concentrate at the posterior pole, ensuring vertical transmission to the next generation. This precise localization reflects a well-coordinated process critical for successful endosymbiont inheritance.

In the second mode, core gut symbionts in ants achieve codiversification with their hosts through alternative social transmission mechanisms, unlike the mode for endosymbionts, which are strictly transmitted to offspring via transovarial transmission. As social insects, ants maintain partner fidelity at the colony level through trophallactic transmission and transgenerational inheritance facilitated by independent colony founders. A study of gut bacterial microbiota across 13 *Cephalotes* species, spanning different castes and developmental stages, revealed that unmated, alate queens harbor microbiomes resembling those of workers before dispersal and mating flights. This allows for the vertical transfer of symbionts to the newly founded colony. After colony establishment, young queens transmit gut symbionts to newly emerged workers through trophallaxis, ensuring the continuity of beneficial microbiomes (23, 30). In ant colonies that reproduce through fission, such as *Diacamma* cf. *indicum*, unclassified *Firmicutes* symbionts are predominantly associated with worker ants and are rarely found in gamergates. This finding suggests that during colony

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splitting, older workers in the subcolony may pass the *Firmicutes* symbionts to newly emerged workers via social behaviors, such as fecal contact, rather than through direct transmission via reproductive castes (52). In these modes of ant colony founding, social symbiont transmission enables the preservation and stability of microbial communities critical to the colony's nutrition and resilience, highlighting its evolutionary significance in ants.

Although not yet experimentally confirmed, in the third mode the conserved gut symbionts in *Cephalotes* ant larvae are likely acquired through a conserved environmental filtering mechanism (23). The gut microbiome composition in larvae is highly conserved across different *Cephalotes* species. The dominant microbes are phylogenetically closer to free-living environmental bacteria. Unlike the adult gut microbiome, which coevolves with the host, no such phylosymbiosis pattern has been observed in the larval microbiome. However, the stability and conservation of the larval gut microbiome among different *Cephalotes* species across their geographic range suggest an alternative mechanism. This environmental filtering mechanism likely plays a crucial role in shaping the larval microbiome of *Cephalotes* ants.

6. CONCLUSIONS AND OUTLOOK

Over the past two decades, significant advances have been made in understanding ant–microbe symbioses. While many ant species host few or no microbes, some ant lineages exhibit high abundances of bacterial symbionts with consistent associations. These symbionts play critical roles in host nutrition, growth, and development by conferring various nutritional benefits. A general pattern observed is that ant lineages with abundant, ant-specialized microbial clades often occupy specialized dietary niches characterized by nutritional imbalances, such as herbivorous diets low in nitrogen and carnivorous diets high in protein. Evidence from genomic sequencing and experimental validation suggests that symbionts help mitigate these challenges.

However, current studies are limited largely to a few genera, such as *Cephalotes*, *Tetraponera*, and *Dolichoderus*, and ants in the Camponotini tribe. Moreover, most research has been restricted to functional predictions derived from metagenomic data, with relatively few studies extending to experimental validation. Future research should expand to include a broader range of ant lineages and integrate genomic analyses with functional experiments to better understand how ants establish and maintain nutritional symbioses. This integrated approach will provide a more comprehensive perspective on the metabolic strategies ants employ through their symbiotic partnerships. In addition, ants exhibit a division of labor, with different caste members performing specialized roles. For example, the queen is responsible for reproduction, and the larvae can liquefy solid food and regurgitate it to adult ants (53). Worker ants forage for food, care for the young, and contribute to other essential tasks within the colony. Despite the crucial roles these different castes play in maintaining the colony, research on ant–microbe symbiosis has focused predominantly on worker ants. This focus is largely due to sampling limitations and the challenges of maintaining sexually reproducing ant colonies under laboratory conditions. Future studies should expand to include ants from various castes within the colony to better understand the dynamics of ant–microbe symbioses across different castes and developmental stages of ants. Furthermore, a defining feature of nutritional symbioses is the metabolic complementarity between host and microbes—a phenomenon exemplified by the aphid–*Buchnera* system. Similarly, in ant–microbe nutritional symbioses, it is crucial to uncover the molecular mechanisms that have maintained these partnerships over millions of years. Fortunately, with the rapid expansion of available ant genomes, we can now perform comparative analyses to identify host genomic signatures of coevolution. For example, retained host genes encoding metabolite shuttles (e.g., amino acid transporters) may interface directly with symbiont biosynthetic pathways, while parallel losses of redundant functions (e.g.,

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host loss of essential amino acid biosynthesis when symbionts encode complete pathways) will further illuminate mutual dependence. By combining these correlative genomic predictions with targeted functional assays, such work will advance our understanding from descriptive association to mechanistic validation of coevolved metabolic modules.

The nutritional symbiosis between ants and microbes has permitted one of the most ecologically dominant groups of animals on the planet to move into new ecological niches and take advantage of novel food sources. These often ancient and obligate associations have permitted ants to transition to specialized diets with limited nutrition. Although new sequencing technologies allow us to better understand the diversity of microbes associated with many hosts, we are only beginning to understand the important functional roles these symbionts play. These systems range from single bacterial systems contained in host-derived bacteriocytes, which are transmitted through the eggs, to diverse communities within the midgut and hindgut, which rely on complex social behaviors to ensure vertical transmission among members of the colony. We are only beginning to discover and understand the important role microbes play in the most species-rich group of social animals on the planet.

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