Intestinal Symbionts

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Synonyms

Gut biome; Gut fauna; Gut symbionts; Intestinal biome; Intestinal fauna

Host-microbe interactions are ubiquitous across the tree of life and can range from mutualistic to parasitic. In social insects, a diversity of host-associated microbes has been identified, including maternally transmitted bacteria that selfishly manipulate the host's reproduction to cuticular bacteria that help fungus-gardening ants in the fight against parasitic fungi. Although microbes can be found in many places on and in the host, the majority of symbiotic microbes are associated with the digestive tract. Symbiotic microbes in the intestinal tract can benefit the host through a myriad of ways, including nutritional upregulation, defense from pathogens and parasites, and by increasing environmental tolerance [4]. Internal microbial communities can not only provide immediate ecological benefits to the host but in some cases may even benefit the host on an evolutionary scale. Gut microbial symbionts are best known from termites, but they are found across the social insects (Fig. 1).

Termites

Termite gut symbionts contain members from all three domains of life (Archaea, Bacteria, and Eukarya). Termites exhibit different ▶ feeding syndromes, with diets comprising lignocellulose (cellulose and lignin) plant material including wood, various stages of decaying plant material, animal dung, and soil rich in organic material. As termites, like almost all other animals, cannot digest these food sources and these food sources are limited in their nutritional quality and access, intestinal symbionts are responsible for the breakdown of cellulose and for nitrogen acquisition [1, 2]. In fact, termites that have had their gut symbionts removed, but are otherwise healthy, die even in the presence of ample wood or cellulose.

The two major groups of termites host different extracellular gut community members. The lower termites host dense communities of Bacteria, Archaea, and flagellate protozoa, many of which host their own prokaryotic symbionts, while the higher termites have diverse bacterial gut communities, but almost always lack protozoa. In the lower termites, the protozoa are primarily responsible for the degradation of cellulose into digestible sugars, which are then converted into short-chain fatty acids. In the higher termites, in

C. Starr (ed.), *Encyclopedia of Social Insects*,
https://doi.org/10.1007/978-3-319-90306-4_65-1

Intestinal Symbionts, Fig. 1 Gut microbial symbionts have been documented and studied in several social insect groups including termites, cockroaches, social aphids, bees, and ants. (Photos by Alex Wild)

contrast, lignocellulose moves through various specialized gut chambers where it is decomposed through chemical processes. The gut-associated bacteria are responsible for providing nitrogen to the host primarily through N-fixation, although recycling of uric acid has also been observed. During these digestive processes, a major product is methane gas, and termites are considered a major contributor of methane in our atmosphere.

These microbial communities are not evenly distributed across the digestive tract. Although there are some bacteria associated with the foregut and midgut, the majority of the intestinal microbiota are found in the hindgut. As these microbial communities are extracellular and not strictly maternally transmitted, termites must acquire these essential symbionts through behavioral transmission. This is primarily accomplished through oral-anal ▶ trophallaxis. Associations with intestinal symbionts have permitted termites to feed on an abundant food source that is undigestible to most of life, which may account for their high abundance in many ecosystems.

▶ Wood-Feeding Cockroaches

A close phylogenetic relationship between cockroaches and termites was first suggested by the observation that wood-eating cockroaches (▶ *Cryptocercus*) harbor a similar fauna of gut flagellates. It is now accepted that termites are a special group of social cockroaches, with *Cryptocercus* as their sister group. The latter's intestinal communities comprise bacteria and protozoans which enable them to digest cellulose. Gut microbial symbionts in some other cockroach species are responsible for the production of pheromones secreted in the feces, which serve as aggregation cues.

▶ Social Aphids

Social aphids are plant-feeding hemipterans that rely on an obligate nutrient-provisioning bacterium, *Buchnera aphidicola* [3, 5]. These bacteria are housed in host-derived bacteriocyte cells and are maternally transmitted through the egg. These bacteriocytes are aggregated into specialized organs called bacteriomes that are located near the host's midgut. This obligate intracellular endosymbiont has been co-diversifying with its aphid hosts for 150–250 million years. *Buchnera* produce essential amino acids for their insect host. As this bacterium is found only within aphid hosts, it has lost many of the genes required for free-living and has one of the smallest genomes recorded.

There is also a range of facultative microbes that have been found associated with aphids that often provide benefits to the host in specific ecological contexts. For example, the maternally transmitted bacterium, *Hamiltonella defensa*, protects aphids from parasitoids by causing mortality of parasitoid larvae. Two other facultative bacteria, *Regiella insecticola* and *Serratia symbiotica*, also provide protection against these natural enemies. In addition to its role in protection from parasitoids, *S. symbiotica* has also been shown to protect aphids from the detrimental effects of heat stress, an example of host-associated microbes increasing environmental tolerance for the host. Interestingly, although these facultative bacteria are maternally transmitted, they are found at variable frequencies in natural populations of the host aphid. This suggests that there is a net cost to maintaining the symbiosis if the ecological pressure is not high.

