

Review

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Posted Date: 19 June 2023

doi: 10.20944/preprints202306.1339.v1

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Review

From Beneficial Arthropods to Soil-Dwelling Organisms: A Review on Millipedes

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Simple Summary: Millipedes are known to be pests of various crops, and their distribution and damage can be affected by several climatic and environmental factors. In addition to natural enemies, the use of chemical pesticides and other control methods can also impact millipede populations and their interactions with crops and other vegetation. The present review provides recent research progress on the important soil-dwelling organisms that play a vital role in maintaining healthy ecosystems, their biology and ecology of agricultural pests, and their impact on crop damage.

Abstract: Millipedes are soil-dwelling organisms that play a crucial role in nutrient cycling and soil health. They can increase the availability of nitrogen and phosphorus and accelerate the decomposition of organic matter in the soil. However, millipedes can also cause considerable damage to crop, leading to yield losses and indirect effects on soil quality and plant health. Effective management of millipedes may involve a combination of cultural and chemical control methods tailored to specific crops and environmental conditions. Integrated pest management strategies, emphasizing a holistic, ecosystem-based approach, may be particularly effective for managing millipede populations while minimizing negative impacts on the environment. Monitoring is also essential for identifying areas of high millipede activity and targeting control measures accordingly. This review provides recent research progress on millipedes' biology, ecology, and agricultural pest status, as well as IPM strategies to control their infestation in agricultural crops and beyond.

Keywords: millipedes; beneficial insects; pests; yield loss; management

1. Introduction

Millipedes are fascinating creatures that belong to the class Diplopoda, which means “double-footed” in Greek, and global species diversity is estimated between 50,000 and 80,000 species [1,2]. They are arthropods, which means they have an exoskeleton, jointed legs, and segmented bodies. Millipedes are commonly found in soil and leaf litter, where they play an important role in nutrient cycling and soil health. Millipedes play an important role in decomposing organic matter in the soil. A study found that millipedes increased the rate of decomposition by up to 45% in some cases [3]. Another study found that millipedes can increase the availability of nutrients such as nitrogen and phosphorus in the soil. The researchers found that millipedes increased the mineralization rate of nitrogen by up to 42%, and the availability of phosphorus by up to 23% [4].

The ability of millipedes to regenerate lost body parts is a well-documented phenomenon. For example, a study conducted by VandenSpiegel [5] found that a species of millipede called *Glomeris marginata* can regenerate its antennae, legs, and even segments of its body. Bioluminescence in millipedes has been observed in several different species. A study conducted by Lewis et al. [6] found

that the millipede *Motyxia* produces a blue-green light through a chemical reaction involving luciferin and luciferase.

Millipede infestations in crops can cause significant damage by feeding on the above-ground plant tissues such as leaves, stems, and fruits. The extent of millipede damage to germinating maize seeds during the first and second rainy seasons was recorded at 34% and 29%, respectively [7]. The species *O. sudanica*, *Spirostreptus ibanda*, and *Tibiomus* spp. cfr. *ambitus* were present near the maize seeds, but they were observed feeding on them only during the second rainy season [7].

In addition to the direct damage caused by millipedes, their presence in crops can also have indirect effects on soil quality and plant health. Millipedes are known to increase soil nitrogen and phosphorus levels, which can have both positive and negative effects on plants [8]. While increased soil fertility can promote plant growth and development, excessive levels of nutrients can lead to nutrient imbalances and toxicity, which can damage or kill plants [8]. In addition to feeding damage, millipedes can also cause indirect damage by creating entry points for secondary pathogens such as fungi and bacteria. These pathogens can further damage the plants and cause additional yield losses [9]. In a study conducted to investigate the impact of millipedes on maize crops in South Africa, and they found that millipedes can cause significant damage to maize seedlings and that the extent of damage is influenced by factors such as soil type, planting date, and seedling age [10].

In severe cases, millipede infestations can even lead to plant death. A study conducted in Malaysia showed that millipede damage on seedlings of oil palm trees resulted in seedling mortality rates of up to 40% [11–13].

To prevent and control millipede infestations in crops, various methods can be used. These include cultural practices such as crop rotation and proper soil management, chemical control using insecticides, and biological control using natural predators such as birds or predatory insects [14]. According to a review by Cruz-Rodríguez et al. [15], effective management of millipedes may involve a combination of cultural and chemical control methods, tailored to the specific crop and environmental conditions. Additionally, integrated pest management (IPM) strategies, which incorporate a range of control methods and emphasize a holistic, ecosystem-based approach, may be particularly effective for managing millipede populations while minimizing negative impacts on the environment.

