



Review Article

Bacterial Diversity Associated with Dung Beetles: Ecological Perspectives

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Abstract | This study reviews the bacterial diversity associated with the gut microbiota of dung beetles, focusing on the microbial ecology, taxonomy, and environmental factors influencing the composition and functionality of these bacterial populations. Dung beetles are among the most diverse organisms, harboring a wide variety of bacterial phyla in their gut. The genetic diversity within these bacteria is astounding, with bacteria possessing 100 times more genes than the host dung beetle. Dung beetles use dung (incomplete diet) for their development and require symbiotic relationships with microorganisms to synthesize and use nutrients. The gut microbiota includes bacterial phyla such as *Lactobacillus*, *Bifidobacterium*, *Clostridium*, *Firmicutes*, *Proteobacteria*, *Bacteroidetes*, *Deltaproteobacteria*, *Betaproteobacteria*, *Streptomyces*, *Actinobacteria*, with variations linked to diet, geographical location, and beetle species. The gut microbiota plays a crucial role in breaking down complex organic compounds, neutralizing toxins, and supporting the overall ecology of the beetle. This paper examines the bacterial population within dung beetles, focusing on their taxonomy, functionality, and ecological roles. It also explores how these gut bacteria vary based on the beetle's environment and its symbiotic relationship with them. The bacterial taxa and their metabolic pathways related to dung decomposition, nitrogen fixation, and antimicrobial synthesis show distinct specificity. These findings reinforce the symbiotic relationship between dung beetles and their gut bacteria, contributing to a deeper understanding of microbial diversity and its ecological significance. The study also offers valuable insights with implications for bioconversion, soil management, and the preservation of beneficial microbes.

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Introduction

Dung beetles (Coleoptera: Scarabaeidae) immensely to the ecosystems by providing ecological services such as soil aeration, nutrient

recycling, and seed dispersal (Hajji *et al.*, 2024) which ultimately improves environmental health and biodiversity (Hussain *et al.*, 2022; Torabian *et al.*, 2024). The symbiotic association of dung beetles with microbiota with their gut microbiota helps to

address any nutritional deficiencies of a dung-based diet (Bashir *et al.*, 2013). The microbial communities associated with the gut of various species are involved in organic matter breakdown, and decomposition of dung, thus, ensuring the survival and fitness (Suman *et al.*, 2022).

The composition and function of bacterial communities associated with the gut are dependent on the species, environmental factors, and diet of the dung beetles (Kucuk, 2020). Ecological significance, taxonomic diversity, functional roles, and environmental dynamics of gut microbiota emphasize on more elaborative studies to understand sustainable impact of microbiota (Hernández *et al.*, 2015).

Taxonomic and functional diversity of dung beetles

Dung beetles (Coleoptera: Scarabaeidae) have about 8000 species belonging to 12 tribes reported from different landscapes of the globe (Davis *et al.*, 2008; Halffter *et al.*, 2013; Tarasov and Dimitrov, 2016; Tonelli, 2021). Dung beetles are classified into four groups based on their feeding and nesting behaviour: telocoprid (dung rollers), paracoprid (tunnelers), endocoprid (dwellers), and kleptocoprid (which use telocoprid dung balls) (Byk and Piętko, 2018; Halffter and Edmonds, 1982).

Gut microbiota of dung beetles

The taxonomic composition of gut bacterial communities in beetles have been reported in various studies indicating variations in the assemblages depend on species, dung type, and region (Chen *et al.*, 2024; Ebert *et al.*, 2021; Jácome-Hernández *et al.*, 2023). The bacterial communities of dung beetle are symbiotic and play a vital role in digestion, detoxification of foods, behaviour modulation, and pathogenicity (Boucias *et al.*, 2018; Douglas, 2015; Wernegreen, 2012). The gut of an insect contains more microbial cells than the host cells resulting in more microbial genes (> 100 times) (Krishnan *et al.*, 2014; Lederberg, 2000). The taxonomic composition of bacterial assemblages depends on life cycle of the dung beetle species. Some bacterial species may be linked with specific developmental stage (Suárez-Moo *et al.*, 2020), and associated with the need for acquiring essential nutrients that are absent in nutrition (Jácome-Hernández *et al.*, 2023).

