WITHDRAWN: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

Kahsay Tadesse Mawcha

tadesekahsay@gmail.com

Aksum University https://orcid.org/0000-0002-7310-8085

Research Article

Keywords: Beneficial, Crop, Ecosystem, Management, Millipedes, Pest

Posted Date: August 25th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3257909/v1

EDITORIAL NOTE:

The full text of this preprint has been withdrawn by the authors while they make corrections to the work. Therefore, the authors do not wish this work to be cited as a reference. Questions should be directed to the corresponding author.

Abstract

Millipedes are important soil-dwelling organisms that play a vital role in the soil's nutrient cycling and overall health. They can increase the availability of nitrogen and phosphorus and accelerate the decomposition of organic matter in the soil. However, they can also cause significant damage to crop plants, which can lead to reduced yields and negatively impact both soil quality and plant health. Integrated Pest Management (IPM) strategies may be necessary to effectively manage millipedes. These strategies involve a combination of cultural and chemical control methods that are tailored to specific crops and environmental conditions. By taking a holistic, ecosystem-based approach, IPM strategies can effectively manage millipede populations while minimizing negative impacts on the environment. Monitoring millipede activity and implementing control measures in areas with a high infestation is a crucial measure. This review provides recent research progress on millipede's biology, ecology, and agriculture pest status of millipedes in Africa and beyond and IPM strategies to control their infestation in agricultural crops.

1. Introduction

Millipedes, captivating creatures belonging to the class *Diplopoda*, derived from the Greek term "double-footed," boast a remarkable global species diversity, estimated to range between 50,000 and 80,000 species (Stašiov et al. 2012, Sierwald and Bond 2007). As arthropods, they feature exoskeletons, jointed legs, and segmented bodies. Typically, inhabiting soil and leaf litter, millipedes play a crucial role in the ecosystem by contributing to nutrient cycling and soil health. Their presence aids in decomposing organic matter, with a study indicating that millipedes can accelerate decomposition rates by up to 45% in certain cases (Dangerfield and Milner 1996). Moreover, these remarkable organisms facilitate the availability of vital nutrients like nitrogen and phosphorus in the soil. Researchers discovered that millipedes enhance nitrogen mineralization by up to 42% and phosphorus availability by up to 23% (Vohland and Hamer 2013). Such findings underscore the significant ecological impact of millipedes as essential contributors to soil enrichment and overall ecosystem functioning (Vohland and Hamer 2013).

Millipedes have a special behavior of regenerating lost body parts. The phenomenon of millipedes regenerating lost body parts has been extensively documented. An illustration of this is seen in a study by Vohland and Hamer (Vohland and Hamer 2013) which revealed that the *Glomeris marginata* species of millipede can regenerate its antennae, legs, and even body segments. Additionally, bioluminescence has been observed in various millipede species (Nabil and Del 1969). Shelle (1997) conducted a study that demonstrated how the millipede *Motyxia* emits blue-green light by undergoing a chemical reaction involving luciferin and luciferase. Millipedes are also common pests of crops, and they can cause significant damage by feeding on above-ground plant tissues. In one study, millipede damage to germinating maize seeds was recorded at 34% and 29% during the first and second rainy seasons, respectively. This level of damage can significantly reduce crop yields, and it is important to take steps to control millipede populations (Ebregt et al. 2005). The species *Omopyge 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 (Ebregt et al. 2005).

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 (Dangerfieldand Milner1996, Mengru et al. 2018). While increased soil fertility can promote plant growth and development, however, excessive levels of nutrients can lead to nutrient imbalances and toxicity, which can damage or kill plants (Mengru et al. 2018). 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 (Michael 2023). 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 (Ferreira et al. 2015).

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% (Rajkumar 2021).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 (Cabi 2020). According to a review by Elango (2017), 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 millipedes that play a vital role in maintaining healthy ecosystems, their biology, ecology, and their impact on crop damage. Several studies have shown the importance of monitoring as an IPM strategy for millipedes in agricultural crops and have demonstrated that monitoring is important for identifying areas of high millipede activity and targeting control measures accordingly (Ebregt et al. 2005). 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. Sexual reproduction in millipedes involves the transfer of sperm packets, or spermatophores, from males to females (Hopkin 1992). Some species of millipedes are known to engage in multiple mating, where females mate with multiple males and males mate with multiple female set (Ferreira et al. 2015).

Asexual reproduction in millipedes can occur through parthenogenesis, where females are able to produce offspring without fertilization by a male (Mesibov 2008).The gonopods of male millipedes are essential for species identification, making them of significant diagnostic importance (Miley 1925). While genitalia are not traditionally viewed as adaptive structures, they can evolve as a secondary outcome of ecological divergence. This evolution is driven by variations in environmental conditions, which directly influence mating preferences and signals (Bond et al. 2003, Tanabe et al. 2001).