The present review provides recent research progress on the important soil-dwelling organisms that play a vital role in maintaining healthy ecosystems, their biology and ecology of the agricultural pests of millipedes, and their impact on crop damage. Several studies have shown the importance of monitoring as an IPM strategy for millipedes in agricultural crop plants and have demonstrated that monitoring is important for identifying areas of high millipede activity and targeting control measures accordingly [7,16]. Furthermore, this review provides IPM strategies to control millipede infestation in agricultural crops and beyond.

2. Biology and Ecology of Millipedes

2.1. Reproduction and feeding behavior of Millipedes

Millipedes exhibit a variety of reproductive modes, including sexual and asexual reproduction [17]. Sexual reproduction in millipedes involves the transfer of sperm packets, or spermatophores, from males to females [18,19]. Some species of millipedes are known to engage in multiple mating, where females mate with multiple males and males mate with multiple females [19,20]. Asexual reproduction in millipedes can occur through parthenogenesis, where females are able to produce offspring without fertilization by a male [21].

Life cycle: the life cycle of millipedes typically includes an egg stage, several larval stages, and the adult stage [22,23]. The number of molts between larval stages varies among species and can range from a few to more than a dozen. The length of the life cycle can also vary depending on the species and environmental conditions [24,25].

Feeding behavior: According to a study by Hopkin and Read [26], millipedes are mainly detritivores, feeding on dead plant material and other decaying organic matter and play an important

role in the breakdown and recycling of organic matter in soil ecosystems [26,27]. They consume dead plant material, such as fallen leaves, twigs, and bark, as well as other decaying organic matter, such as animal remains and feces [6]. Some species may also feed on live plant material, fungi, or other invertebrates, depending on the availability of food and their specific dietary requirements [6,26].

In addition to their role in nutrient cycling, millipedes have been found to have other beneficial effects on the soil ecosystem, such as improving soil structure and moisture retention, increasing nutrient availability, and enhancing microbial activity [28,29].

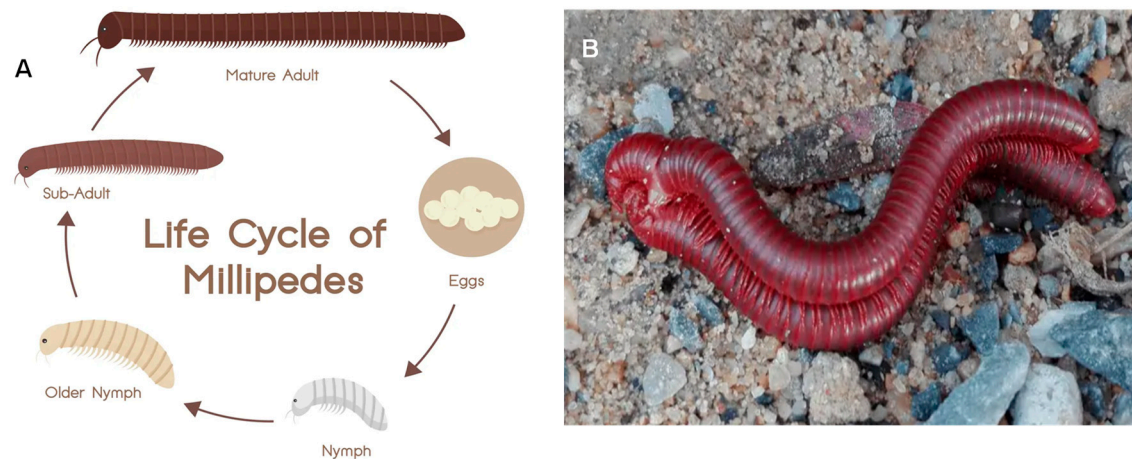


Figure 1. Millipede life cycle (A) on the left side, and on the right-side millipedes clamped to each other during mating (B) (modified from <https://keepingbugs.com/life-cycle-and-lifespan-of-giant-millipedes-explained/>).

Habitat: Millipedes are known to inhabit a wide range of terrestrial environments, including forests, grasslands, wetlands, caves, and deserts, with many species being found in moist habitats such as leaf litter, soil, and decaying wood [30–33]. Millipedes play an important role in the decomposition process of organic matter in their respective ecosystems, contributing to nutrient cycling and soil health [34].