Dung beetles harbor rich and diverse gut bacterial communities to support critical biomasses, nutrient

equalization, and digestion (Shukla *et al.*, 2016). Bacterial community structures vary not only with the dung beetle species but also with changes in gender. For example, microbial communities found within the *Onthophagus taurus* brood balls resemble the composition found on the male dung beetles, not female dung beetles. The gut bacterial community of *Catharsius molossus* differs in various developmental stages of the dung beetle. Recent studies have highlighted the significant roles of mutualistic microbes, such as *Lactococcus lactis* and *Enterococcus* species, in the gut ecosystem. For instance, *Lactococcus lactis* has been identified as a core prokaryote in the guts of certain wood-boring beetle larvae, suggesting its potential in food fermentation processes due to its probiotic properties (Chen *et al.*, 2024). The gut microbiota of the adult *Copris incertus* included *Enterobacter*, *Serratia*, and *Ochrobactrum*. In contrast, *Parabacteroides* and *Dysgonomonas* were predominantly found in larvae and pupae, while eggs harbored *Hydrogenophaga* and *Nocardioidea*. The microbial communities varied significantly across the adult and intermediate life stages, including larvae, pupae, and eggs (Suárez-Moo *et al.*, 2020). The dominant genera of bacteria in the gut of *Onthophagus taurus* are *Clostridium*, *Bacillus*, *Lactobacillus*, *Enterococcus*, and *Bacteroides*. Such microbes assist in the degradation of multiple composite matters present in dung, inclusive of cellulose and hemicellulose, which are then metamorphosed to simpler compounds surmountable by the beetle. Microbiota is a complex consortium of microorganisms constituted according to the diet, developmental stage, and other conditions. Developmental effects have also been reported whereby gut bacteria play a role in larval development, as well as the morphology of the adult beetles (Macagno and Moczek, 2023).

Ecological relationships

Scarab beetles form mutualistic relationships with gut bacteria that aid in regulating metabolism, facilitating nutritional interconversion, and enhancing nutrient assimilation (Thiyonila *et al.*, 2018). Symbiotic gut bacteria facilitate the decomposition of dung and hindgut morphology determines the bacterial community composition in association with food type (Ebert *et al.*, 2021). For instance in *O. gazella*, microbiota enhanced growth and developmental rate (Schwab *et al.*, 2016).

Dung is a poor source of nourishment because it lacks some essential amino acids, such as histidine,

methionine, tryptophan, and arginine (Müller, 1980). For the full utilization of nutrients, insects and commensal microorganisms establish a symbiotic interaction, and the complication of bacteria varies among species (Benson *et al.*, 2010; Ventura *et al.*, 2009; Wu *et al.*, 2011). The gut microbiota in dung beetles plays a vital role in the survival, development, and ecological success of dung beetles. Nutrient cycling is enhanced by microbes that are considered mutualism digestion aids of manure (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Hernández *et al.*, 2015; Price, 2004). Dung beetle species and associated bacterial gut microbiota has been presented in Table 1. Many scientists have also demonstrated that endogenous microbiotas synthesize a variety of smart compounds to help the host immunity should there be a pathogenic invasion, as well as improved defence machinery in insects (Holmes *et al.*, 2012; Lee and Hase, 2014).