Life cycle

the life cycle of millipedes typically includes an egg stage, several larval stages, and the adult stage (Fig. 1), (Brewer 2018). The number of molts between larval stages varies among millipede species, ranging from a few to more than a dozen. The length of the life cycle also varies depending on the species and environmental conditions. Millipede larvae are born with only three pairs of legs and four fully developed body segments (Lawrence1984, Blower 1985). They are lighter in color than mature individuals, and it typically takes over a year for them to reach their full size as adults. Most millipedes undergo a purely anamorphic development, meaning that they do not undergo a complete metamorphosis (Lawrence1984, Blower1985).

Feeding behavior

According to a study by Hopkin, 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 (Hopkin 1991, Lewis and Sutherland 2001a). 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 (Lewis and Sutherland 2001b). Some species may also feed on live plant material, fungi, or other invertebrates, depending on the availability of food and their specific dietary requirements (Hopkin, 1991, Lewis and Sutherland 2001b). 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 (Kevan 2020).

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 (Enghoff et al.1993, Hopkin 2015).

2.2. Ecological role of millipedes

Millipedes serve crucial functions within ecosystems, acting as decomposers and nutrient recyclers. Their sensitivity to environmental changes, including alterations in temperature, moisture, and soil composition, has been well-documented (Enghoff et al. 1993). Certain millipede species display distinct seasonal and diurnal activity patterns. As important prey for various predators, including birds, mammals, and invertebrates, millipedes play a key role in the ecological food web (Ebregt 2005). Their significance extends to ecological processes, as they play a vital role in breaking down deceased plant material and other organic matter, ultimately aiding in the release of nutrients into the soil. Numerous studies have emphasized the importance of millipedes in facilitating decomposition and nutrient cycling in forest ecosystems. For instance, the study by Alagesan (Alagesan 2016) highlighted that millipedes are recognized as the primary decomposers of leaf litter within the intricate ecosystem of a tropical rainforest.. In summary, millipedes contribute significantly to the overall balance and functioning of ecosystems through their diverse ecological roles.

Millipedes also serve as a critical food source for a wide range of predators. For instance, a study by Blower et al. (2015) 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 (Tuf 2019). 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 (Tuf 2019). Furthermore, millipedes are important indicators of soil health and can be used as bio-indicators of environmental stressors such as pollution and habitat disturbance. Their presence or absence can provide insight into the health and stability of an ecosystem (Hopkin 1991, Snyder,and Hendrix 2008, Tuf 2019). 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 bio-remediation efforts to clean up contaminated soils (Hopkin 1991, Snyder et al. 2015, Tuf 2019).

Behavior

Millipedes are typically nocturnal and spend most of their time hiding in dark, moist habitats, such as soil, leaf litter, and rotting wood (Lawrence 1984). They typically stay in the shallow topsoil layer, but during hot, dry weather they may burrow deeper to escape the heat (Dangerfield 1991) found that millipedes can overwinter in burrows up to 30 centimeters (12 inches) deep. Millipedes have a variety of defensive mechanisms, including curling into a tight spiral, secreting chemicals, and using their hard exoskeletons. When threatened, some species curl into a tight spiral, using their hard exoskeletons to protect their soft undersides. This defensive behavior is known as conglobation. Benzoquinones are the most common chemicals produced by millipedes (Zagrobelny 2008, Smolanoff et al. 1975). They are found only in the orders *Spirobolida, Spirostreptida*, and *Julida*. Benzoquinones are toxic to many predators, and they can cause skin irritation and respiratory problems (Lawrence 1984). The defensive mechanisms of millipedes are an important part of their survival. These mechanisms help to protect millipedes from predators and allow them to live in a variety of habitats (Shear and Jones 2007, Hopkin 1992).

2.3. Managing soil fertility: The impact of millipedes

Detritivores are creatures that feed on dead and decaying organic matter, such as millipedes. They consume leaf litter, soil, and other remnants of plants and animals, and some also browsing on fungal mycelia (Blower 1985). As they eat, they break down this matter into smaller pieces, making it more digestible for other living organisms. Furthermore, they release nutrients into the soil, which can enhance its fertility (Mark et al. 1999). Overall, the effect of millipedes on soil fertility is complex and depends on a number of factors, including the species of millipede, the type of soil, and the presence of other organisms. In general, millipedes can be beneficial to soil fertility, but they can also have a negative impact in some cases (Culliney 2013,Tian et al. 1995).

Millipedes can contribute to soil fertility in various ways. Firstly, they break down organic matter, leading to the release of nutrients into the soil. This, in turn, enhances soil fertility and promotes plant growth. Secondly, millipedes burrow through the soil, improving aeration and drainage, which minimizes soil compaction. Thirdly, some millipedes produce toxins that can prevent plant diseases, safeguarding plants from infection. Lastly, millipedes can reduce pest populations, such as slugs and snails, which can protect plants from damage (Culliney 2013, Hopkin 1992), Raw1967, Dangerfield 1996). However, it is important to note that millipedes can also have a negative impact on soil fertility in some cases. For example, they can consume large amounts of organic matter, which can deplete the soil of nutrients. They can also release toxins that can be harmful to plants (Dangerfield 1996,Tian et al. 1995).