2.2. Ecology

Millipedes play important roles in ecosystems as decomposers and nutrient recyclers (Hopkin, 2015). They are sensitive to changes in environmental conditions, such as changes in temperature, moisture, and soil composition [32]. Some species of millipedes are known to exhibit seasonal and diurnal activity patterns [35]. Millipedes have been found to be important prey for a variety of predators, including birds, mammals, and invertebrates [7].

Ecological role: Millipedes play a significant ecological role in the ecosystem by breaking down dead plant material and other organic matter, which helps to release nutrients into the soil. Several studies have documented the importance of millipedes in facilitating decomposition and nutrient cycling in forest ecosystems, such as the study by Snyder et al. [36] which found that millipedes were the primary decomposers of leaf litter in a tropical rainforest.

Millipedes also serve as a critical food source for a wide range of predators. For instance, a study by Blower and Shotbolt [37] found that millipedes were the primary prey item for the *Eurasian woodcock*, a bird species found in European forests.

Millipedes are also known to have a mutualistic relationship with certain fungi, particularly mycorrhizal fungi [38]. These fungi can form associations with plant roots, helping to enhance their nutrient uptake. Millipedes can transport the spores of these fungi, aiding in their dispersal and facilitating their association with new plant hosts [38].

Furthermore, millipedes are important indicators of soil health and can be used as bioindicators of environmental stressors such as pollution and habitat disturbance. Their presence or absence can provide insight into the health and stability of an ecosystem [26,38,39].

Studies have also shown that millipedes can contribute to the suppression of plant diseases through their interactions with soil microorganisms. They may also have the potential for use in bioremediation efforts to clean up contaminated soils [26,36,38].

Behavior: Millipedes are generally nocturnal and spend most of their time hiding in soil, leaf litter, or other dark and moist habitats [40,41]. They can curl into a tight spiral when threatened, using their hard exoskeletons to protect themselves. Some species also release a defensive chemical called hydrogen cyanide, which can deter predators [26,40,41].

2.3. Negative impacts of millipedes

Millipedes can also have negative impacts on the environment and human activities. For example, some species can cause damage to crop plants and gardens by feeding on live plant material and can even become pests in agricultural systems [42,43]. Additionally, millipedes can become a nuisance pest in homes and buildings, as they may enter in large numbers and produce a foul odor [43].

2.4. Medicinal values of millipedes

One interesting ecological role of millipedes is their use in traditional medicine in some cultures. In China, for example, millipedes have been used for centuries in traditional medicine to treat a variety of ailments, including inflammation, rheumatism, and hemorrhoids [44,45]. Millipedes contain a compound called *diplopodin*, which has been found to have anti-inflammatory and analgesic properties [42,46].

2.5. Distribution and plant damage caused by millipedes

Wesener and Enghoff [47] did a comprehensive overview of the global distribution of millipedes, including patterns of diversity, biogeography, and ecology. Another study by Enghoff [32] carried out on the distribution of millipedes in Southeast Asia, is known to have high levels of species richness and endemism. The distribution and ecology of millipedes and other arthropods, and notes that millipedes are found on all continents except Antarctica [48].

Millipedes can cause damage to plant roots, stems, and leaves, particularly in agricultural settings, and understanding their distribution and potential impact on crops is important for managing these pests. One way in which millipedes can cause plant damage is by feeding on the roots, stems, and leaves of plants. John [7] investigated the feeding behavior of the greenhouse millipede *Oxidus gracilis* and its potential as a pest in greenhouse crops. They found that the millipedes fed on the roots, stems, and leaves of several greenhouse crops, including cucumber, tomato, and chrysanthemum [7]. The presence of millipedes in the soil was negatively correlated with plant growth and biomass, suggesting that millipedes may play a role in limiting the productivity of these plantations [49]. The feeding damage caused by the millipedes resulted in stunted growth, wilting, and reduced yield of the crops [30,49,50]. In addition, some species of millipedes can secrete toxic compounds that can further damage plant tissues. For example, the North American millipede, *Narceus americanus*, secretes hydrogen cyanide which can cause necrosis in plant tissues [51]. Furthermore, millipede infestation caused significant changes in the levels of various biochemicals, including total phenolics, flavonoids, and proline, suggesting that millipedes can cause damage to plant tissues by disrupting normal physiological processes [52].

3. What are the climatic factors that affect millipedes' distribution and damage?

Millipedes are known to be pests of various crops, and their distribution and damage can be affected by several climatic factors. Some of the factors that have been reported to influence their population dynamics include temperature, humidity, rainfall, and soil moisture levels.

