The Role of Earthworms in Grasslands

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Abstract Grasslands are among the most important ecosystems for human livelihoods. Besides their irreplaceable role in human food production, grasslands provide a wide range of ecosystem services at different scales. Earthworms, being soil ecosystem engineers, can play a key role in affecting the capacity of grassland soils to provide ecosystem services. Earthworms are known to improve soil physical properties, nutrient availability, plant biomass production, and soil water balance. Specifically, a high earthworm abundance and diversity in grasslands is often related to high soil porosity and water retention, low soil compaction, formation of soil biogenic aggregates with great stability, high availability of nutrients, and accelerated soil organic matter cycling, leading to high plant biomass production. This, in turn, encourages the maintenance of large and diverse earthworm populations in grasslands.

Most of the world's managed grasslands sustain livestock production (as opposed to natural grasslands without human intervention). Earthworms are sensitive to agricultural management. For instance, fertilization, grazing and manure management, soil compaction, and modification of the plant community composition (i.e., introduction of improved forages, trees, or legumes) can affect earthworm communities

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in direct and indirect (and often interrelated) ways. Here, we summarize the potential of different grassland management practices and their possible effects on earthworm populations and communities, as well as the subsequent soil properties and functions that underpin sustainable intensification.

Based on their importance for soil functions and high sensitivity to grassland management, we encourage the inclusion of the earthworm communities among the studied factors for the assessment of grassland management practices' effects on soil health. Furthermore, we suggest that using earthworms as bioindicators of soil health in grassland is practically accessible and easily interpretable by farmers and agriculture services. The development of a standardized method of earthworm assessment, adapted to different edaphoclimatic conditions and types of grassland management, could help to transfer scientific knowledge generated during the last decades to final users and managers of grasslands.

1 Grasslands

1.1 Importance of Grasslands

Grasslands cover about 40% of the ice-free area on Earth and are one of the most important ecosystems (Suttie et al. 2005; Lemaire et al. 2011; Bengtsson et al. 2019). The grassland biome is characterized by the dominance of graminoids and the presence of broadleaves forbs, in addition to less than 10% coverage by tree canopy in temperate regions or up to 40% in tropical regions (Suttie et al. 2005; Jones 2019). Grasslands were formed by processes related to climate, fire, and wildlife grazing, and they occur naturally in temperate regions (steppes and prairies) and along desert borders. In more humid regions, grasslands have been generated anthropogenically by forest clearance for grazing domesticated animals (Jones 2019; Bengtsson et al. 2019). Globally, grassland areas have decreased during the last century because of increasing food demand and the related land use change to cropland (Manuel-Navarrete et al. 2009; Peeters 2009). Nevertheless, in some regions of Europe and North America, the abandonment of marginal croplands with low productivity contributes to grassland and prairie restoration (Cramer et al. 2008; Török et al. 2011).

The importance of grasslands for human livelihood is primarily related to fodder and forage production for the livestock sector (Herrero et al. 2013; Rao et al. 2015; Bengtsson et al. 2019; Notenbaert et al. 2021). Grasslands produce plant biomass that is the basis for meat and dairy production, particularly in the Global South where the livestock sector is based on mixed crop-livestock systems and family farms (Herrero et al. 2013; Rao et al. 2015; Notenbaert et al. 2021). The most important role of grasslands, nevertheless, lies in their ecological functions. Grasslands provide a wide array of ecosystem services affecting ecological processes and human welfare at the landscape, regional, and global scale (Lamarque et al. 2011;

Bengtsson et al. 2019). At the landscape scale, grasslands are considered reservoirs for the maintenance of above and belowground biodiversity, which is also linked to other ecosystem services such as providing floral support for pollinators and biological pest control (Lamarque et al. 2011; Bengtsson et al. 2019). At the regional scale, grasslands provide water services by storing, purifying, and regulating the water flows and reservoirs. They also limit erosion and deliver cultural services, such as tourism; recreation and sport areas; hunting; landscape heritage; and social cohesion (Lamarque et al. 2011; Bengtsson et al. 2019; Notenbaert et al. 2021). Finally, at the global scale, grassland ecosystems are crucial for climate regulation because their soils store about 20% of global carbon (C) stocks and can become a sink or source of CO_2 depending on the grassland status (Lal 2004; Wang and Fang 2009; Bengtsson et al. 2019). However, all of these ecosystem services are endangered by land use change, climate change, and unsustainable grassland management practices (Egoh et al. 2016; Bengtsson et al. 2019; Notenbaert et al. 2021). Therefore, the understanding, conservation, and restoration of grasslands in an agroecology framework are crucial to ensure biodiversity conservation, food security, and sustainable livelihoods at the global scale (Bengtsson et al. 2019; Notenbaert et al. 2021).