2.3. Other benefits of millipedes

One interesting ecological role of millipedes is their use in traditional medicine in some cultures. Millipedes have been used in traditional medicine for centuries, and there is some scientific evidence to support their medicinal value (Pemberton 2005, Paoletti 2005). For example, some millipedes produce chemicals that have anti-inflammatory, antimicrobial, and insecticidal properties. These chemicals have been shown to be effective against a variety of bacteria, fungi, and parasites (Hopkin 1992).

In addition, millipedes are known to possess substantial amounts of essential nutrients, including calcium, iron, and unsaturated fatty acids. Among the Bobo population, certain millipede species belonging to the families *Gomphodesmidae* and *Spirostreptidae* are utilized as a food source for human consumption et al. 2014). These nutrients have been linked to several health benefits, including improved bone health, immune function, and cardiovascular health. However, it is important to note that millipedes can also produce toxic chemicals, (Zagrobelny 2008) and their use in traditional medicine is not without risk. In some cases, millipede poisoning has been reported, and it is important to use caution when handling or consuming millipedes (Eisner et al. 1978).

2.4. Distribution and plant damage caused by millipedes.

Sara (2013) did a comprehensive overview of the global distribution of millipedes, including patterns of diversity, biogeography, and ecology. The distribution and ecology of millipedes and other arthropods, and notes that millipedes are found on all continents except Antarctica (CSIRO 2002, Redman 2003, Shelley and Golovatch 2011, Hopkin 2013, Iniesta and Ferreira 2013, Nefedieva et al. 2015). 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. Ebregt et al. (2005) 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 (Ebregt 2005).

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. The feeding damage caused by the millipedes resulted in stunted growth, wilting, and reduced yield of the crops (ECHO 2018, Hopkin 2015). 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 (Stacheland Zalik 1976). 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 (Chakraborty et al. 2016).

3. Climatic factors that impact distribution and damage by millipedes

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. Higher temperatures may lead to increased metabolic rates and feeding activity, but prolonged exposure to temperatures above their upper thermal limit can be lethal (Mark et al. 1999, Hoffman, 2000).

Humidity

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 (Graça et al. 2017a), 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 (Hamer 1999). 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 (Mwabvu 1997,De Araujo 2018). Atmospheric pressure changes may also impact their distribution, with millipedes more active during low-pressure weather systems (Mwabvu 1997, Graça 2017b).

Photoperiod, or the duration of light exposure in a day, can also influence millipede behavior and activity (Jewe and 1957). Some species may be more active during certain times of the day, with peak activity occurring at dawn or dusk (Jeweand 1957, Jean 2009). 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 (Jean 2009). 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 (Jean 2009). 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 properties and Organic Matter on Millipede Population

Soil type can also impact millipede distribution, with certain species preferring specific soil types or soil moisture levels (Slavomír Stašiov et al. 2021). 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. Soil properties, such as pH, conductivity, and litter quality, have a significant impact on the structure and composition of millipede communities in forest stands (Slavomír et al. 2021). The total activity density of millipedes is negatively correlated with the pH of the soil, meaning that the more acidic the soil, the fewer millipedes there are. This is likely because acidic soils are less suitable for the decomposition of organic matter, which is a major food source for millipedes (Slavomír et al. 2021).

Millipedes can have a significant impact on the concentrations of selected soil elements, such as magnesium (Mg), potassium (K), nitrogen (N), and carbon (C) (Smit 2001). The magnitude of the impact of millipedes on soil element concentrations depends on the species of millipede, the amount of millipede biomass, and the duration of millipede activity. Millipedes can increase the concentrations of these nutrients in soil by ingesting and breaking down organic matter. The increase in soil nutrient concentrations caused by millipedes can have a positive impact on plant growth (Smit 2001). For example, the train millipede *Parafontaria laminata* prefers to feed on litter that is high in nitrogen and low in lignin, and it also consumes soil that is rich in organic matter (Minori et al. 2004). The millipedes can reduce the thickness of the litter layer by up to 50%, and they can also increase the litter decomposition rate by up to 30% (Minori et al. 2004) .

In a study by de Carcamo et al. (2000) in a Canadian tropical dry forest, the researchers found that greater millipede abundance and diversity were associated with higher levels of soil organic matter. 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 (Kuczynski et al. 2012). The study by Hashimoto et al. (2004) offers valuable perspectives on the involvement of millipedes in the decomposition of organic matter and nutrient cycling specifically in larch plantation forests. The study's results indicate that millipedes have a noteworthy impact on the overall well-being of these forests. They contribute to essential processes such as the breakdown of organic matter and the cycling of nutrients, ultimately playing a crucial role in maintaining the health and functionality of the forest ecosystem (Minori -Hashimoto et al. 2004). Millipedes are important decomposers that break down dead plant and animal matter, releasing nutrients that plants can use (Dangerfield 1989). They also help to aerate the soil, which allows water and air to penetrate more easily. This improves the overall health of the soil and makes it more productive (Dangerfield 1989).