Temperature: is a crucial factor affecting the activity and growth of millipedes. They are typically active at temperatures ranging from 15°C to 30°C, with optimal activity occurring at temperatures

around 25°C [53]. Higher temperatures may lead to increased metabolic rates and feeding activity, but prolonged exposure to temperatures above their upper thermal limit can be lethal.

Humidity levels also play an important role in millipede behavior and distribution. They are known to be more active and feed more actively under high humidity conditions [54]. However, excessively high moisture levels can also negatively impact millipede populations by promoting the growth of fungal pathogens that may infect them.

Rainfall patterns and soil moisture levels can also impact the distribution and damage caused by millipedes. Heavy rainfall events can lead to an increase in soil moisture levels, which in turn can stimulate millipede activity and population growth [55]. However, prolonged periods of high moisture levels can lead to waterlogged soils, which may negatively impact crop growth and productivity.

In addition to temperature, humidity, rainfall, and soil moisture levels, other climatic factors such as wind speed, atmospheric pressure, and photoperiod can also affect millipede distribution and damage. Wind speed can impact the movement of millipedes, with strong winds potentially dislodging them from their habitats and dispersing them to new areas [53]. Atmospheric pressure changes may also impact their distribution, with millipedes more active during low-pressure weather systems [56].

Photoperiod, or the duration of light exposure in a day, can also influence millipede behavior and activity. Some species may be more active during certain times of the day, with peak activity occurring at dawn or dusk [55]. Changes in photoperiod may also trigger molting, reproductive activity, and other physiological processes in millipedes.

Understanding how these climatic factors interact with each other and with other environmental factors such as vegetation, soil type, and land use practices can provide insights into the distribution and dynamics of millipede populations. This information can help inform pest management strategies that minimize the damage caused by millipedes to crops and other vegetation.

In addition to the climatic factors discussed earlier, other environmental factors such as land use practices, vegetation cover, and soil type can also influence millipede distribution and damage. Land use practices such as tillage and crop rotation can affect soil moisture levels and soil structure, which may impact millipede populations. For instance, reduced tillage practices can lead to higher soil moisture levels and increased organic matter, which may promote millipede activity and population growth [55]. Conversely, frequent tillage can disrupt millipede habitats and reduce their populations.

Vegetation cover can also play a role in millipede distribution and damage. Millipedes may be more abundant in areas with high vegetation cover, as vegetation provides them with shelter and food resources [56]. However, certain plant species may be more susceptible to millipede damage, and their abundance may vary depending on the type of vegetation cover present in the area.

4. Impact of Soil Type and Soil Organic Matter Content on Millipede Population

Soil type can also impact millipede distribution, with certain species preferring specific soil types or soil moisture levels [57]. For example, some millipede species may be more abundant in sandy soils, while others may prefer clay soils. Soil pH and nutrient levels may also impact millipede populations indirectly by affecting the growth and productivity of plants, which may in turn affect the availability of food resources for millipedes.

A study conducted by Kuczynski et al. [58] in a tropical rainforest found that soil organic matter content was the most important factor influencing millipede distribution and abundance. The study suggested that millipedes were more commonly found in soils with high organic matter content. In a study by de Oliveira et al. [59] in a Brazilian tropical dry forest, the researchers found that higher levels of soil organic matter were associated with greater millipede abundance and diversity. Verchot et al. [60] conducted a study in western Kenya that examined the relationship between soil properties and the abundance of earthworms and termites, which are also important decomposers in soil ecosystems. The study found that soil organic matter content was a key factor influencing earthworm and termite abundance, with higher levels of organic matter supporting greater populations. These studies provide evidence to support the idea that soil type and soil organic matter can have a

significant effect on millipede distribution and damage. They suggest that higher levels of soil organic matter are generally associated with greater millipede abundance, while the specific type of soil can also play a role [58–60].

Generally, understanding the complex interactions between climatic and environmental factors can help inform strategies for managing millipede populations and minimizing their damage to crops and other vegetation. Another environmental factor that can influence millipede distribution and damage is the presence of natural enemies and predators. Some natural enemies of millipedes include birds, mammals, reptiles, and other arthropods, which can feed on them and help regulate their populations [53]. However, the effectiveness of natural enemies in controlling millipede populations can vary depending on the species and environmental conditions.

