

Behavioural ecology and soil engineering potential of millipedes (Diplopoda)

Yashwant Patne^{1*}, Ravi Barde²

¹ Department of Zoology, N.E.S Science College, Nanded, Maharashtra, India

² Department of Zoology, Shri Guru Buddhiswami Mahavidhyalaya, Purna, Parbhani, Maharashtra, India

Corresponding Author: Yashwant Patne

Abstract

Millipedes (Class Diplopoda) are important components of soil macrofauna and contribute significantly to decomposition and nutrient cycling in terrestrial ecosystems. This review provides a critical synthesis of the behavioural ecology of millipedes and re-evaluates their role as behaviourally driven regulators and ecosystem engineers in soil ecosystems. Relevant literature published on millipede behavior, feeding ecology, aggregation, reproductive adaptations, chemical defense, and environmental stress responses was critically reviewed using published peer-reviewed sources. Millipedes exhibit behavioral adaptations such as moisture tracking, aggregation, selective detritivory, and defensive chemical secretion, which strongly influence litter decomposition, microbial succession, nutrient mineralization, and soil structure. Their responses to climatic and anthropogenic stressors also support their importance as ecological indicators. Millipedes function as detritivores, ecosystem engineers, and behavioral regulators of soil ecological processes. Their ecological significance highlights the need for greater integration of Diplopoda into soil biodiversity and sustainability studies.

Keywords: Diplopoda, detritivore behaviour, soil engineering, chemical defense, bioindicators

Introduction

Millipedes are one of the earliest successful terrestrial arthropod lineages (Shear, 2015) [16]. Their evolutionary persistence is closely linked to detritivory and adaptation to soil-associated microhabitats within the leaf litter layer. Although over 12,000 species have been formally described, global diversity is likely far higher (Golovatch & Kime, 2009) [9]. For decades, diplopod research has remained largely descriptive. However, modern soil ecology has shifted its attention toward functional roles and behavioral

mechanisms. Millipede behavior, including moisture tracking, aggregation, selective feeding, and chemical defense, directly shapes decomposition dynamics, nutrient cycling, and soil structural properties. Therefore, this review argues that millipedes should not be regarded merely as passive decomposers, but as behaviourally driven regulators and ecosystem engineers influencing multiple soil ecological processes. This review presents the latest research in millipede behavioural ecology and the role they play in soil ecosystem stability and resilience.

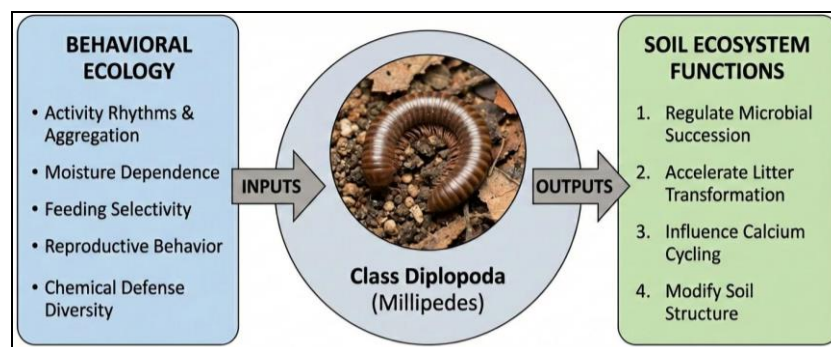


Fig 1: Conceptual overview of behavioural ecology and ecosystem roles of millipedes

Literature Search Strategy

Scientific databases such as Google Scholar, Scopus, Web of Science, and PubMed were used to gather relevant literature published between 2000 and 2025. Keywords like “Diplopoda,” “millipede behavior,” “soil macrofauna,” “detritivore ecology,” “aggregation behavior,” and “soil ecosystem engineering” guided the search. Peer-reviewed articles focusing on behavioral ecology, decomposition dynamics, nutrient cycling, chemical defense, and environmental stress responses in millipedes were critically evaluated and synthesized for this review.