Gaining a comprehensive understanding of the intricate interplay between climatic conditions and environmental factors is crucial for developing effective approaches to manage millipede populations and mitigate the potential harm they can inflict on crops and other plant life. Millipedes hold significant importance as they actively contribute to the well-being of both soil and ecosystems. By recognizing their pivotal role and implementing protective measures, we can guarantee their continued positive impact on our planet, promoting a harmonious balance between these fascinating creatures and the environment they inhabit.

5. Genetic Diversity of Millipedes in Africa

The *Spirostreptida* order of millipedes is exceptionally abundant and widely distributed across Africa, encompassing approximately 71 recorded genera. Extensive research on *spirostreptid* millipedes has revealed significant genetic divergence among these organisms, with an average pairwise distance of 10.7% observed (Hamer 1999, Mwabvu et al. 2015). Among the numerous millipede genera in Africa, *Bicoxidens* stands out as one of the most extensively studied. This genus is exclusively endemic to the southern regions of the continent and thrives in diverse habitats such as savanna woodlands, forests, and riverine vegetation (Mwabvu et al.2009, Mwabvu et al., 2010, Mwabvu et al. 2015). *Bicoxidens* predominantly occur in Zimbabwe's eastern, southern, and central areas, as documented by Mwabvu et al. (2009). Nine distinct species have been identified within this genus, with *Bicoxidens flavicollis* exhibiting noteworthy phenotypic variation across different populations (Tinago et al. 2017).

In a comprehensive study conducted by Tinago et al. et al.(2017), mitochondrial DNA sequences were employed to investigate the genetic diversity of *Bicoxidens* populations in Zimbabwe. The findings unveiled the existence of several distinct mitochondrial lineages within the genus, indicating potential geographic isolation and/or ecological adaptation as contributing factors to their divergence. These multiple lineages strongly suggest the presence of cryptic species concealed within the genus *Bicoxidens.* The research results highlighted the presence of numerous divergent lineages within the *Bicoxidens* genus. Remarkably, some lineages were found to be more closely related to each other than to other lineages within the same genus. Such a pattern indicates prolonged geographic isolation among the various populations of *Bicoxidens*, suggesting that these lineages have been evolving independently for an extended period (Tinago et al 2017).

A molecular phylogenetic analysis of the millipede family *Spirostreptidae* in Africa revealed a complex pattern of diversification and radiation. Several genera within the *Spirostreptida* have undergone thorough revision, shedding light on their taxonomy and characteristics. Among these revised genera are *Archispirostreptus, Doratogonus, Cacuminostreptus, Spirostreptus, Plagiotaphrus*, and *Bicoxidens*, as documented by (Hamer 2000, Mwabvuet al. 2009, Mwabvu 2010, Mwabvu et al. 2015). The millipede fauna of North Africa has been relatively well-studied, with the Julida order being the richest and most diverse group (Akkar et al 2009). This order encompasses 58 species distributed among 12 genera and 3 families, and is predominantly found in Algeria, Egypt, Morocco, Tunisia, and Libya (Akkaret al. 2009). In contrast, the millipede fauna of Sub-Saharan Africa is less well-studied, with a considerable gap in our knowledge. However, the region hosts a remarkably rich diplopod fauna, boasting approximately 552 species belonging to 71 genera. Among these, the *Spirostreptida* order is the most recognizable, conspicuous, and frequently encountered group of diplopods in urban areas of Southern Africa (Hamer 1999).

Mitochondrial DNA (mtDNA) is a frequently utilized tool in genetic research due to its haploid nature, which facilitates its amplification across diverse taxa without the need for cloning procedures (Hurst and Jiggins 2005). mtDNA is also valuable for researchers because its structure and sequence can provide insights into evolution, gene flow, phylogenetics, and molecular evolution (Mandal et al. 2014). Despite constituting only a small fraction of an organism's entire genome, mtDNA remains the most commonly employed marker for studying molecular genetic diversity (Galtier et al 2009).

Ribosomal RNA (rRNA) genes have gained significant importance in phylogenetic studies because they have a high gene copy number per cell, which facilitates efficient gene amplification and sequencing (Galtier et al 2009). These genes contain conserved regions and variable regions, including expansion segments, which provide valuable information on evolutionary rates of base substitutions within the rRNA gene (Gillespieet al. 2006). Specifically, the 16S rRNA gene, a component of the ribosomal subunit, plays a crucial role in phylogenetic analysis. Its conserved secondary structure, in conjunction with associated proteins, forms the large mitochondrial RNA sub-unit (Schubart, et al. 2000).

The 16S rRNA region is a valuable tool for studying interspecific differentiation because it exhibits relatively low evolutionary rates, meaning that it changes slowly over time (Calo–Mata et al. 2009). This makes it ideal for comparing the genetic sequences of different species, even if they are closely related. The presence of conserved and variable regions within the same gene also makes 16S rRNA a favored marker for investigating separation events and conducting phylogenetic reconstructions (Schubart et al. 2000). In many phylogenetic studies involving diverse species, the genes 12S and 16S rRNA are commonly employed in conjunction with each other, as this provides a more complete picture of the evolutionary relationships between the species (Kuznetsova et al, 2002). The highly accelerated evolutionary rate of mitochondrial DNA (mtDNA) allows for the observation of substantial variation between closely related species (Yang and Bielawski 2000).