4.1. Chemical pesticides and Human activities

In addition to natural enemies, the use of chemical pesticides and other control methods can also impact millipede populations and their interactions with crops and other vegetation. Pesticides may be effective in reducing millipede damage in the short term, but they can also have negative impacts on non-target organisms and the environment [54]. Therefore, integrated pest management strategies that combine multiple control methods may be more effective and sustainable in the long term.

Finally, human activities such as urbanization and land-use change can also impact millipede distribution and damage. Urbanization can lead to the destruction of millipede habitats and fragmentation of their populations, while land-use change such as conversion of natural habitats to agriculture can alter the availability of food resources and other environmental factors that influence millipede populations [55]. Another factor that can influence millipede distribution and damage is the diversity and composition of plant communities. Studies have shown that millipede populations and their interactions with crops can be affected by the diversity and quality of the plant species in the surrounding area [15]. For example, some plant species may release chemicals that deter millipedes or attract their natural enemies, while others may provide a more suitable habitat or food source for millipedes.

Furthermore, global climate change may also have significant impacts on millipede populations and their interactions with crops. Climate change can alter temperature and rainfall patterns, which can influence the distribution and abundance of millipedes and their natural enemies. For example, warmer temperatures may increase millipede reproduction rates and survival, while changes in precipitation patterns may affect the availability of food and water resources [61].

Finally, the genetic variability of millipede populations can also play a role in their distribution and damage. Genetic diversity can influence a species' ability to adapt to changing environmental conditions and interact with other organisms in its ecosystem. Therefore, understanding the genetic diversity and population structure of millipedes can provide insights into their potential for adaptation and response to environmental change [7].

In conclusion, a range of factors can influence millipede distribution and damage, including climate, plant communities, natural enemies, human activities, and genetic diversity. Understanding the complex interactions between these factors is important for developing effective pest management strategies that balance the needs of agriculture with the preservation of ecosystem health and biodiversity.

5. Genetic Diversity of Millipedes

The genetic diversity of the millipede genus *Tymbodesmus* in Africa was studied using mitochondrial DNA markers. The results showed that the species within the genus had high genetic diversity, with some species showing distinct genetic lineages [62]. A study by Wesener et al. [63] used DNA barcoding to analyze the genetic diversity of millipedes across Africa. The researchers found that the millipede species in Africa exhibited high levels of genetic diversity, with some species showing significant differences between populations from different geographic regions. The millipede family *Spirostreptidae* was studied in South Africa using molecular markers and revealed high genetic diversity within and among species. The study also suggested that some species may

have experienced recent population expansions [64]. Genetic analysis of the millipede genus *Tonkinbolus* in East Africa showed that the species were genetically diverse, with some species showing high levels of genetic divergence. The study also suggested that the genus may have undergone recent radiation and diversification [47].

A molecular phylogenetic analysis of the millipede family *Spirostreptidae* in Africa revealed a complex pattern of diversification and radiation. The study suggested that the family had undergone multiple radiations in Africa, with some lineages showing rapid diversification [65]. The phylogenetic relationships and biogeography of the millipede genus *Orthomorpha* in Africa were investigated using molecular markers. The study revealed a complex pattern of diversification and radiation in this genus, with some lineages showing rapid diversification and others having a more ancient origin [65].

A study by Nguyen et al. [66] examined the genetic diversity of the millipede family *Xystodesmidae* in eastern North America. The researchers used molecular markers to analyze the genetic relationships among different species and populations and found high levels of genetic diversity within and among populations. The study suggested that the genetic diversity of millipedes in this region may have been influenced by historical climate change and landscape evolution. In a study by Golovatch et al. [67] the researchers analyzed the genetic diversity of the millipede family *Paradoxosomatidae* in Southeast Asia. The study used molecular markers to examine the phylogenetic relationships among different species and found high levels of genetic diversity within and among populations. The researchers suggested that the complex geological and climatic history of Southeast Asia may have played a role in shaping the genetic diversity of millipedes in this region. A study by Marek et al. [68] examined the genetic diversity of millipedes in the family Polydesmida in the United States. The study used a combination of molecular markers and morphological traits to analyze the genetic relationships among different species and populations and found high levels of genetic diversity within and among populations. The researchers suggested that the complex geological history and biogeographical patterns of the United States may have influenced the evolution and diversification of millipedes in this region.

Overall, these studies suggest that millipedes exhibit high levels of genetic diversity, both within and among populations. The specific patterns of genetic diversity may be influenced by a variety of factors, including historical climate change, landscape evolution, and biogeographical patterns.

