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Review Articles

Dung-Associated Insects: Ecological Roles and Potential Benefits in Agricultural

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ABSTRACT

Dung-associated insects, often referred as coprophagous insects and detritivores, help break down organic matter, returning essential nutrients to the soil and promoting plant growth. Their activities not only enhance soil structure and fertility but also aid in pest control by reducing the populations of parasites and pathogens associated with animal waste. Understanding the complex relationships between dung-inhabiting insects and their environment highlights the crucial role these creatures play in maintaining ecological balance. These insects facilitate nutrient cycling and contribute to overall biodiversity. It plays a crucial role in promoting healthy ecosystems, as its presence can lead to improved soil health and increased agricultural productivity. Implementing integrated pest management practices that encourage the presence of dung-inhabiting insects can further enhance their role in sustainable agriculture, promoting a balanced ecosystem where both crops and beneficial organisms grow well. This approach not only promotes biodiversity but also enables farmers to adopt more environmentally friendly practices that contribute to long-term agricultural resilience.

Keywords: Coprophagy, ecosystem balance, nutrient cycling, sustainable agriculture, soil health

1. INTRODUCTION

Dung-associated insects are integral components of ecosystems, playing crucial roles in nutrient recycling, pest control, and ecosystem maintenance. They contribute to the decomposition process, control pests, and enhance biodiversity. Dung attracts various insect species, such as dung beetles and flies, which are essential for sustaining ecological balance by managing organic waste. Found across diverse climatic regions, the composition and functionality of dung-associated insect communities vary based on environmental conditions, substrate characteristics, and ecological interactions (Saha et al., 2021; Piñero & Avila, 2004).

The diversity and abundance of these insects are profoundly influenced by factors such as moisture levels, climate, and proximity to water sources. Their interactions with microbial communities further enhance their ecological functions, such as decomposition, aeration, and nutrient cycling (Viegas et al., 2014). These processes contribute significantly to soil fertility, sustainable agriculture, and the overall health of ecosystems (Liang et al., 2024).

The following sections examine the ecological roles, functional interactions, and economic significance of dung-associated insects, highlighting their importance in maintaining ecological balance and promoting sustainable agricultural practices.

2. FACTORS INFLUENCING THE DIVERSITY AND ABUNDANCE OF DUNG-ASSOCIATED INSECTS

Dung-associated insects exhibit remarkable diversity, encompassing numerous species adapted to exploit dung as a primary resource for feeding, reproduction, and habitat. These insects are found globally, varying across ecological zones and climatic conditions, and play essential roles in nutrient recycling, pest control, and biodiversity maintenance (Saha et al., 2021). The dung-associated insect community is primarily dominated by dung beetles (Scarabaeinae and Aphodiinae) (Figure 1) and flies (Diptera), with other insect groups such as termites and ants contributing to specific ecological functions (Piñero & Avila, 2004).

Dung-associated insects exhibit immense diversity, with approximately 6000 to 8000 species of dung beetles alone (Arellano, 2016). In general, there are three functional groups in the dung beetle's classification: dwellers, tunnellers, and rollers (Maldonado et al., 2019). The division of competitively subordinate guilds from more excellent ones may be due to the dynamic limitations that permit them to endure sympatrically with the competitive supremacy hierarchy of dwellers < tunnellers < rollers defined by reducing ecological tolerance and rising energetic costs (Scholtz et al., 2009).

Furthermore, this hierarchy further explains the evolution and diverse functionality among the dung beetle community through their physical structures. For example, the dwellers possess smaller protibial and thinner tibia that could be brittle for digging hardened soil but plausible for dwelling in the highly moistured cow dung (DeCastro-Arrazola et al., 2020). Although the tunnellers and rollers are similar in their general behaviour (Table 1), physically the rollers have bigger pronotum: to balance the bigger dung balls while rolling, 'the bigger the pronotum, the larger the size of their dung balls'; bigger protibial: to bear the entire biomass of dung beetle with the ball weight; with many tibial teeth: to create friction to stabilize themself while rolling the balls upside down; thicker femur: to spin the dung ball throughout the transportation and longer tibia: to speed up the relocation process (DeCastro-Arrazola et al., 2020; Reid & Storey, 2000; Scholtz et al., 2009).