Microsatellites are widely dispersed throughout the genome and consist of short tandem repeat sequences, such as di-, tri-, or tetranucleotide repeats, with variable lengths ranging from one to five base pairs (Abdul Muneer 2014).This unique feature makes microsatellites a popular choice for molecular studies and the assessment of genetic population structures (Richard and Thorpe 2001, Abdul Muneer 2014). While most population genetic studies rely on data obtained from mitochondrial and nuclear markers, the information derived from evaluating microsatellites is crucial (Abdul Muneer 2014). Microsatellite sequences can be classified into minisatellites, and microsatellites based on their size. Microsatellites are particularly useful in identifying closely related populations due to their high variability levels, ability to isolate numerous loci, and fast processing speed (Abdul Muneer 2014).

Microsatellites are abundant in eukaryotic genomes, and their alleles are inherited according to Mendelian genetics. Each microsatellite locus is characterized by a known DNA sequence, consisting of both unique and repetitive DNA segments (Richard and Thorpe 2001, Abdul Muneer 2014). In a study by (Wojcieszek and Simmons 2009), 25 novel microsatellite markers were isolated from the millipede species *Antichiropu*s variables to investigate patterns of paternity. These markers represented the first microsatellite loci identified in a millipede species. Among the 25 loci, eleven were found to be polymorphic, and eight loci successfully amplified in other species of *Antichiropus* (Wojcieszek. and Simmons 2009). Similarly, Hasegawa et al. (2011) examined thirteen newly isolated polymorphic microsatellite loci in *Brachycybe nodulosa*. Out of these thirteen loci, only two showed lower-than-expected heterozygosity. These new loci hold potential for conservation efforts not only for *Brachycybe nodulosa* but also for other species within the same taxonomic group (Hasegawa et al. 2011). A study by Marek et al. (2012) 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.

A study conducted by Marek et al. (2012) that was used DNA sequencing to identify several distinct genetic lineages within the species (*Pachybolus ligulatus*) 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. A study by Vladimír et al. (2013) 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. 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.

6. Agricultural pests of millipede species

Millipedes can sometimes cause significant damage to crops (Fig. 2), so understanding the pest species and their impact on agriculture is important for pest management and control strategies. While most millipedes are known to be saprophagous, meaning they feed on decaying organic matter, certain species have been observed consuming living plant parts. They target soft and easily digestible plant tissues, such as young shoots or fine roots (Hopkin 1992). Numerous reports have highlighted the destructive nature of millipedes in agricultural crops. Kuria, et al. (1981) documented instances of millipedes causing crop damage in Ghana (guinea corn, cotton, millet, and groundnut), Central African Republic (cotton and groundnut), and South Africa (Irish potato, beetroot, carrot, turnip, and various ornamental plants). Mercer (Mercer 1978) even implicated millipedes as one of Malawi's culprits responsible for poor groundnut crop stands. Later, Lizzy (2021) described the impact of millipede feeding on the inflorescence of green gram (*Vigna* spp.) in India, particularly in areas surrounded by fallow land.

Blaniulus guttulatus Fabricius (*Julida, Blaniudae*) and *Brachydesmus superus* Latzel (*Polydesmida, Polydesmidae*) are species known to pose a notable economic threat to root crops in various regions worldwide. Specifically, these millipede species have been observed to cause significant damage to crop plants. They are frequently found in Irish potato tubers that show signs of partial hollowing-out (Blower 1985). Millipedes can cause significant damage to planting material, storage roots, and germinating seeds (Ebregt et al. 2004). The same study indicated that the incidence of millipede damage is highest in areas where sweet potato is grown in succession with other host crops, such as cassava and maize (Ebregt et al. 2004), apart from sweet potato, millipedes are a major pest of groundnut, and maize in Uganda (Ebregt et al 2005, Ebregt et al. 2007a). *Omopyge sudanica* is a voracious feeder that can cause significant damage to a variety of crop products, including sweet potato, cassava, groundnut, and maize (Abidin and Odongo 2007), and its activity peaks during the night and in periods of high humidity. Factors such as temperature, humidity levels, and the type of crop product influence the millipede's feeding behavior. Of concern is the significant damage it can cause to crop products, particularly when they are young or stored in humid conditions (Abidin and Odongo 2007). Farmers should remain vigilant in managing millipede populations and implementing appropriate control measures to mitigate the potential harm they can inflict on crops.