A study published in the journal *Ecology and Evolution* in 2020 investigated the genetic diversity and population structure of a tropical millipede species (*Pachybolus ligulatus*) in Costa Rica. The researchers used DNA sequencing to identify several distinct genetic lineages within the species and suggested that this diversity may be linked to differences in environmental conditions such as temperature and rainfall. They also found evidence of limited gene flow between populations, which could have implications for the species' ability to adapt to changing environmental conditions [69]. A study by Brewer et al. [70] used genotyping-by-sequencing to investigate the genetic diversity and population structure of the millipede species *Narceus americanus* in the southeastern United States. The researchers found evidence of high genetic diversity within populations, with limited gene flow between populations.

6. Agricultural pests of millipede species

Millipedes can sometimes cause significant damage to crops (Figure 2), so understanding the pest species and their impact on agriculture is important for pest management and control strategies. Table 1. summarizes the various species of millipedes that are reported as pests of agricultural crops in different agroecosystems.

Table 1. list of agricultural pests of millipede species, affected crops, and their geographical distributions.

| <i>Millipede species</i> | Host crop | Geographic distribution | References |
|---|--|--------------------------------|-------------------|
| <i>Ommatoiulus moreletii</i> | citrus, grapes, and vegetables, lettuce and cabbage | Portugal and Spain, | [71] |
| <i>Parafontaria laminata</i> | wheat, barley, and corn | North Africa | [4] |
| <i>Eurymerodesmus bleemensis</i> | potatoes and sweet potatoes | Japan | [72] |
| <i>Spirostreptus sp.</i> | cassava crops, | Brazil, | [73] |
| <i>Boreviulisma inflatum</i> | rice | Indonesia | [74] |
| <i>Nopoiulus kochii</i> , | cocoa | Cameroon | [75] |
| <i>Xystodesmidae</i> | lettuce and celery | Australia | [76] |
| <i>Chersastus millipede</i> | corn, soybeans, and wheat | the United States | [7] |
| <i>Polydesmus angustus</i> | maize and beans | southern Brazil | [77] |
| <i>Glyphiulus granulatus</i> , | soybean crops, | North America, | [78] |
| <i>Ptyoiulus impressus</i> | maize, cassava, and potato | Indonesia | [79] |
| <i>Ommatoiulus sabulosus</i> | turf | New Zealand | [80] |
| <i>Sigmoria aberrans</i> , | tomato, lettuce, and cabbage, | Spain and Portuga | [81] |
| <i>Oxidus gracilis</i> , | Soybean | southeastern United States | [82] |
| <i>Tachypodoiulus niger</i> , | rice | Japan | [83] |
| <i>Pachyiulus flavipes</i> | peas, beans, and corn | Europe and North America | [84] |
| <i>Cylindroiulus caeruleocinctus</i> , | nursery crops | North America | [85] |
| <i>Aphistogoniulus corallipes</i> , | potatoes and carrots | Europe | [86] |
| <i>Anadenobolus monilicornis</i> | Cocoa | West Africa | [87] |
| <i>Tonkinbolus dollfusi</i> , | sugar cane | southern Africa | [88] |
| <i>Euryarthrum sp.</i> | maize | East Africa | [89] |
| <i>Orthomorpha gracilis</i> | maize | Southern Africa | [90] |
| <i>Archispirostreptus syriacus</i> | cassava | West Africa | [91] |
| <i>Ommatoiulus sabulosus</i> , | maize | East Africa, | [92] |
| <i>Tonkinbolus caudulanus</i> , | wheat and barley | North Africa | [4]. |
| <i>Pachyiulus flavipes</i> | Groundnut (peanut) | West Africa | [93] |
| <i>Archispirostreptus tumuliporus</i> | Coffee | East Africa, | [94] |
| <i>Ommatoiulus moreleti</i> , | Maize | East Africa | [95] |
| <i>Tonkinbolus caudulanus</i> : | Tomato and potato | North Africa | [96] |
| <i>Archispirostreptus tumuliporus</i> | Groundnut | Nigeria | [93] |
| <i>Polydesmid millipedes</i> | maize | Kenya | [95] |
| <i>Unknown species:</i> | maize, cabbage, and tomato | Zimbabwe | [97] |
| <i>Euryurus leachii and Telodeinopus aoutii</i> | banana, beans, cassava, maize, and sweet potato | Tanzania | [98] |
| <i>Tymbodesmus africanus</i> | wheat and barley | Ethiopia | [99] |
| <i>Hyleoglomeris diemenensis</i> | maize, sorghum, and sugarcane | South Africa | [100] |
| <i>Orthomorpha coarctata</i> | sugarcane and pineapple | South Africa | |
| <i>Spirostreptus sp.</i> | cassava and maize | Cameroon | [101] |
| <i>Ommatoiulus moreletii</i> | maize, cassava, and yams | Nigeria | [102] |
| <i>Orthoporus ornatus</i> | citrus, cocoa, and coffee | Kenya, Tanzania, and Uganda | [7] |
| <i>Anadenobolus sp. Rhinocricus sp.</i> | cotton, corn, and soybean | United States | [103] |
| <i>Tonkinbolus caudulanus</i> | cassava | Benin | [104] |
| | beans, peas, and tomatoes | Tanzania | [105] |