1.2 Natural Versus Managed Grasslands

Grasslands generally require a certain degree of management to support the increasing demand for livestock production worldwide (Herrero et al. 2013). Natural and managed grasslands differ in the intensity of human intervention. Natural or semi-natural grasslands have a low level of human intervention and are only grazed by wild herbivores or sparsely by domestic herbivores (Bengtsson et al. 2019; Chang et al. 2021). In contrast, managed grasslands or pasturelands have been anthropogenically modified to support livestock production (Bengtsson et al. 2019; Chang et al. 2021). Grassland management includes practices such as tree and shrubs clearance; construction of farm infrastructures including fences, shelters, or watering places; introduction of improved grasses or legumes to replace the natural floral composition; fertilization with chemical fertilizers or manure; and/or periodical burnings. Within the managed grasslands, we could distinguish between pastures (permanent grasslands under grazing by domestic herbivores) and meadows (permanent grasslands used for mechanical harvesting of grass by mowing), but in this chapter, we will refer indistinctly to pastures and meadows as managed grasslands, except when differences between types of managed grasslands are expected. The trend of globally increasing demand for livestock products has been accelerating the management intensification of these ecosystems, resulting in the replacement of wild herbivores and natural grasslands with managed grasslands grazed by domestic herbivores (Smith et al. 2016; Chang et al. 2021).

2 Earthworms in Grasslands

2.1 Occurrence of Earthworms in Grasslands

Earthworms are probably the most studied soil invertebrates in grasslands because of their pivotal role in providing or maintaining many soil ecosystem services and their relative ease of evaluation (Phillips et al. 2021). Earthworms are more abundant in grasslands than in any other ecosystem (Decaëns et al. 1994; Lavelle et al. 1997; Paoletti 1999). Earthworm biomass can be as high as 200 g m^{-2} in temperate grasslands (Curry et al. 2008; Hoeffner et al. 2021b) or up to 150 g m^{-2} in tropical pastures (Decaëns et al. 1994; Feijoo et al. 2011), exceeding the biomass of any other invertebrate. At the global scale, the average biomass of earthworms in pastures and grasslands is approximately 100 g m^{-2} (Paoletti 1999). Similarly, earthworm abundance in grasslands and pastures is approximately 300 individuals m^{-2}, although it can range between 0 and 500 individuals m^{-2}, while the earthworm species diversity commonly ranges between 6 and 15 species (Lavelle et al. 1997; Paoletti 1999; Feijoo et al. 2011; Hoeffner et al. 2021b; van de Logt et al. 2023). Earthworms in grasslands compared with those in croplands or forests benefit particularly from higher and continuous availability of food (organic matter inputs to soil, including animal manure) (compared with croplands), absence of soil tillage (compared with croplands), and high-quality litter (compared with forests), although exceptions can be found in both cases.

2.2 Impacts of Earthworms on Grassland Soils

Earthworm activity is crucial for grassland soil functioning: they regulate litter decomposition and nutrient availability; maintain soil structure and water retention; and affect the greenhouse gas (GHG) balance (Lavelle 1988; Lavelle et al. 1997; Eisenhauer and Scheu 2008; Pulleman et al. 2012; Blouin et al. 2013). In addition, due to their impact on soil properties and nutrient availability, earthworms affect the ecosystem's primary production or even the competition between different plant functional groups (Lavelle 1988; Brown et al. 2004; Eisenhauer and Scheu 2008; Blouin et al. 2013). Therefore, the study of earthworm communities in grasslands can help to understand the soil health status and ecosystem functioning (Pulleman et al. 2012; Blouin et al. 2013). In this section, we will summarize the main impacts of earthworms on grassland soils as well as on plant community composition and biomass production. The main relationships among soil properties, earthworms, plant biomass production, grazing animals, and anthropogenic inputs are summarized in Fig. 1.