Figure 1. An example of common dung beetle from genus *Catharsius* (Family Scarabaeinae). Source of image: voucher specimen from Zoollery (Museum of Zoology) Department of Biology, Faculty of Science, Universiti Putra Malaysia.

Table 1. Differences between dweller, tunneller and roller dung beetles

Functional groups	Dweller (Endocoprids)	Tunneller (Paracoprids)	Roller (Telecoprids)
Tribe Species name Locality Body size	Eurysternini *Eurysternus caribaeus* Herbst, 1789 Costa Rica 15mm	Dichotomiini *Heliocopris neptunus* Boheman, 1857 Botswana 35mm	Canthonin Circellium bacchus Fabricius, 1781 South Africa 40mm
Tribes	Oniticellini (Some)	Coprini, Dichotomiini, Onitini, Phanaeini, Onthophagini, Oniticellini	Canthonini, Eucraniini, Eurysternini, Gymnopleurini, Scarabaeini, Sisyphini
Physical key (major)	Smaller pronotum Smaller protibial Thinner tibia	Small pronotum Protibia with tibial teeth Smaller and thinner femur	Bigger pronotum Bigger protibial and more tibial teeth Thicker femur Longer tibia
General behaviour			
Dung management	No burying Bury (if) between pat and soil interference	Burying ball-shaped dung Tunnel below dung pile	Rolling and burying ball-shaped dung in soil tunnel piles
Life cycle	Live and develop within the dung/ just beneath it	Live under the soil after transporting vast dung balls/no dung left	Live under the soil after transporting vast dung balls/no dung left
Nesting/ brooding chamber	No nesting/brooding chamber	At the end of the tunnel	At the end of the tunnel
Burrow	No burrow	Burrow the eggs under soil	Burrow the eggs under the soil
Eggs	Lay eggs within the dung	Lay eggs with the dung ball (one in each)	Lay eggs with the dung ball (one in each)
Larvae	Hatches and grows within the dung	Hatches within the dung ball	Hatches within the dung ball
Larval feed	The entire dung	The dung ball	The dung ball
Degradation	Larvae feeding (mainly)	Relocation of the dung soil beneath the dung (under soil -10cm) Larvae feeding (dung ball)	Relocation of the dung far from the source (From the source ~1.2m) Larvae feeding (dung ball)
Modification of dung	Changes dung into lightweight granular material	Removes the dung from its location	Removes the dung from its location

(Source: Byk & Piętka, 2018; Dellacasa & Dellacasa, 2005; Floate, 2011; Nemes & Price, 2015; Pokhrel et al., 2020; Tomkins et al., 1999; Scholtz et al., 2009)

The diversity and abundance of dung-associated insects are influenced by environmental factors such as moisture, temperature, and grazing intensity (Manning et al., 2016). These insects adapt their behavior and physiology to varying habitats, influencing the decomposition rates and nutrient cycles. Studies have shown that tropical regions host a higher diversity of dung beetles compared to temperate zones due to the favorable climatic conditions and greater availability of herbivore dung. In fact, moisture levels, vegetation type, and proximity to water sources affected insect distribution and activity (Nichols et al., 2008).

Dung-associated insect abundance and diversity decline markedly within a week of dung deposition, necessitating adaptive strategies for the survival of adult beetles and their progeny. Adult beetles typically feed on fresh herbivore dung, whereas larvae utilize older dung (>7 days) (Holter, 2016). Due to the limited digestive capacity of insects, fibrous content from ruminant dung is largely unsuitable as food (Vannier & Chen, 2002). Instead, beetles ingest fine particles, generally no larger than 0.2% of their body length (Madzivhe et al., 2020), which are rich in microbial biomass, steroids, and amino acids that provide essential nutrients (Sládeček et al., 2021). Nevertheless, specialized mouthparts allow dung beetles to filter out indigestible polysaccharides and excess fluid, thereby concentrating digestible particles, a mechanism comparable to that of dung flies (Vannier & Chen, 2002).