Behavioural Adaptations and Microclimate Regulation

1. Moisture Dependence and Hydrotaxis

Millipedes display a pronounced affinity for moisture due to their vulnerability to drying out. Experimental studies have shown that their surface activity is closely linked to high relative humidity. The Tomosvary organ acts as a hygroreceptive structure, facilitating movement toward moist substrates (Ilić *et al.*, 2019) [10]. Kinematic analyses have shown that coordinated leg-wave movements enhance stability and mobility during substrate navigation (Garcia *et al.*, 2015) [8]. This behavioral sensitivity ensures; Reduced

water loss Optimized feeding periods Synchronization with microbial activity Moisture-dependent activity creates temporal pulses in litter processing

2. Aggregation and Microhabitat Buffering

Aggregation, once viewed just as social behaviour, is now recognised as a tactic for stabilising microclimates. The relationship between moisture preference and directional movement in millipedes is illustrated in Figure 2A. Clustering reduces evaporative losses and may enhance

chemical defense efficiency (Kania & Wesener, 2021)^[11, 19]. Such behavior becomes particularly significant in fragmented or drought-prone habitats, where microenvironmental buffering determines survival. Recent biomechanical studies have further demonstrated that millipede body organization and locomotion dynamics contribute significantly to movement efficiency in complex soil microhabitats (Garcia *et al.*, 2020)^[7]. Aggregation-mediated microclimate stabilization and habitat buffering are represented in Figure 2B.

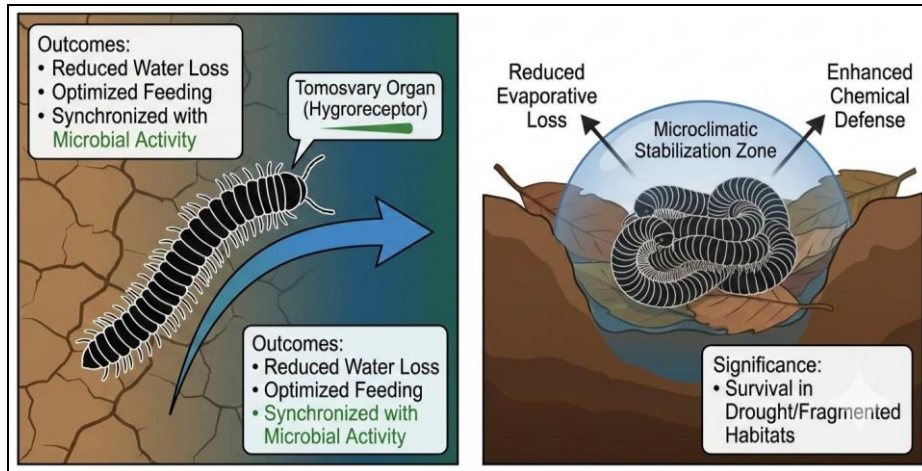


Fig 2: Behavioural adaptations of millipedes associated with microclimate regulation

- (A) Moisture dependence and hydrotaxis behaviour
- (B) Aggregation and microhabitat buffering in soil habitats

Feeding Ecology and Ecosystem Engineering

1. Selective Detritivory

Millipedes are not indiscriminate detritivores; isotopic evidence suggests they selectively consume fungus-conditioned litter. Microbial conditioning of substrates offers a more nutritious food source and enhances the animals' digestive efficiency. Millipede-induced litter fragmentation results in the following: increased surface area for microbial growth, accelerated nutrient mineralization, and heightened carbon turnover. Improved efficiency in the breakdown of organic matter has been observed in the presence of active millipedes (David *et al.*, 2020)^[4]. Figure 3A summarizes the ecological role of selective litter feeding and microbial regulation by millipedes. Thus, millipedes function as moderators of microbial succession rather than merely passive litter

processors. Morphological adaptations associated with feeding specialization have also been documented in certain diplopod groups, indicating evolutionary diversification in feeding mechanisms (Moritz *et al.*, 2021)^[13].

2. Calcium and Biogeochemical Cycling

Millipedes contribute to the soil mineral pool because of the calcium content in their cuticles, which becomes available after molting and cuticle decay. Millipede biomass has a quantifiable impact on the redistribution of calcium in the upper soil layers of temperate hardwood ecosystems. Millipede-mediated calcium redistribution and nutrient cycling processes are illustrated in Figure 3B. This activity is critical in scenarios of soil acidification stress. (Sagi *et al.*, 2019; Snyder & Hendrix, 2008)^[15, 17]