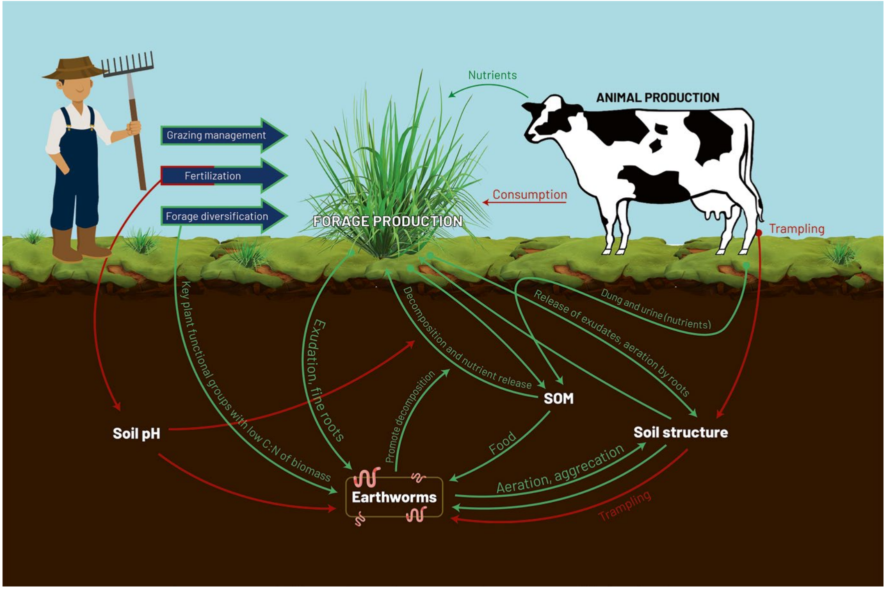

Fig. 1 The reciprocal impacts of grazing management, grassland fertilization, and forage diversification (blue arrows) on forage production and earthworms mediated by effects on soil pH, soil organic matter (SOM), and soil structure. Positive and negative effects are represented by green and red color, respectively (figure made by José Luis Urrea and Anny Isabella Yedra (Alliance Bioversity-CIAT))

2.2.1 Soil Physical Properties

The life strategy of earthworms affects the physical properties of soil in many ways. They dig burrows and tunnels, deposit casts with a particular physical structure, and contribute to the mixing of soil horizons, which subsequently incorporate plant litter into deeper soil layers (Lavelle 1988). In this way, earthworms improve soil porosity and aeration, water infiltration and storage, and soil aggregation and structural stability (Lavelle 1988; Spurgeon et al. 2013) (Fig. 1).

Many studies have found a higher soil porosity in grasslands with a higher earthworm abundance (Drewry 2006; Lamandé et al. 2011; Velásquez et al. 2012; Schon et al. 2017; Vázquez et al. 2020; Teutscherová et al. 2021b). Earthworms can increase macropores by burrowing, while meso- and microporosity is mainly affected by casting. Variation occurs between different earthworm species in the extent to which they impact soil porosity (Brown et al. 2004). Surface-casting species, like *Lumbricus terrestris*, are recognized for their prolific production of surface casts in compacted soils, which can alleviate soil compaction (Piearce 1984; Joschko et al. 1989). Although exceptional, some invasive species, such as *Pontoscolex corenthrurus*, have been observed to colonize grasslands established after Amazonian Forest clearance leading to soil compaction as a result of their uncontrolled casting activity that reduces the soil macroporosity (Chauvel et al.

1999). In general, the ability of earthworms to maintain adequate soil aeration and reduce soil compaction is of particular interest in managed grasslands threatened by soil compaction from animal trampling or mechanical traffic (Piearce 1984; Herrick and Lal 1995; Drewry 2006; da Silva et al. 2019; Arrázola-Vásquez et al. 2022) (Fig. 1). In relatively compacted soils, earthworms can restore soil porosity when burrowing via ingestion and deposition the soil cast on the soil surface (Piearce 1984; Joschko et al. 1989; Arrázola-Vásquez et al. 2022).

Higher soil porosity generated by earthworms coincides with increased soil aeration and soil hydraulic conductivity, thereby affecting some important ecosystem services provided by grasslands, such as plant biomass production, water fluxes regulation, and soil erosion control (Blouin et al. 2013; Spurgeon et al. 2013) (Fig. 1). The relationship between higher earthworm abundance and water infiltration and storage has been observed in experimental grasslands (Clements et al. 1991; Bouché and Al-Addan 1997; Velásquez et al. 2012; Fischer et al. 2014) and real farm grasslands (Teutscherová et al. 2021b). Higher water infiltration is mainly caused by the continuous macropores created by earthworm burrowing activity, primarily by anecic species. This can contribute to reduced soil erosion through superficial water runoff (Weiler and Naef 2003; Blouin et al. 2013) or waterlogging conditions on flat surfaces (Teutscherová et al. 2021b). In addition, earthworm surface casting can reduce soil erosion by increasing surface roughness (Blouin et al. 2013); however, this seems to be more important in agricultural soils with abundant bare soil areas than in permanent grasslands.