Coprophagous insect abundance and diversity are also dependent on the properties and exposure of the cow dung and the environmental and chemical cues (Sládeček et al., 2021). When dung is excluded from the accessibility of the insects, a significant decline in the rate of decomposition is noticed compared to the uncaged dung samples (Pecenka & Lundgren, 2018). Nonetheless, in both inclusion and exclusion conditions, the insect abundance and complexity reduced drastically to 28% and 17% respectively, during the second week (7–14 days) (Lee & Wall, 2006). Because the insects prefer the high moisture of the freshly excreted dung to colonize and consume, when the moisture content drops, the insects leave the dung samples, allowing them to colonize.

Furthermore, the succession of dung-inhabiting beetles and flies reflects the succession of dung-emitted volatile compounds (Sládeček et al., 2021). Abundance and diversity of dung-attracted insects are also strongly influenced by climatic conditions, with early summer supporting richer insect communities than late summer due to moisture loss at higher temperatures (Viegas et al., 2014). A further explanation for the decline in coprophagous insects after a period of a week is increased predation pressure on the dung community (Noriega & Navarrete-Heredia, 2013). Overall, insect diversity, abundance, and biomass are positively associated with substrate moisture; the composition of dung itself, shaped by host digestibility, also regulates coprophagous arthropod populations (Holter, 2016). Moreover, dung deposited near water sources supports fewer insects, except endocoprids, likely due to intensive grazing that lowers carbon and nitrogen levels within 100 m of the source, reducing plant and insect diversity (Maldonado et al., 2019).

Despite their ecological importance, dung-associated insect diversity is threatened by habitat loss, pesticide use, and climate change. Land-use changes and intensive agricultural practices disrupt their habitats and, reduce dung availability, leading to population declines (Maldonado et al., 2019). Understanding and preserving the diversity of dung-associated insects is critical for maintaining ecological balance and sustaining their contributions to ecosystem health and agricultural productivity. Further research is needed to explore the drivers of diversity and the functional roles of less-studied species within this group.

3. ECOLOGICAL ROLES OF DUNG-ASSOCIATED INSECTS

Dung-associated insects play a fundamental role in nutrient recycling and maintaining soil health, making them indispensable components of both natural and agricultural ecosystems. By facilitating the decomposition of manure and other organic matter, these insects break down complex materials into simpler, bioavailable nutrients, significantly enriching soil fertility and promoting plant growth (Arellano, 2016). Their activities help to aerate the soil, enhance water infiltration, and reduce the build-up of organic waste, contributing to healthier and more productive environments.

In addition to their contributions to nutrient cycling, dung-associated insects are crucial in regulating pest populations. *Aphodius* spp. and other dung beetles reduce livestock gastrointestinal parasite availability on pasture by modifying cow-pat micro-environment and reducing parasite larval survival (Sands & Wall, 2017).

Furthermore, these insects play an integral role in food webs, serving as a primary food source for a wide range of predators, including birds, mammals, and reptiles (Huerta et al., 2013). This creates a vital link between organic waste management and higher trophic levels, supporting biodiversity and ecological resilience.

Cow dung supports diverse insect communities dominated by dung beetles (*Aphodius fimetarius, Onthophagus gazella, Labarrus pseudolividus, Sphaeridium* spp.) and coprophagous flies (*Sepsis cynipsea*), whose composition changes with dung age and contributes to nutrient recycling, soil aeration, and pest control (Sládeček et al., 2021; Sands & Wall, 2017; Viegas et al., 2014; Liang, 2024).

Dung-associated insects play a crucial role in biogeochemical cycling and soil fertility, making them effective decomposers of cow dung (Maldonado et al., 2019). Their ecological functions include nutrient recycling, bioturbation, seed dispersal, parasite suppression, and dung decomposition (Lee & Wall, 2006; Pecenka & Lundgren, 2018). Through dung burial and bioturbation, they enhance ecosystem productivity by increasing nutrient accessibility to plants beyond the dung patch (>10 cm) (Nichols et al., 2008; Yamada et al., 2007). Importantly, dung beetles reduce pest fly populations and cattle gastrointestinal parasites by limiting resource availability (Wise et al., 2020). Collectively, these contributions highlight the indispensable ecological and economic value of dung-associated insects.