Bees

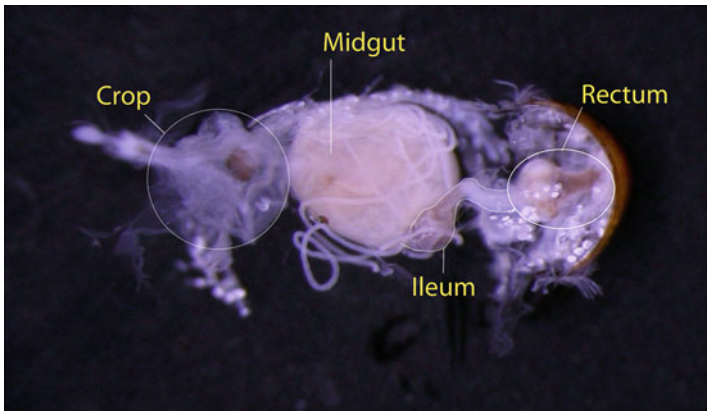
▶ Honey bees are the most thoroughly studied of all insects, and, not surprisingly, the majority of what we know about bee gut-associated microbiomes comes from honey bees. Their intestinal tracts contain a distinctive, yet relatively simple community of bacteria of only a few species. The majority of these bacteria reside in the ileum, but some species are found predominately in the rectum. The gut microbiota of honey bees has been shown to increase body weight gain and confer resistance to ▶ pathogens. Additionally, one of the most notable roles of the honey bee gut community is that these bacteria likely permit their hosts to digest pollen.

Along with honey bees, ▶ bumble bees also appear to have a stable, socially transmitted (through interactions with other members of the colony or direct contact with the nest substrate), and functionally important gut bacterial community that overlaps in some of its core components with that of honey bees. As in honey bees, the gut bacterial community of bumble bees also protects the host from parasitic infections.

Ants

Although we know many details about the gut-associated microbial community for individual social insects, in the ants we have a better understanding of the diversity of host-associated microbes across many species [6]. Ants have a great diversity of diets, with some species being entirely predatory, others having strict fungal- or plant-derived diets, while the majority are omnivores. This provides the opportunity to investigate the role of gut microbial communities and host diet in a comparative framework. The best-studied gut-bacterial interactions among the ants comes from the ▶ carpenter ants (*Camponotus*), ▶ spiny ants (*Polyrhachis*), and their close relatives.

In this ancient symbiosis, maternally transmitted intracellular bacteria from the genus *Blochmannia* have been co-diversifying with their ant hosts for over 40 million years. This midgut-associated bacterium resides in bacteriocytes and supplements the host's nutrition through nitrogen recycling and amino acid synthesis. To date the majority of gut-associated microbes have been shown to be extracellular and, as in termites, these microbial communities are not evenly distributed throughout the digestive tract. For ants feeding low on the trophic scale, there appear to be multiple independent origins of putative nutrient-provisioning bacteria. Bacteria



Intestinal Symbionts, Fig. 2 The digestive tract of a turtle ant (*Cephalotes varians*) showing the distinct comparts. Typically, the crop, or social stomach, does not seem to harbor a persistent functional bacterial community, while the midgut, ileum, and rectum have all been shown to harbor diverse and stable gut communities with functional roles for the host

of the order Rhizobiales have been shown to be associated with a diversity of distantly related ants, including *Cataulacus*, *Cephalotes*, *Dolichoderus*, and *Tetraponera*. Among the ► turtle ants (*Cephalotes*), the gut-associated bacterial community is stable, has been co-evolving with the host for over 46 million years, and provides amino acids through nitrogen-recycling. These bacteria are associated with the midgut, ileum, and hindgut and are socially transmitted through oral-anal trophallaxis, as also seen in termites. At the other end of the spectrum of feeding habits, ► army ants, which are entirely predatory, have also been shown to have mid- and hindgut associated bacteria, although the functional role of these are not known. Of major importance to our understanding of gut-associated microbial communities, many species of ants with generalized diets seem to have no or only low densities of bacterial communities in their intestinal tracts, suggesting that microbial associations are not ubiquitous. This survey across a biologically and ecologically diverse group of animals throws some light onto the gain and loss of specialized symbionts and their connection with host ecology and evolution (Fig. 2).

Stability and Function of Gut Microbes in Social Insects

The majority of intestinal microbes observed across the tree of life are transient. To establish long-term associations, there must be dependable transmission mechanisms among individuals. Social interactions provide opportunities for the transmission of gut microbial communities, which may explain the diversity, stability over evolutionary time, and functional importance of gut-associated microbes across the social insects. Not only do the majority of microbial species found in the intestinal tract of social insects exist nowhere else, but these microbes often have important functional roles for the host. At present, our knowledge of these functions is still very limited. This highlights the importance of understanding the diversity and role of intestinal symbionts in social insects, as these may shed light on not only their role in host health but also provide insights into transitions in host ecology and evolutionary diversification.

Cross-References

► *Cryptocercus*

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