Earthworms are well known for increasing soil aggregation in grasslands (Guggenberger et al. 1996; Fonte et al. 2012; Velásquez et al. 2012; Vázquez et al. 2020; Lavelle et al. 2020; Garcia-Franco et al. 2021; Rodríguez et al. 2021b). The positive effect of earthworms on soil aggregation can be caused directly by the production of highly stable casts or indirectly through the promotion of the root colonization of nutrient-rich casts (Pulleman et al. 2005a, b; Fonte et al. 2012). Generally, earthworm casts are very rich in C and other nutrients, and these structures remain stable upon drying (Guggenberger et al. 1996; Pulleman et al. 2005a, b; Jouquet et al. 2008; Fonte et al. 2012; Lavelle et al. 2020).

2.2.2 SOM and Nutrient Cycling

Among the most studied and accepted impacts of earthworm activity in grasslands is, without a doubt, their capacity to enhance soil C sequestration by improving soil aggregation and organic matter mineralization (Lavelle et al. 2020) (Fig. 1). Earthworm casts are formed by resistant aggregates enriched in C stabilized with soil particles (Lavelle and Martin 1992; Guggenberger et al. 1996; Pulleman et al. 2005b). Plant debris is decomposed in the earthworm gut and mixed with mucus and soil particles that promote the physical stabilization of organic matter (Lavelle and Martin 1992; Guggenberger et al. 1996). After release, casts are enriched in nutrients and show a high microbial activity; however, after a few days/weeks, the microbial activity decreases, resulting in organic matter that is stabilized and protected from further mineralization within the aggregates (Lavelle and Martin 1992; Guggenberger et al. 1996). This occlusion of organic matter within stable aggregates created by earthworms suggests that casts may influence positively long-term C sequestration in soils (Lavelle and Martin 1992; Guggenberger et al. 1996; Pulleman et al. 2005a, b; Lavelle et al. 2020). Yet, some studies have suggested that earthworms only increase the soil C sequestration in the long term when organic matter inputs are also increased compared with the previous management (Don et al. 2008; Fonte and Six 2010).

2.2.3 Plant Biomass Productivity and Plant Community

The positive effect of earthworms on plant biomass productivity (Fig. 1) was already described by Darwin in 1881. Since then, many studies, reviews, and meta-analyses have confirmed such observation (Curry 1987; Brown et al. 1999; Scheu 2003; Blouin et al. 2013; van Groenigen et al. 2014) and at least five mechanisms have been identified to justify the observed effects of earthworms on plant biomass productivity (Brown et al. 1999; Scheu 2003; Blouin et al. 2013): (1) higher nutrient availability due to accelerated organic matter mineralization, (2) improved water retention and soil structure, (3) pest control, (4) increased microbial activity, and (5) promotion of symbiotic relationships. In addition, earthworms can affect the plant diversity of grassland by modifying the competition between different plant functional groups, such as grasses and legumes (Eisenhauer and Scheu 2008; Eisenhauer et al. 2009a) or by affecting the seed bank dispersion (Decaëns et al. 2003; Zaller and Saxler 2007). However, the understanding of these mechanisms and their relevance under real grassland conditions remains a challenge because earthworms both affect and are affected by plant biomass and diversity in a positive feedback loop (Brussard 1999). In Sect. 3, the different management practices that simultaneously promote plant biomass or diversity and earthworm abundance in managed grasslands are discussed.

3 Earthworms in Managed Grasslands

As the earthworm abundance and distribution in soil are primarily driven by the presence of food supply, earthworm communities are affected by, for instance, sward composition and diversity; the quantity and quality of produced plant biomass; the type and intensity of grazing or cutting events; the dung deposition; and the application of both organic and inorganic fertilizers (Lavelle et al. 2001; Curry 2004; Curry et al. 2008; Singh et al. 2021). Therefore, all grassland management practices affecting these grassland properties can affect the earthworm community (Lavelle et al. 2001; Curry 2004). Not only does grassland management affect organic matter supply in soil, but it also affects earthworm communities by changing the soil's physical structure, microclimatic conditions, and/or chemical composition (which includes toxic substances) (Ma et al. 1990; Drewry 2006; Curry et al. 2008; Birkhofer et al. 2008; Schon et al. 2017; Vázquez et al. 2020).