Globally, dung beetles are one of the largest insect groups that feed on herbivore dung, utilizing and moulding the dung throughout their life stages (adult beetles and larvae) (Holter et al., 2016). Their specific importance is described with their relocation of the herbivore dung and burying it for nesting purposes by rolling the balls using their hind legs (Ocampo & Hawks, 2006). The relocation of dung balls assists in the inhibition of ammonia volatilization, improvement of soil fertility, prevention of nutrient loss, and the activation of decomposing microbes that are responsible for nitrogen fixation (Nichols et al., 2008). Therefore, it encourages nitrogen absorption of the plants, moisture loss in the manure, proliferation of aerobic microbes and nitrification.

On the other hand, the larvae are bulk feeders (>380% and >175% of their dry body weight during instar II and III, respectively) over the old dung samples (>7 days old). In general, three major groups of dung beetles dominate over cow dung: telecoprids, paracoprids, and endocoprids. The telecoprids and paracoprids usually have limited access to the food within their nests compared to the endocoprids. Unlike adult beetles, larvae are unselective over food moisture, thus, they feed on dry cow dung during the hatching stage. Although ingestion is rapid, assimilation is only responsible for 7–10% of the ingestion (Holter, 2016). The rapidity in energy gaining is primarily for its growth and development.

Furthermore, though beetles contributed only 1.5–3% of coprophagous arthropods but are actively associated with the entire arthropod community (Pecenka & Lundgren, 2018). Interestingly, the dung beetles deposit the egg beneath cow dung, which will then hatch and feed on the dried fibrous materials that remain in the cattle dung (Holter, 2016). Because they are responsible for bioturbation and tunnelling, they aerate the cow dung, exposing the interior surface to other microbes, driving it to decompose even faster (Forgie et al., 2018).

Rolling the dung balls is a mating signal among the roller beetles, such as *Kheper nigroaeneus*. The male beetles build the balls; the larger they can attract their mating pair (Tomkins et al., 1999). Then, the female settles herself on the dung for a chariot roll by the male beetles until the translocation of the cow dung. After the relocation, the female lays an egg sealed with an excrement cap within each nesting ball upon burrowing (Scholtz et al., 2009). Like every other organism, the dung beetles specifically dwellers, confront active intraspecific competition for food and habitat with the advanced tunnellers and rollers. Therefore, to evade competition, the dwellers breed within the dung when the substrate becomes less attractive to other beetles during cool and dry periods, as their larvae feed on older dung samples (Lee & Wall, 2006).

4. FUNCTIONAL INTERACTIONS IN DUNG ECOSYSTEMS

The interspecific relationship is a must whenever there is a coexistence of more than two organisms in the same niche. Similarly, when the dung beetle is present since the first day of deposition, the association between the early-stage decomposers, like dung bacteria and coprophils, is significant. In other contexts, the contribution of dung beetles to the dung might not only be subjected to the arthropods alone, perhaps due to the presence of microflora found within their digestive tract. In general, the dung beetles possess diverse microflora within the guts, including Bacteriodes, Firmicutes, and Proteobacteria covering about 967 taxa overall (Ebert et al., 2021). This latest identification proves the endosymbiotic coexistence of these bacterial colonies in the dung since its inception. According to Viegas et al. (2014), when the colonization of dung beetles accelerates in the first week due to the highest moisture level in the substratum, the discharge of the bacterial strains into the dung is also boosted to aid in further decomposition and conditioning for fungal invasion.