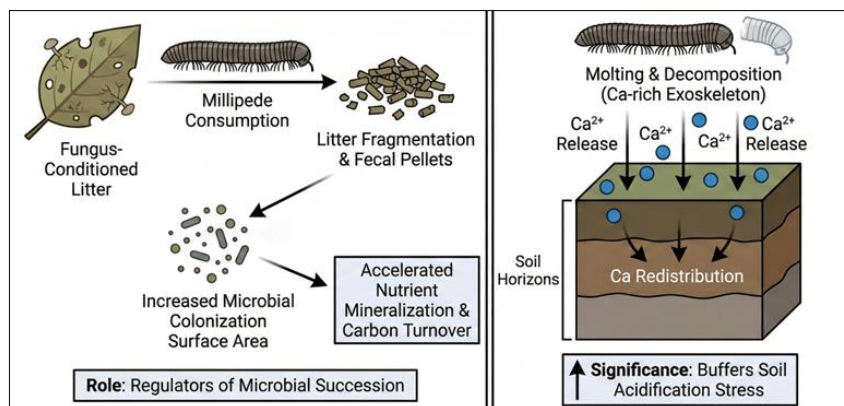


Fig 3: Ecosystem engineering functions of millipedes

- (A) Selective detritivory and microbial regulation
- (B) Calcium cycling and biogeochemical contributions in soil ecosystems

Reproductive and Social Behaviour

1. Courtship and Chemical Signalling

Millipedes use specialized gonopods to transfer their gametes. The courtship ritual involves tactile antennation and chemical communication, as reported by (Ilić *et al.*, 2019) [10]. The chemical components of the courtship ritual serve to further reinforce species integrity and reproductive isolation.

2. Maternal Investment

Maternal care, as reported by Wesener (2021) [19] for the Glomerida order, involves the guarding of eggs and the creation of capsules from soil and fecal matter, thus improving the chances of offspring survival in different moisture regimes. The presence of this type of parental care in millipedes argues against the general assumption of millipedes as low-investment invertebrates (Paoletti *et al.*, 2007) [14].

Defense Ecology

1. Mechanical Protection

Millipedes have a range of morphological and behavioural adaptations to protect them against predators and harsh conditions. Perhaps the most typical defence is volvation, where the body curls into a tight spiral to protect the vulnerable ventral surface and appendages. This is most common in pill millipedes (Order Glomerida). Furthermore, the sclerotized tergites provide a protective armour to minimise injury and predation. The round body and jointed armour-like tergites also provide protection against predators. Mechanical defence in millipedes is therefore an effective initial survival mechanism, prior to chemical defence. Behavioral studies have also demonstrated that defensive coiling responses vary depending on environmental conditions and disturbance intensity (Srinivasa & Mohanraju, 2011) [18].

2. Chemical Defense Diversity

Chemical compounds are synthesized by millipedes. Recent metabolomic studies have identified considerable diversity, which implies ecological specialization and pharmaceutical potential. There is also an effect on predator learning. Recent chemical analyses of *Brachycybe* species have further revealed considerable diversity in defensive secretions, suggesting ecological specialization among millipede taxa (David & Hand, 2009) [3]. Major classes of defensive compounds and their ecological functions in Diplopoda are summarized in Table 1.

Table 1: Major chemical defense compounds reported in millipedes and their ecological functions

Compound Type	Ecological Function	Representative Groups
Benzoquinones	Irritant defense	<i>Julida</i>
Phenols	Antimicrobial activity	<i>Glomerida</i>
Alkaloids	Toxic deterrents	<i>Brachycybe</i>
Hydrogen cyanide	Lethal chemical defense	<i>Polydesmida</i>

Responses to Environmental Stress

1. Climate Stress

When faced with drought, millipedes withdraw from the surface and burrow deeper into the ground to avoid

desiccation. Their behavioral flexibility is advantageous for coping with harsh environmental conditions, although high levels of stress can affect feeding and reproductive activities (Custodio *et al.*, 2022) [2].

2. Heavy Metal Contamination

Millipedes accumulate heavy metals, such as cadmium and lead, in their bodies, making them good bioindicators of their ecosystem. High levels of stress proteins in millipedes exposed to pollutants confirm their sensitivity to contaminated environments.

3. Habitat Fragmentation

Habitat fragmentation is associated with reduced species richness, but decomposition is maintained, implying that detritivore guilds exhibit functional redundancy (Edo *et al.*, 2024) [6].