Millipedes pose a significant threat to tuber crops, such as sweet potato, cassava, and yam, as they can cause extensive damage to their roots, stems, and leaves (Alagesanand Ganga 1989). This damage results in yield losses and facilitates the spread of diseases among the affected crops. Various factors contribute to millipede infestations, including moist conditions, making areas with high rainfall or irrigation more susceptible to their presence (Alagesan and Ganga 1989). Furthermore, certain host crops, like sweet potato, are more attractive to millipedes, leading to higher infestation rates in these fields. Additionally, the soil type plays a role, as millipedes show a preference for sandy or loamy soils, which provide an easier environment for their burrowing activities. Similar reports on soil borne pests including millipedes have been reported from South Africa (Govender et al. 1996). Farmers must monitor millipede populations and implement appropriate pest control measures to safeguard their tuber crops and ensure optimal yields (Alagesan and Ganga 1989). 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.

Millipede species	**Host crop**	**Geographic distribution**	**References**
Anadenobolus sp. Rhinocricus sp.,	Cassava	Benin	(Sogbedji et al. 2009)
Archispirostreptus syriacus	Potato crops	Israel and East Africa,	(Mrema and Kidanemariam 1987)
Archispirostreptus tumuliporus (tulip-root millipede)	Maize, citrus crops	USA, Florida	(Odhiambo 2003)
Bandeirenica caboverda	Potato, sweet potato, papaya, and mango.	Cape Verde	(Hoffman 2000)
Boreviulisoma inflatum	Corn plants, soybean	United States	(Apple and. Wood 2004),
Cylindroiulus caeruleocinctus,	Corn and lettuce plants	Europe, North America.	(Program 2023)
Euryarthrum sp.	Trees, maize	North America, Europe, and Asia.	(Chapman and Hill 1976)
Euryurus leachii and *Telodeinopus aoutii*	Wheat and barley	Ethiopia	(Abebe-Erko 2015)
Hyleoglomeris diemenensis	Sugarcane and pineapple	South Africa	(Govender et al. 1996)
*Nopoiulus kochii (*sugarcane millipede*)*	Sugarcane, strawberry, and tomato crops	Southeast Asia, Australia, the United States, and Europe.,	(Manoa 2023)
Odontopygidae	Groundnut	West Africa	(Umeh et al. 1999)
Ommatoiulus moreletii	Citrus, cocoa, and coffee	Kenya, Tanzania, and Uganda	(Ebreg et al. 2005)
Ommatoiulus sabulosus,	Wheat and barley	Europe, Asia, North America.	(El-Borolossy et al. 2017).
*Omopyge sudanica (*black millipede*)*	Sweet potato storage roots, and germinating seeds.	Native to East Africa, South Africa	(Ebregt et al. 2004, Govender et al. 1996)
Orthomorpha coarctata (large millipede)	Cassava and maize	Cameroon	(Tchuenguem et al. 2015)

Millipede species	Host crop	Geographic distribution	References
Orthomorpha gracilis (greenhouse millipede)	Home garden	found in areas where there is decaying organic matter,	(Kwoseh et al. 2012)
Orthoporus ornatus	Cotton, corn, and soybean	United States	(Easton 1984)
Oxidus gracilis,	Corn and lettuce plants	Europe, Asia, North America, and Australia.	(University of California Statewide Integrated Pest Management Program 2023)
Pachyiulus flavipes	Coffee	Europe, Asia, North America, and North Ameria.	(Wardhaugh 1996)
Parafontaria laminata	Strawberry and tomato crops and sweet potatoes	Southeast Asia, Japan	(Shimizu et al. 2006)
Polydesmid millipedes	maize, cabbage, and tomato	Zimbabwe	(Hauser 1995)
Ptyoiulus impressus	Corn seedlings	Europe and North America	(Brockerhoff & Heenan 2002)
Rhinocyphus bicolor (black millipede)	Roots, stems, and leaves of tuber crops.	Native to India	(Alagesan and. Ganga 1989).
Rhinocyphus bicolor (brown millipede)	Sweet potato crops	Native to East Africa, South Africa	(Ebregt et al. 2004,Govender 1996)
Spirostreptus ibanda *(Brown millipede)*	Sweet potato and groundnut crops	Native to East Africa	(Ebregt et al. 2007a. Ebregt 2005).
Spirostreptus sp.	Coffee, crone, forests	Brazil, India	(Mulyadi et al. 2017)
Spirostreptus sp.	Maize, cassava, and yams	Africa and Asia.	(Dede et al. 2018)
Tachypodoiulus niger,	lettuce plants, corn plants	Europe and North America	(Blower 1971) (University of Kentucky Cooperative Extension Service 2023)
Tibiomus spp. cfr. Ambitus (brown millipede)	Maize crops	Native to East Africa	(Ebregt et al. 2007a, Ebregt et al. 2005)

Millipede species	Host crop	Geographic distribution	References
Tonkinbolus caudulanus	Beans, peas, and tomatoes	Tanzania	(Mashimba 2017)
Tonkinbolus caudulanus,	Groundnut (peanut)	West Africa	(Chakupurakal Isichei 1982)
*Tonkinbolus caudulanus:(*South China giant millipede)	It can cause up to 80% crop loss in a cabbage field.	China, Kenya, Nigeria	(Chakupurakal Isichei 1982, Odhiambo 2003)
Tymbodesmus africanus	Maize, sorghum, and sugarcane	South Africa	(Govender et al. 1996)
*Xenobolus carnifex (*brown millipede)	Tuber crops	Native to India	(Alagesan and. Ganga 1989)
Xystodesmidae millipedes	Cotton, tobacco, vegetable crops, Corn, soybeans, and wheat	North America	(Ebregt et al. 2005)

The species affected by millipede damage are numerous, including beans, cabbage, carrots, corn, potatoes, strawberries, tomatoes, and more. Millipede damage is most 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, botanical, cultural, biological, and chemical control methods.