Interestingly, among the dung beetles of different functional groups and in the same species, the diversity of the microbiota colony is not the same due to the environmental acquisition and adaptability of the species over the different locations. Correspondingly, the flying dung beetles of paracoprids and telecoprids can switch to various habitats and food resources by modifying the gut microbe colonies for divergent nutrient degradation (Ebert et al., 2021). However, in the flightless dwellers, the microbiota seemed to be more stable, indicating a mutualistic association with the consumption of the dung particles. Changes in microbiota diversity are closely linked with evolutionary adaptations, and the unique gut morphology of *Cephalodesmius* may provide a fermentation chamber that supports microflora involved in the digestion of organic matter, nutrient assimilation, and detoxification of plant compounds, while ensuring the retention of vital microbial taxa (Ziganshina et al., 2018).

Surprisingly, during every stage of dung beetles, they seemed to possess diverse and dissimilar bacterial colonies to break down their dietary molecules. For instance, the most typical microbial class in the guts of *Melolontha hippocastani* Fabricius 1801, adult beetle and larval midgut was recognized as Gammaproteobacteria, whereas the hindgut of *Melolontha melolontha* L. 1758, larvae were inhabited by *Clostridiales* and *Methanobrevibacter* sp. (Ziganshina et al., 2018). Likewise, the hindgut of *Amphimallon solstitiale* L. 1758, and *Oryctes nasicornis* L. 1758, larvae revealed a notable level of *Bacteriodes, Bacillaceae, Desulfovibrionaceae, Parabacteriodes, Porphyromonadaceae, Parabacteroides*, and *Ruminococcaceae*.

These Bacteroides and Porphyromonadaceae are responsible for the fermentation of carbohydrates, creating a pool of energy sources not only for the beetles but also for other fungal colonies inhabiting the dung after being expelled from the intestinal guts. On the other hand, those from the family Ruminococcaceae are accountable for hydrolyzing the polysaccharides (cellulose and hemicellulose) by secreting cellulosomal enzymes and cellulose-binding proteins. In other words, this is the family responsible for breaking down the cellulolytic compounds within and outside the gut of these arthropods. Hence, these phyla aid in the decomposition of the refractory part of the dung. Since the larvae possess abundant bacteria responsible for cellulase secretion, the larvae's diet preference falls after the adult dung beetle (>7 days) when lesser moisture and higher fiber content are present in the dung (Shukla et al., 2016).

Besides, the beetle possesses a variety of bacterial genera throughout its developmental stage of the life cycle. The adult beetle gut is dominated by Enterobacter and Serratia (uric acid metabolism), pupae and larvae are abundant with *Parabacteroides* and *Dsygnomonas* (nitrogen fixation and cell wall degradation), whereas the eggs possess *Nocardioides* and *Hydrogenophaga*. This justifies the diversity of microbiota due to the life demands of beetles in different stages and dietary requirements at each stage (Suárez-Moo et al., 2020). Corresponding to the dietary aspects, gut structure, and microbiota diversity, the adult beetles *Euoniticellus triangulates* Harold 1873, and *E. intermedius* Reiche 1849, possess mandibles to assimilate nutrient-rich dung (1–7 days) and infiltrate the moisture content of the water. On the other hand, the larvae depict sclerotized mandibles to grind coarser particles of plant materials from the dung with higher carbon and nitrogen ratios (Shukla et al., 2016).

In addition, female dung beetles tend to discard their feces upon the broods before burrowing. Since the hindgut of these beetles consists of tremendous decomposing microbial species, don't they decompose the broods, which are supposed to be consumed by larvae upon hatching? Potentially, the larvae might feed on microbial colonies as their food source or on the simplest form of nutrients broken down by the microbial decomposers. Therefore, the translocation of these microbial colonies on the brood ensues to expedite the decomposition of cow dung.

Apart from the microbiota found in the gut, the tunnellers and rollers from the environment aid fungal and bacterial colonies in traveling from one niche to another by attaching to their tarsi and tarsal claws of the hind legs. Furthermore, dung beetles roll dung balls away from the deposition site to burrow, making the dung an available resource for immobile bacteria and fungi to facilitate rapid disintegration (Holter, 2016; Shukla et al., 2016). Clearly, the mutualistic and commensal relationships between these organisms warrant further examination to enhance the understanding of interspecific interactions between the microflora and macrofauna in cow dung. The observed differences in gut microbiota between the adults and larvae of *Euoniticellus intermedius* and *E. triangulatus* are likely to influence nutrient assimilation from ingested dung at different life stages (Shukla et al., 2016).