To better understand the earthworm ecology and to predict potential impacts of grassland management on earthworm communities, several studies have provided interesting information on the different drivers of earthworm abundance and activity using data collected from experimental plots with different levels of plant richness (Milcu et al. 2008; Eisenhauer et al. 2009b; Velásquez et al. 2012) or N fertilization type/dose (Ma et al. 1990; King et al. 2007; van Eekeren et al. 2009; Hoeffner et al. 2021a). Nevertheless, under real farm conditions, several management practices are generally applied simultaneously to optimize the productivity and/or sustainability of a managed grassland (intensification or sustainable intensification of a grassland) (Dumont et al. 2018). For instance, grassland fertilization is commonly accompanied by increased livestock stocking rates or the frequency of cuttings, both possibly influencing soil earthworms. Thus, the response of earthworm communities to grassland management is more complex in comparison to effects caused by a single treatment applied in experimental plots (Curry et al. 2008; Singh et al. 2021). In addition, suitable grassland management practices are strongly dependent on the region, the climatic conditions, the type of farming, and/or the aim of the farmer. The principal aim of this section is to provide an overview of the potential effects of different management practices on earthworm communities and their interactions under real farm conditions. In the next four sections, different effects are evaluated separately, and at the end, the combination of different common management practices in temperate and tropical regions is discussed, aiming to provide an overview of the potential impact of sustainable intensification of grasslands on earthworm communities.

3.1 Impact of Grassland Establishment

Land use change has a profound impact on soil ecosystem functioning including the earthworm community and its functions in soil (Decaëns et al. 2004; Postma-Blaauw et al. 2012; Spurgeon et al. 2013). In the last century, the growing human population and food demand have forced the intensification of agricultural production, which, on one hand, has led to the transformation of grasslands into agricultural fields, and on the other hand, the establishment of newly managed grasslands in formerly forested areas (Fragoso et al. 1999; Ellis and Ramankutty 2008; Peres et al. 2010; Graesser et al. 2015; Dumont et al. 2018; Notenbaert et al. 2021). The latter land use change is particularly true in Latin America, where the growing demand for meat has dramatically moved the deforestation barrier into the tropical forests and savannas to establish new grasslands or man-made pasturelands (Rodrigues et al. 2009; Rao et al. 2015). In contrast, in temperate regions of Europe and North America, a trend of land management de-intensification to restore grasslands and prairies in abandoned agricultural areas (Cramer et al. 2008; Török et al. 2011; Postma-Blaauw et al. 2012; Spurgeon et al. 2013; Wodika et al. 2014) or introduction of temporal grass leys in crop rotations (Karwat et al. 2017; Rodríguez et al. 2020; Hoeffner et al. 2021a) has been observed.

The effect of grassland establishment on earthworm communities depends on the previous land use, particularly on the degree to which there is a similarity between the previous land use and vegetation and the newly established grassland. For instance, the impact of grassland establishment on earthworm communities will drastically differ in grasslands formed in previously forested areas versus grasslands that were previously savannas (Decaëns et al. 1994, 2004; Fragoso et al. 1999). In tropical savannas (one of the predominant ecosystems in Latin America), the man-made pastures used for intensive livestock production are established by replacing the native grasses with African grasses and forage legumes, hence simplifying the plant community but increasing the biomass production (Fragoso et al. 1999; Notenbaert et al. 2021). Nevertheless, if the vegetation structure and functionality remain similar, the taxonomic richness and earthworm community composition can be preserved (Decaëns et al. 1994, 2004; Fragoso et al. 1999). In fact, earthworm abundance and biomass can even augment after such intervention as a result of higher organic matter inputs from plant biomass, higher quality plant litter (especially in case of legume inclusion), absence of periodic burning, and higher animal dung deposition (Decaëns et al. 1994, 2004; Jiménez et al. 1998; Fragoso et al. 1999).

In contrast, earthworm communities are usually drastically altered when tropical rainforests (such as in the case of the Amazon Basin) are substituted with pasturelands, as native earthworm species are commonly depleted and replaced by a single exotic peregrine species (Fragoso et al. 1999; Decaëns et al. 2004; Marichal et al. 2010). The exotic replacement species seem to benefit from the following changes to the soil environment, the removal of the soil litter layer (affecting in particular anecic and epigeic species) and high soil organic C availability in managed pasturelands (Fragoso et al. 1999; Decaëns et al. 2004; Mathieu et al. 2005; Peres et al. 2010; Marichal et al. 2010). Such a strong reduction of earthworm diversity inevitably leads to the loss of healthy soil structure, as the role of earthworms as soil engineers is lacking. This is reflected in a rapid degradation of soils as commonly observed across Latin America pasturelands (Chauvel et al. 1999; Marichal et al. 2014). This highlights the importance of considering earthworm communities during the assessment of the impact of land use change on ecosystem services and sustainability.