7.1. Mechanical and cultural control methods

This involves physically removing millipedes from the affected area. This can be done by handpicking, vacuuming, or using sticky traps (Ebregt et al. 2005). 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 (Kharusi et al. 2019). Several studies reported that sticky traps were effective at reducing the number of millipedes in a house, while vacuum cleaners were less effective (Abbot and Brennan 2014, (Akinwumi,et al. 2013). 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 (Abbotand Brennan 2014, Akinwumi et al. 2013).

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(Michael et al. 2018). To effectively minimize the entry of millipedes (as well as other pests), the most recommended and sustainable approach is to address the factors of excess moisture and hiding spots, particularly near the foundation (Michael et al. 2018). Cultural control methods can be effective in reducing millipede populations, but they may take longer to show results than chemical control methods (Wang 2014, Adis Harvey 2017, Oliveir a 2017).

7.2. Controlling millipedes using botanicals

Neem, a renowned natural pesticide, has emerged as a promising solution in the battle against pests. In addition to neem, various other organic pesticides have proven to be effective repellants against millipedes (ECHO 2018). Preliminary research conducted in north-eastern Uganda has highlighted the potential of plant extracts derived from the neem tree (*Azadirachta indica*), goat weed (*Ageratum conyzoides*), African marigold (*Tagetes* spp.), tobacco (*Nicotiana tabacum*), and chilies (*Capsicum* spp.) as potent pest deterrents (ECHO 2018). These organic alternatives offer sustainable and environmentally friendly options for managing millipede infestations, aligning with the growing interest in eco-conscious and natural pest control methods.

7.3. 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 (Pocockand Hassall 2010). However, the effectiveness of biological control methods can be limited by the availability and suitability of natural enemies.

Millipedes have a specific covert development cycle and defensive chemicals that make them difficult for most predators to eat. However, some parasites could be used as biological control agents against *S. caboverdus*. Laboratory tests have shown that the fungi *Beauveria*, *Metarhizium flavoviride* could be effective biological control agents for the millipede in Cape Verde (Nascimento 2002). 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 (Van den and Janssens 2017). 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 (Sij 2021, Kostanjšek et al. 2014). Centipedes are predatory arthropods that have been observed feeding on millipedes in both laboratory and field settings (Kime 1982). Some species of nematodes have been found to infect and kill millipedes. For example, *Rhabditis necromena, Steinernema carpocapsae* has been shown to be effective against the millipede *Ommatoiulus moreletii* in laboratory experiments (Nascimento 2002,riments (Baker 1985, Albrecht M. Koppenhöfer 2000, Nascimento 2002).

Pelidnoptera nigripennis, a parasitoid fly, is a promising candidate for biological control of the invasive Portuguese millipede, *Ommatoiulus moreleti*, in Australia (Eter 1989). The fly is specific to julid millipedes, and it has been shown to be effective in laboratory trials. The main benefit of using *P. nigripennis* is that it could be an effective way to control *O. moreleti*, which is a serious pest in Australia. However, further research is needed to assess the risks and benefits of releasing the fly into the environment (Eter 1989). The Portuguese millipede, *O. moreletii*, is an introduced pest in Australia. This millipede has several parasites in its native range in Portugal, including a nematomorphan worm (*Gordium* sp.) and a muscoid fly (*Eginia* sp.) (Baker 1985). These parasites are specific to *O. moreletii* and have the potential to be used as biological control agents in Australia (Baker 1985). It is 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 to control millipedes.

7.4. Natural enemies

Another 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 (Orkin 2022). Predatory beetles belonging to the Carabidae (ground beetles) and Staphylinidae (rove beetles) families are commonly found in agroecosystems, and some of these species have been observed to feed on millipedes in laboratory experiments(Rem 1984, Baker 1985). In the carrot and sweet potato Fields, eight species of generalist predators that are linked to the millipede population have been identified (Brunke et al. 2009). However, the effectiveness of natural enemies in controlling millipede populations can vary depending on the species and environmental conditions.

7.5. 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 (Michael 2023, Chapman 2016).

Foliar-applied chlorpyrifos and beta-cyfluthrin, such as diazinon and chlorpyrifos, have also been used to control millipedes (Ashley and Erin 2020). The same study evaluated the effectiveness of several insecticides, including organophosphates and pyrethroids, 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 (Ashley and Erin 2020, Park 2015). 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.