The primary two ecological functions the dung beetles perform together with their gut microorganisms are nitrogen counterpart and mineral. There is also a potential for the ammonifier bacteria so associated with dung beetles to enhance N-mineralization by breaking down dung matter (Holter and Scholtz, 2007; Kazuhira *et al.*, 1991; Nichols *et al.*, 2008). Gut microbes of termites utilize nitrogen that is abundantly present in the atmosphere and reduces waste material recycling (French *et al.*, 1976; Hongoh *et al.*, 2008; Thong-On *et al.*, 2012). The metabolically significant compounds generated by the gut microbial load of the insect are assumed to be advantageous for the insect and its symbionts. The process of digestion of cellulose in insects is an example of synergism, the cooperation of specific enzymes that form cellulase complex make it easier to break this material. The cellulolytic enzymes that are found in gut fungi and bacteria include endoglucanases, 3-glucosidases, exoglucanases, and cellobiohydrolases (Vaheri *et al.*, 1979; Wood, 1985). This diet requires specialized bacteria that can break down complex polysaccharides for nutrient extraction. For instance, *Holotrichia parallela* larvae harbor cellulolytic bacteria such as *Clostridium* and *Cellulomonas* which secrete enzymes to help in degrading cellulose and hemicellulose since fibrous plant materials become a rich source of food for the larvae (Huang *et al.*, 2012). This is especially because *Onthophagus* species have been known to change their gut microbiota based on diet. These beetles, whose diet consists primarily of dung, host

bacteria such as *Clostridia* and *Firmicutes*, which are highly effective at degrading polysaccharides in dung. However, since dung is teeming with microbial bacteria that feed on it, shifting from a dung-based diet to decaying plant matter introduces a new set of bacterial demands for the digestion of plant material (Shukla *et al.*, 2016). Facultative coprophagous scarab beetles, including those that feed on dung, harbor a genuine community of microorganisms adapted and specialized for decomposing plant material in dung. For instance, the short chain of fatty acids-producing bacterial populations of *Scarabaeus sacer* dung beetle include bacteria belonging to *Lactobacillus*, *Bifidobacterium*, and *Clostridium*; these bacteria are involved in the fermentation of complex carbohydrates, celluloses in this case, derived from dung (Table 2). Many bacteria found in the gut of dung beetles are responsible for breaking down the cellulose and other complex plant materials into easily assimilable food, which dung beetles. Several factors, including diet, habitat, and environmental conditions influence the diversity of bacteria linked with gut of dung beetles. Some of these bacteria are species from the genera *Lactobacillus*, *Bifidobacterium*, and *Clostridium* that are used in fermenting the fiber components of dung. In *Scarabaeus sacer*, a dung beetle, the bacterial communities contribute by fermenting cellulose and other polysaccharides with the potential of the beetle extracting nutrients from dung materials that are hard to digest. Disturbances in this mutual relationship, like conventional antimicrobial therapy, may affect the capacity of beetles to break down nutrients and, hence, augment their development and fertility (Gotcha, 2022). The bacterial communities associated with the gut of dung beetles depends on various factors such as environment, habitat, biological interactions, feeding habits and food availability (Figure 1).

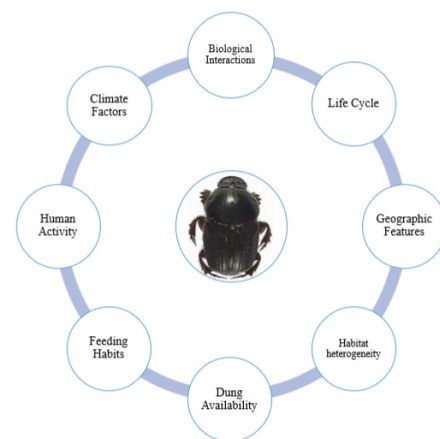


Figure 1: Factors affecting bacterial microbiome associated with the gut of scarab beetles.