Unlike in the tropics, temperate grassland areas have tended to diminish during the last century because of the increasing demand for agricultural lands (Manuel-Navarrete et al. 2009; Peeters 2009). This agriculturalization process of grasslands, which is still in progress in some regions (e.g., the Argentinian pampas), has led to the reduction of earthworm abundance and the invasion of exotic or opportunistic earthworms and, therefore, soil degradation (Manuel-Navarrete et al. 2009; Domínguez et al. 2010; Falco et al. 2015). In contrast, in many regions of Europe and North America, land with low agricultural productivity and marginal croplands have been abandoned, which contributes to grassland and prairie restoration (Cramer et al. 2008; Török et al. 2011). Even though the success of the grassland plant community recovery in such abandoned agricultural fields may require some human support to reach the native vegetation diversity status (the success seems to be dependent on the intensity of previous agricultural management) (Cramer et al. 2008; Török et al. 2011), a shift toward grasslands at the expense of an agricultural field generally leads to an increase in earthworm abundance (van Eekeren et al. 2008; Postma-Blaauw et al. 2012; Spurgeon et al. 2013; Wodika et al. 2014). This effect derives from the higher organic matter input in grasslands compared with croplands, lack of tillage or pesticide application, and the continuous soil cover that buffers the soil microclimatic conditions (van Eekeren et al. 2008; Domínguez et al. 2010; Postma-Blaauw et al. 2012; Spurgeon et al. 2013; Wodika et al. 2014). It has been observed that earthworm abundance can react to land use change as early as 0–3 years after a transition (van Eekeren et al. 2008; Spurgeon et al. 2013). However, the earthworm species composition in restored grasslands is not always the same as in a native grassland. For instance, in restored prairies of Illinois (USA), the earthworm community was dominated by exotic European earthworm species, which may affect the soil and grassland functioning (Wodika et al. 2014). Similarly, van Eekeren et al. (2008) described a recovery of earthworm abundance and biomass in Belgium after 3 years of grassland establishment, but the dominance of anecic species, as in older grasslands, was not achieved. In general, earthworm communities in croplands are dominated by endogeic (feeding on deeper soil layers) species, which are likely the first earthworm group that reacts positively to grassland conversion as they can recruit new progeny from the standing arable crop community. Anecic and epigeic species, on the contrary, likely need a longer period of time after grassland restoration until their microhabitat is recovered (especially surface litter) and they can recolonize the area (Spurgeon et al. 2013).

In recent years, the introduction of temporal grass ley phase in crop rotations has gained attention as an alternative to continuous cropping systems (particularly in organic farming) that can reduce soil degradation, loss of biodiversity, and N losses and increase the soil C sequestration (Tsiafouli et al. 2015; Lemaire et al. 2015; Karwat et al. 2017; Hoeffner et al. 2021a). The grassland period, which commonly ranges between a season to several years, temporally modifies the soil ecosystem and subsequently can affect the earthworm community (van Eekeren et al. 2008; Postma-Blaauw et al. 2012; Rodríguez et al. 2020; Hoeffner et al. 2021a). Hoeffner et al. (2021a) observed that the increase in earthworm abundance and shift in community composition depended on the time since grassland establishment. In particular, they observed that anecic species benefited from grassland establishment only after 6 years, indicating that the effects on soil earthworm communities and their ecosystem services may differ depending on the extent of the grassland period in the rotation. Therefore, the introduction of temporal grasslands in crop rotations can have a positive effect on soil earthworm communities compared with continuous cropping; however, the positive effects would not reach the level of permanent grasslands due to the short term of the grassland period and the consequent returned to cropland including tillage and other agricultural practices. Further studies should evaluate possible legacy effects on the earthworm communities established during the grassland period in the next cropping periods of the rotation.

In summary, a shift toward managed grasslands depends on the previous land use type and can have a positive or negative impact on earthworm communities. When a grassland is established on a recently deforested area, expansion of exogenic species and soil degradation are often observed. Nevertheless, the substitution of native grasslands, savannas, or agricultural areas with managed grasslands may have a positive impact on earthworms due to an increase in organic inputs to the soil via higher plant biomass production or livestock dung deposition and/or the reduction of periodical burnings, tillage, and pesticide application. However, the composition and diversity of the earthworm community can differ compared with the native community, particularly when the ecosystem functioning of the former land use is different, which can have strong implications for soil properties and soil health. Therefore, we encourage consideration of the potential responses of earthworm communities to grassland establishment in order to minimize negative impacts on newly established soil earthworm communities.