The type of insecticide that you choose will depend on the severity of the millipede infestation and the specific area that you need to treat. If you have a large infestation, you may need to use a combination of different types of insecticides, such as contact pesticides, residual pesticides, insect dust, and perimeter pesticides (Powell 2023).

Contact pesticides work when they encounter the millipede's body. They are quick-acting and effective against large groups of millipedes. However, they can also be harmful to other insects and animals, so they should be used with caution (Powell 2023). Residual pesticides are designed to kill millipedes over a longer period. They are applied to surfaces where millipedes are likely to crawl, such as floors, walls, and furniture. Residual pesticides can be effective in preventing millipedes from returning, but they can also be harmful to other insects and animals (Powell 2023). Insect dust is a fine powder that can be used to kill millipedes in cracks and crevices. It is a good choice for hard-to-reach areas, but it can be messy to apply. 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. For example, to prevent millipedes and other pests from entering your home and agricultural fields, it is best to minimize moisture and remove debris. This can be done by reducing excess moisture and hiding places, especially near the foundation and greenhouse. It is also important to seal any cracks or openings in the outside foundation wall and prevent water from accumulating near the foundation, in basement walls, or in the crawl space. By taking these measures, you can effectively reduce the entry of pests into your home (Michael Waldvogel 2023).

Monitoring was an important component of the integrated pest management approach and helped to guide the use of other control tactics (Ashley and Erin 2020, Firas 2002). Regular monitoring of crop fields can help to identify millipede infestations early before they become widespread and difficult to control (Firas 2002).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 (Van Driesche 2008, Ashley and Erin 2020). A study investigated millipede damage to maize in Brazil and the use of pitfall trapping as a monitoring technique (Firas 2002, Pimentel 2014). 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 consider 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.

Declarations

Authors contribution

Conceptualization: K.T.M.; Original draft preparation: K.T.M and A.H.; Writing: K.T.M and A.H; Editing and formatting: J.K and Reviewed drafts of the paper: NG; Language editing and preparation of tables and/or figures: W.Y.; Final approval of the review to be published:

All authors have read and agreed to the published version of the manuscript.

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.

Competing Interests

The authors declare no competing interests.

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Figures

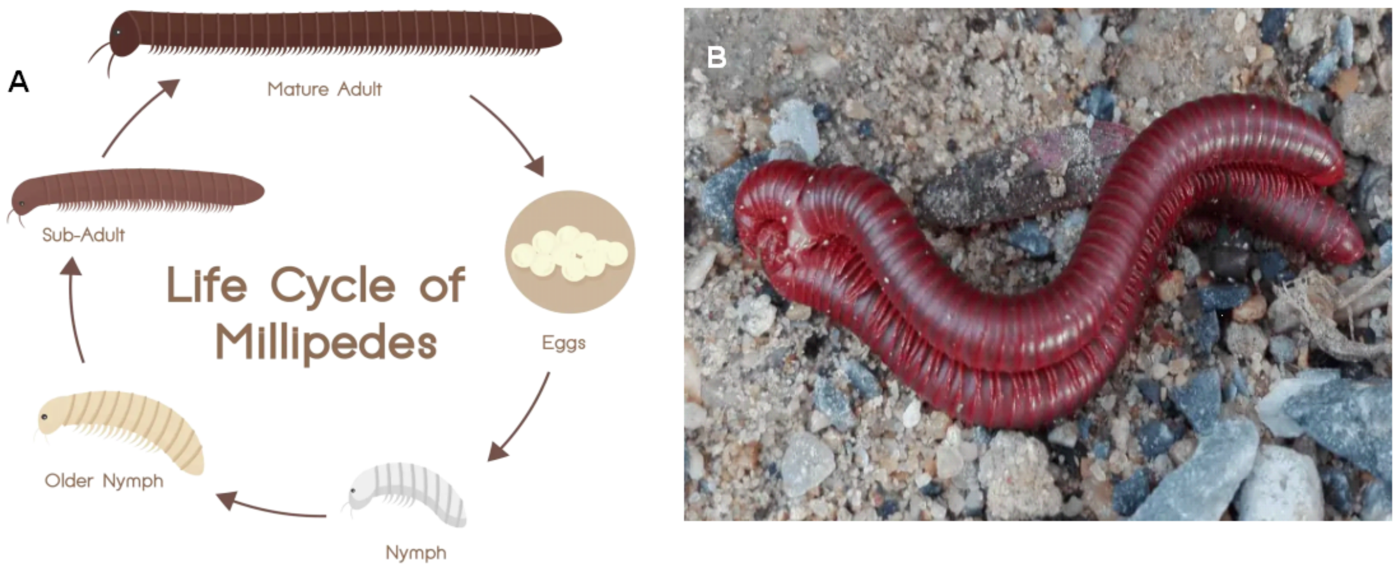

Figure 1

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/).

Figure 2

Millipede damage on various root and tuber crops (A-D) (taken from Eastern Rwanda, in 2021/22 crop season). 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 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 plant protection research group.