Figure 2. Millipede damage on various root and tuber crops (A-D): Millipedes tunnel into and completely consume young plants, as shown in the images (A). They feed on the roots of a wide variety of plants (A-D) and also target bulbs and tubers (C and D). Additionally, they enlarge the holes left by slugs, wireworms, and other pests (A and D). The photos were taken during a millipede survey conducted in Rwanda by our research group.

The species affected by millipede damage are numerous, including beans, cabbage, carrots, corn, potatoes, strawberries, tomatoes, and more. Millipede damage is most commonly observed under extreme humidity conditions, such as during periods of drought or in overly saturated soil. Root and tuber crops are more susceptible to attack in soggy soil. An unintended consequence of millipede damage is the increased likelihood of fungal diseases appearing.

7. Management of Agricultural Pests of Millipedes

There are several IPM strategies that can be used to manage millipedes in agricultural crop plants and minimize plant damage. These include:

Mechanical control: This involves physically removing millipedes from the affected area. This can be done by handpicking, vacuuming, or using sticky traps [7]. The role of integrated pest management strategies in and around structures and recommended that mechanical control methods such as handpicking and vacuuming can be used as ways to physically remove millipedes from affected areas. However, they note that these methods may not be practical for large-scale infestations [106]. Several studies reported that sticky traps were effective at reducing the number of millipedes in a house, while vacuum cleaners were less effective [107,108]. They conclude that sticky traps can be a useful tool for controlling millipedes in homes. The use of sticky traps as a mechanical control method for small infestations of millipedes. They note that this method may not be practical for large infestations but can be useful for monitoring the presence and abundance of millipedes in an area [107,108].

Cultural control: This involves modifying the environment to make it less suitable for millipedes by reducing the amount of organic matter in the soil and improving drainage and removing debris and leaf litter from the area. Cultural control methods can be effective in reducing millipede populations, but they may take longer to show results than chemical control methods [35,44,109].

They note that cultural control methods can be effective in reducing millipede populations but may take longer to show results than chemical control methods.

Biological control: This involves using natural enemies of millipedes to control their populations. Some predators that feed on millipedes include birds, small mammals, and other arthropods [110]. However, the effectiveness of biological control methods can be limited by the availability and suitability of natural enemies.

A study found that predators such as centipedes and spiders were important natural enemies of millipedes, and that the effectiveness of biological control methods was influenced by the presence of co-evolved bacterial and fungal communities [111]. Another study investigated the prey selection of a spider species that feed on millipedes, among other arthropods, and they found that millipedes were a preferred prey item for the spider, suggesting that they may be an effective natural enemy of millipedes in some ecosystems [112]. Ground beetles are generalist predators that feed on a wide range of soil-dwelling arthropods, including millipedes. *Carabus* ground beetles, which thrive in temperate environments, have evolved to excel in vineyards as efficient predators of millipedes [113,114]. Centipedes are predatory arthropods that have been observed feeding on millipedes in both laboratory and field settings [115]. Some species of nematodes have been found to infect and kill millipedes. For example, the nematode *Steinernema carpocapsae* has been shown to be effective against the millipede *Ommatoiulus moreletii* in laboratory experiments [116,117].

Some species of parasitic wasps lay their eggs inside millipedes, where the developing larvae feed on the host's tissues. For example, the wasp *Cylloceria* sp. has been observed parasitizing the millipede *Apheloria virginiensis* [25]. It's important to note that while biological control can be an effective method for managing pest populations, it is not always a reliable or sustainable solution. It is also important to carefully consider the potential environmental impacts of introducing non-native natural enemies into a given ecosystem.