5. ECONOMIC AND AGRICULTURAL BENEFITS

Dung-associated insects play a crucial role in nutrient recycling, promoting soil health and enhancing agricultural productivity through their activities (Bertone et al., 2006). These insects, especially dung beetles, break down organic matter and facilitate the decomposition process, increase the availability of nitrogen, phosphorus and other mineral nutrients in the rooting zone, which in turn improves plant nutrient uptake and aboveground biomass. Meanwhile, their bioturbation also improves soil structure, fertility, and porosity, promoting water infiltration and reducing surface nutrient loss through runoff, processes. Moreover, their presence in agricultural ecosystems not only supports sustainable farming practices but also contributes to biodiversity, as they create habitats for other organisms, particularly the pollinators, which then help to increase the yield production (Saha et al., 2021). Most importantly, by recycling nutrients into the soil, dung insects boost crop yields and enhance soil health, reducing the need for synthetic fertilizers thus lowering the cost for agricultural management (Saha et al., 2021).

Apart from nutrient provider, dung beetles also play a significant role in suppressing pest populations in agricultural ecosystems by eliminating the breeding substrates of many harmful insects. Fresh dung serves as the primary oviposition and developmental site for pestiferous flies, such as *Musca domestica* (house fly) and *Haematobia irritans* (horn fly), which are notorious for reducing livestock productivity and transmitting pathogens (Espinoza et al., 2025). By burying and fragmenting dung pats rapidly after deposition, dung beetles drastically reduce the availability of moist, nutrient-rich material that supports fly larval development. In addition, some beetle species directly predate on eggs and larvae of dung-breeding flies, thereby exerting both habitat-removal and biotic-regulation pressures on pest populations (Ix-Balam et al., 2018).

Dung beetles also play a pivotal role in secondary seed dispersal, a process that significantly influences vegetation dynamics in both natural and agricultural ecosystems. Many herbivorous mammals ingest seeds during grazing, which later pass through the digestive tract and are deposited in dung. Dung beetles utilize these fecal resources by burying and relocating dung beneath the soil surface, often transporting intact seeds along with it. This behavior effectively removes seeds from the exposed dung surface, where they are highly vulnerable to desiccation, predation, and trampling, thereby increasing their probability of germination and successful establishment (Andresen & Levey, 2004; Farias & Hernández, 2017).

The burial of seeds by dung beetles also creates favorable microsites for germination and seedling survival. Seeds deposited in the soil are protected from direct solar radiation and moisture loss, while also being placed in nutrient-enriched microhabitats created by decomposing dung. These conditions promote higher seedling recruitment compared to unburied seeds, enhancing plant regeneration and contributing to plant community diversity (Andresen & Levey, 2004). Moreover, the spatial redistribution of seeds by dung beetles reduces clustering near parent plants and decreases density-dependent mortality (Lawson et al. 2012). This dispersal pattern prevents competitive exclusion and supports the coexistence of multiple plant species within the ecosystem.

In economic aspect, the combined services of dung-associated insects represent substantial, tangible benefits for both agricultural systems and livestock health. These insects mitigate gastrointestinal parasites and disease vectors, promoting livestock well-being. Their presence in the ecosystem can lead to healthier herds, reduce veterinary costs, and enhance overall farm productivity, creating a win-win situation for both farmers and the environment. By fostering a balanced ecosystem, farmers can harness the natural benefits provided by dung insects, reducing reliance on chemical treatments and promoting organic farming practices that align with sustainable agriculture principles (Jones et al., 2019).

6. CONCLUSIONS

In a nutshell, dung-associated insects are indispensable to ecosystem functioning, nutrient cycling and promoting biodiversity. The multifunctional roles of dung-associated insects not only highlighted their ecological importance but their integration into sustainable agricultural management and practices. Their roles in pest control, soil health, and biodiversity maintenance underscore their importance that help in enhancing agricultural productivity. Conservation and research initiatives are crucial to safeguarding these insects and their ecological contributions for future generations.

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