Ecosystem-Level Contributions

Millipedes play a crucial role as ecosystem engineers by decomposing organic matter, facilitating microbial colonization, enhancing soil aggregation, and increasing water infiltration. They also serve as a food source for various organisms, including birds, amphibians, beetles, and mammals. Emerging ecosystem models are increasingly acknowledging their contributions to ecosystem resilience amid environmental changes (Snyder & Hendrix, 2008) [17].

Conceptual Advancement:

Unlike in the past, when millipedes were merely seen as detritivores, the current understanding of Diplopoda categorizes them as behaviorally advanced organisms, regulators of microbial populations, agents of biogeochemical cycling, and indicators of soil health. Their contributions are assessed not by biomass but by their behavioral impact on the ecosystem. This review therefore contributes to the growing ecological perspective that millipedes function as active behavioural regulators of soil ecosystem dynamics rather than merely passive detritivores.

Integrative Ecological Interpretation

Millipedes are more than just bulk detritivores; their behavioral activity is integral to the ecological function. Moisture, aggregation, and selective consumption demonstrate the temporal and spatial control of the detrital process rather than the quantity-based process traditionally assumed (De Smedt *et al.*, 2016; Laakso *et al.*, 2000) [5, 12]. Although millipedes are often associated with accelerated decay, this is due to their behavioral activity that controls microbial succession. Millipede consumption of fungus-conditioned leaf litter and the creation of fragmented microhabitats are behavioral controls on the detrital process, rather than passive shredding activity. (Golovatch & Kime, 2009) [9]. Millipede chemical defense has also been shown to have important ecosystem-level consequences. Metabolomic studies indicate that millipede chemical defenses not only deter predators but may also influence microbial communities and decomposition dynamics within soil microhabitats.

Millipede behavioral responses to stress, such as desiccation and contamination, demonstrate behavioral plasticity and a

hierarchy of stress responses, with activity, burrowing, and aggregation acting as early warning signs of physiological disruption to the millipede's body. Millipedes are thus revealed to be behavioral controllers of the soil ecosystem, with their activity and chemical defense controlling the detrital process and interacting with the microclimate and microbes in the soil ecosystem. (Sagi *et al.*, 2019)^[15] Thus, ecology is more than taxonomy; it is behavioral ecology, with millipedes controlling the soil ecosystem and its sustainability.

Limitations of Current Knowledge

Despite increasing research on millipede ecology, several limitations remain in the current understanding of Diplopoda behavioural ecology. Most available studies are geographically restricted and focus primarily on a limited number of temperate species, while tropical and semi-arid ecosystems remain underexplored. In addition, variations in experimental methodologies, environmental conditions, and taxonomic coverage make cross-study comparisons difficult. Many ecological interpretations are also based on laboratory observations rather than long-term field investigations. Furthermore, molecular ecology, metabolomics, and microbial interaction studies involving millipedes remain limited, restricting a comprehensive understanding of their ecosystem-level functions. These limitations highlight the need for broader interdisciplinary and geographically diverse investigations in future research.

Future Research Perspectives

The behavioural ecology of millipedes needs to consider the molecular ecology, metabolomics and climate change response models to understand their ecological roles in future environments. Novel techniques such as microbial network interactions, soil biochemistry, and ecosystem monitoring will give further knowledge of the Diplopoda role in ecosystem sustainability. Further research is also needed on the use of millipedes as bioindicators for environmental monitoring and soil restoration in varied environments and climatic zones.

Conclusion

Millipedes are important components of terrestrial ecosystems and are active. Their activity in moist environments, aggregation, reproductive strategies, and chemical defense systems all contribute to ecosystem processes. By recognizing millipedes as ecosystem engineers rather than peripheral decomposers, we can expand our understanding of soil biodiversity and ecosystem sustainability. Future studies incorporating molecular ecology and environmental monitoring will provide further insights into their ecological importance. Understanding the knowledge of the behavioural ecology of millipedes is vital for the advancement of modern soil science, biodiversity conservation and ecosystem management.

Declarations

Author Contributions

YP: Conceptualization, literature review, writing-original draft preparation, visualization, editing, and manuscript preparation. **RB:** Supervision, validation, manuscript review, proofreading, and final approval.

Conflict of Interest

The authors declare no conflict of interest.

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Data Availability Statement

No new datasets were generated or analyzed during this review study.

Ethics Statement

This article does not involve human participants or animal experimentation.

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