3.2 Grassland Management and Intensification

3.2.1 Introduction of Improved Grasses

During the last decades, native vegetation of natural tropical savannas has been replaced in large areas by improved tropical grasses with higher potential biomass production in order to increase livestock production systems (Rao et al. 2015; Notenbaert et al. 2021). We use the term "improved grasses" to refer to grass genotypes that have been selected from wild relatives or have gone through a breeding and selection program to obtain desirable traits (Rao et al. 2015; Notenbaert et al. 2021). In Latin America and the Caribbean, and to a lesser extent in Africa, improved cultivars of *Urochloa* or *Megathyrsus* grasses are commonly sown due to their high productivity that can sustain higher livestock stocking rates (Notenbaert et al. 2021). Besides the exceptionally high aboveground biomass production, these cultivars are resistant to pests and provide an array of environmental benefits (Rao et al. 2015; Notenbaert et al. 2021). Several of the improved grasses are characterized by a dense and deep rooting system that contributes to the accumulation of SOM (Fisher et al. 1994; Trujillo et al. 2006) and soil structure build-up. This in turn is often reflected in a higher abundance of soil earthworms feeding on the SOM (Decaëns et al. 1994, 2004; Jiménez et al. 1998; Webster et al. 2019). In addition, the introduction of improved grasses is also an alternative to the common practice of burning pastures (to temporarily increase their fertility), which is also beneficial to earthworm communities because the negative effects of burning are avoided (Decaëns et al. 1994, 2004; Fragoso et al. 1999). However, the potential effects of improved grasses with different traits (such as contrasting above-belowground biomass allocation) on earthworm communities have not yet been evaluated, to our knowledge. On one hand, the denser rooting system of some improved grasses may enhance the earthworm abundance due to the higher root exudation (Decaëns et al. 1994), but, on the other hand, a very dense rooting system may also hamper the development of earthworm communities (Eisenhauer et al. 2009b). We suggest that the effect of the selected grass on the earthworm community should be evaluated and considered when designing the sustainable intensification strategy of a grassland.

3.2.2 Impact of Grassland Diversification

Earthworms benefit from a high plant biomass production (i.e., higher organic matter inputs) and from high-quality organic matter (i.e., a low C/N ratio); hence, the management practices leading to a higher biomass production and organic matter quality can positively affect the earthworm community (Lavelle et al. 2001; Curry 2004; Eisenhauer et al. 2009b; Hoeffner et al. 2024).

Grasslands with higher plant species diversity generally support a higher abundance of earthworms (Spehn et al. 2000; Milcu et al. 2008; Hoeffner et al. 2024), which is often explained by (1) a higher biomass production, (2) a more diverse offering of litter residues with different chemical qualities, and (3) variable timing in the organic matter supply to soil (Spehn et al. 2000). However, more recent studies have suggested that earthworms benefit more from the presence of specific plant functional groups, such as legumes, than strictly from high plant diversity per se (Eisenhauer et al. 2009b; Piotrowska et al. 2013; Singh et al. 2021). Hence, effects on the earthworm population assumed to be a result of higher plant diversity might actually be caused by the increasing likelihood of legumes being present in highly diverse grasslands (Eisenhauer et al. 2009b). This consideration is critical in a scenario of global loss of legumes and their N_2 fixation capacity due to anthropogenic impacts (Tognetti et al. 2021; Vázquez et al. 2022) and may, therefore, also indirectly affect earthworm communities.

Legumes play a key role in grassland ecosystems by increasing plant biodiversity, providing floral support to pollinators, and fixing atmospheric N via symbiotic N_2 fixation (Lamarque et al. 2011; Lüscher et al. 2014). Fixed N is not only used for growth by legumes but also contributes to the nutrition of other grasses and forbs in the sward, which increases the overall biomass productivity and the N content of plant biomass (Herridge et al. 2008). Therefore, legumes are promoted in managed grasslands aiming to boost their N_2 fixation capacity and reduce the use of synthetic fertilizers (Lüscher et al. 2014; Rao et al. 2015). Because earthworms are benefited by organic matter inputs rich in N, the promotion of legumes in grasslands can have a positive effect on earthworm abundance, an observation that has been largely presented in the literature (Milcu et al. 2008; Eisenhauer et al. 2009b; Velásquez et al. 2012; Piotrowska et al. 2013; Vázquez et al. 2020; Hoeffner et al. 2024). In particular, anecic species benefit more from a high legume abundance for several reasons, their proximity to the high-quality residues entering the soil, the abundance of N-rich seeds, and legumes have a less dense root system compared with grasses (Eisenhauer et al. 2009b; Hoeffner et al. 2024). Similarly, the introduction of forage legume grasslands into crop rotations increased the earthworm abundance more than the introduction of grasses into Argentinian pampas as a consequence of the lower C/N ratio of legume residues (Rodríguez et al. 2020). Therefore, a positive effect on earthworm communities can be considered another benefit of legume promotion in grasslands.