Chemical control: This involves using insecticides to kill millipedes. Insecticides can be applied to the soil, foliage, or both. However, care should be taken when using chemical control methods as they can also harm beneficial organisms in the soil ecosystem.

Carbamate insecticides, such as carbaryl and methomyl, have been shown to be effective against millipedes in field trials [118].

Organophosphate insecticides, such as diazinon and chlorpyrifos, have also been used to control millipedes [119]. A study by Tsunoda & Takada [119] evaluated the effectiveness of several insecticides, including chlorpyrifos and diazinon, against the red millipede on golf courses in Okinawa, Japan, and found that both insecticides were effective in controlling millipedes but noted that chlorpyrifos was more persistent in the soil than diazinon.

Another study evaluated the efficacy of several insecticides, including chlorpyrifos, against the soil-burrowing millipede, *Chamberlinius hualienensis*, in a laboratory setting [120]. The authors found that chlorpyrifos was effective in controlling millipedes but noted that its residual activity was limited. It's important to note that organophosphate insecticides can have negative impacts on human health and the environment and should be used judiciously and in accordance with local regulations.

Pyrethroid insecticides: Pyrethroid insecticides, such as cypermethrin and deltamethrin, have been found to be effective against millipedes in laboratory and field experiments [121]. A study by Abu El-Saad & El-Nagar [121] evaluated the efficacy of several insecticides, including cypermethrin and deltamethrin, against the millipede *Harpagophoridae* in laboratory experiments, and found that both pyrethroid insecticides were effective in controlling millipedes.

The efficacy of several insecticides was evaluated, including cypermethrin and deltamethrin, against the millipede *Anadenobolus monilicornis* in turfgrass in a field setting [122]. The authors found that pyrethroid insecticides were effective in controlling millipedes. It's important to note that pyrethroid insecticides can have negative impacts on non-target organisms and the environment and should be used judiciously and in accordance with local regulations.

Fipronil is a broad-spectrum insecticide that has been used to control millipedes in horticultural settings [123]. A study conducted by Tang et al. [124] evaluated the efficacy of fipronil bait against

the millipede *Apheloria corrugata* in horticultural nurseries in the United States. The authors found that the fipronil bait was effective in controlling millipedes and was a viable alternative to traditional insecticide sprays.

It's important to note that the effectiveness of each of these methods can vary depending on the species of millipede and the type of plant affected. In addition, an integrated pest management (IPM) approach that combines multiple methods may be more effective than relying on a single method.

Monitoring was an important component of the integrated pest management approach and helped to guide the use of other control tactics [125,126]. Regular monitoring of crop fields can help to identify millipede infestations early before they become widespread and difficult to control [125]. This can be achieved through visual inspection, the use of traps, and the monitoring of soil moisture levels could help to predict millipede activity and population growth [127,128]. A study investigated millipede damage to maize in Brazil and the use of pitfall trapping as a monitoring technique [125,129]. The study found that pitfall trapping was an effective method for monitoring millipede populations and could be used to predict damage to maize crops.

Establishing long-term monitoring programs can help in tracking millipede populations and identifying patterns of infestation. This data-driven approach can contribute to developing predictive models that assist farmers in making informed decisions regarding pest management interventions. Regular monitoring also allows for the evaluation of the effectiveness of implemented control measures, enabling adjustments and improvements to be made as necessary.

In conclusion, effective pest management measures must take into account the specific millipede species found in Africa, their behavior, and how they interact with crop plants. Researchers can acquire important insights into the ecology of millipedes in the area and create focused strategies to reduce crop damage by examining their feeding preferences, reproductive habits, and habitat needs. Additionally, it is essential to educate farmers about millipedes as possible agricultural pests. Farmers can spot early signs of infestation and take the proper preventive actions by being educated on the biology, identification, and damage symptoms of millipedes. Develop and spread IPM strategies that emphasize a mix of cultural, biological, and chemical control techniques. Crop rotation, habitat alteration, biological control agents, and prudent pesticide usage are some examples of these measures that aim to have the least possible negative effects on the environment.

Generally, millipedes play a significant role in the ecosystem, contributing to nutrient cycling and soil health. However, in certain cases, they can become pests and cause damage to various crops. It is important to address this issue and gather more information on millipedes as crop pests, particularly in Africa, where their impact has been neglected in agricultural research.

Acknowledgments: The authors would like to thank Rwanda Agriculture and Animal Resources and Development for the financial support.

Conflicts of Interest: There is no conflict of interest.

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