Table 1: *Dung beetle species and their associated bacterial gut microbiota.*

Species	Bacterial communities
<i>Copris incertus</i>	1,699 OTUs and 302 genera (Suárez-Moo <i>et al.</i> , 2020)
<i>Copris tripartitus</i>	<i>Streptomyces</i> sp. (Park <i>et al.</i> , 2012)
<i>Cotinis nitida</i>	<i>Clostridium</i> , <i>Betaproteobacteria</i> , <i>Bacteroidetes</i> , <i>Bacillales</i> , and <i>Deltaproteobacteria</i> (Kucuk <i>et al.</i> , 2023)
<i>Euoniticellus intermedius</i>	<i>Comamonadaceae</i> , <i>Dysgonomonas</i> , <i>Entomoplasmatales</i> , <i>Clostridiaceae</i> , 12 OTUs from the <i>Entomoplasmatales</i> group (Shukla <i>et al.</i> , 2016)
<i>Euoniticellus triangulatus</i>	<i>Enterobacteriaceae</i> (Shukla <i>et al.</i> , 2016)
<i>Onitis philemon</i>	12 OTUs (Surabhi <i>et al.</i> , 2018)
<i>Onthophagus taurus</i>	<i>Clostridium</i> , <i>Bacillus</i> , <i>Lactobacillus</i> , <i>Enterococcus</i> , and <i>Bacteroides</i> (Macagno and Moczek, 2023)
<i>Thorectes lusitanicus</i>	<i>Proteobacteria</i> , <i>Firmicutes</i> , and <i>Actinobacteria</i> . <i>Gammaproteobacteria</i> (Hernández <i>et al.</i> , 2015)
<i>Oniticellus cinctus</i>	<i>Firmicutes</i> , <i>Bacteroidetes</i> , <i>Actinobacteria</i> , <i>Aspergillus</i> , <i>Penicillium</i> (Mahboob and Tahseen, 2022)
<i>Catharsius molossus</i>	<i>Lactococcus</i> and <i>Enterococcus</i> (Chen <i>et al.</i> , 2024)
<i>Coprina brunneum</i>	<i>Oxalobacteraceae</i> , <i>Rhizobiales</i> , and <i>Porphyromonadaceae</i> (Lefort <i>et al.</i> , 2023)
<i>Coprina giveni</i>	<i>Oxalobacteraceae</i> , <i>Rhizobiales</i> , and <i>Porphyromonadaceae</i> (Lefort <i>et al.</i> , 2023)

Table 2: *Functions of gut bacteria of some species of dung beetle.*

Gut bacteria/ Dung beetle species	Functions
<i>Bacteroides/ Onthophagus taurus</i>	Digestion of complex polysaccharides (Macagno and Moczek, 2023)
<i>Lactobacillus/ Catharsius molossus</i>	Fermentation and lactic acid production (Mao <i>et al.</i> , 2023)
<i>Enterococcus/ Onthophagus gazella</i>	Nitrogen recycling and ammonia assimilation (Parker, 2021)
<i>Proteobacteria/ Onthophagus gazella</i>	Detoxification of harmful compounds (Parker, 2021)
<i>Firmicutes/ Onthophagus nuchicornis</i>	Enhancing nutrient absorption and energy harvest (Parker <i>et al.</i> , 2020)
<i>Bacillus thuringiensis/ Scarab beetles</i>	The majority of gut bacteria had antibacterial activity against <i>Bacillus thuringiensis</i> (Shan <i>et al.</i> , 2014)

Conclusions and Recommendations

Dung beetles, with their symbiotic relationships with gut microorganisms, form a complex and ecologically significant system crucial for their survival and ecosystem function. The gut microbiota of dung beetles, characterized by bacterial phyla such as *Firmicutes*, *Proteobacteria*, *Bacteroidetes*, and genera like *Lactobacillus*, *Bifidobacterium*, and *Clostridium*, plays a pivotal role in breaking down complex organic compounds, detoxifying toxins, and enhancing nutrient utilization from their dung-based diet. Additionally, the variation in gut microbiota across developmental stages and environmental conditions highlights the specified dietary requirements depending upon larval stage, resilience of dung beetles against habitat, and climate variations. This review presented the different studies of gut bacteria in scarab beetles and their diversity from a new angle. *Firmicutes*, *Proteobacteria*, *Bacteroidetes*, and *Actinobacteria* are dominant bacterial phyla that differ in different species, diets, and habitats, with specific host distribution showing an important host-microbe interaction.

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Novelty Statement

This review highlights the significance of exploring microbial diversity associated with dung decomposition and its ultimate contribution to the distribution and conservation of local biodiversity of dung beetles and associated microbiota.

Author's Contribution

MH and SK conceived the idea, planned, and prepared the original draft.

AI, UZ, AN, and SHS critically reviewed the manuscript.

Conflict of interest

The authors have declared no conflict of interest.

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