A particular case of grassland diversification is the establishment of silvopastoral systems, which consists of the introduction/maintenance of woody perennials in a pastoral system. The *dehesa* (or *montado*) ecosystem covers 3.1 million ha in the Iberian Peninsula (Moreno and Pulido 2009) and is the most emblematic example of a managed silvopastoral system. Dehesa is a silvopastoral system based on livestock rearing and oak exploitation after the partial clearing of oak woodlands (Moreno and Pulido 2009). Dehesa and other silvopastoral systems are characterized by high biodiversity, including earthworms, as a result of the existence of many different microhabitats (Moreno and Pulido 2009; Moreno et al. 2016; Marsden et al. 2020). Similar positive effects on earthworm communities have also been observed in the tropics (Fragoso et al. 1999; Barros et al. 2003; Lavelle et al. 2016; Vázquez et al. 2020; Rodríguez et al. 2021a), where the greatest benefits can be expected in cases where legume woody perennials provide high-quality litter (Murgueitio et al. 2011; Webster et al. 2019).

Altogether, earthworm communities benefit from highly productive grasslands characterized by a high plant diversity including legumes and in the case of silvopastoral systems from high spatial heterogeneity. Thus, grassland management should be directed toward supporting the highest biodiversity and legume abundance, without penalizing biomass production.

3.2.3 Grassland Fertilization

Fertilized grasslands have higher plant biomass production and, therefore, by providing more food supply, can generally sustain a higher biomass of earthworms (Curry 1976; Curry et al. 2008; van Eekeren et al. 2009; Murchie et al. 2015; Schon et al. 2017; Hoeffner et al. 2021a). The positive impact of N fertilization on earthworm abundance is particularly strong when N fertilization is combined with irrigation, which also increases plant biomass growth (Schon et al. 2017). The addition of organic fertilizers can be even more beneficial than synthesized N fertilizers due to the simultaneous supply of organic matter (Birkhofer et al. 2008; van Eekeren et al. 2009; Murchie et al. 2015; Deru et al. 2023). However, in other cases, low or no effect of fertilization on earthworm abundance has been detected due to the already high soil organic content of many grasslands (Edwards and Lofty 1982; Timmerman et al. 2006). Besides the effects on earthworm abundance, fertilization can also alter the earthworm community composition (Edwards and Lofty 1982; Murchie et al. 2015). For example, epigeic earthworms generally benefit more from manure or cattle slurry addition because they feed directly upon surface organic matter (Edwards and Lofty 1982; Murchie et al. 2015; Deru et al. 2023).

However, the positive effects on earthworm abundance through increased plant biomass production can be hindered by changes in soil properties, especially in the case of continuous additions of synthesized N fertilizers, which can strongly reduce soil pH (Ma et al. 1990; van Eekeren et al. 2009; Schon et al. 2017). Similarly, the addition of high doses of manure slurry has been found to be detrimental to earthworm populations due to the high presence of heavy metals or other toxic substances in earthworms (Curry 1976; Edwards and Lofty 1982; Murchie et al. 2015; Segat et al. 2020). Grassland N fertilization can also affect earthworms indirectly by changing plant community composition: grasses and non-N-fixing forbs frequently displace legumes due to their lower competitiveness under high N availability (Tognetti et al. 2021; Vázquez et al. 2022). Therefore, the effect of fertilization depends on the balance between the positive effects of higher biomass production and SOM and the detrimental effects of soil acidification, reduced legume abundance, and potential toxic effects.

3.2.4 Increasing Livestock Stocking Rate and Mowing Frequency

Efforts to increase plant biomass production are almost exclusively directed to higher animal production, e.g., to the increasing stocking rates in grazed pastures or mowing frequency in meadows. Higher stocking rates can negatively affect earthworm communities by increasing the risk of soil compaction and poaching caused by excessive animal trampling (Cluzeau et al. 1992; Drewry 2006; Curry et al. 2008; Schon et al. 2017; Vázquez et al. 2020; Hoeffner et al. 2021b, 2024). In particular, earthworm species living near the soil surface are more affected by the negative effects of excessive trampling (Piearce 1984; Cluzeau et al. 1992). Both direct mortality due to crushing and poor conditions of compacted soils can contribute to earthworm decline and downward shifts in vertical distribution (Piearce 1984; Cluzeau et al. 1992).

The detrimental impacts of trampling on soil properties and earthworm communities depend on the treading pressure; thus, more negative impacts can be observed in grasslands grazed by cattle than by sheep (Schon et al. 2017). It can also be localized to specific areas of the grassland (i.e., under the trees or close to the water sources) due to preferential animal behavior (Vázquez et al. 2020). As earthworms often play a key role in reducing soil compaction, the disappearance of earthworms further stimulates soil physical degradation in a negative feedback loop (Piearce 1984; Herrick and Lal 1995; Drewry 2006).

Nevertheless, it should also be noted that increasing stocking rates can, in some cases, stimulate earthworms by increasing the dung deposition and availability of fresh organic matter rich in nutrients and microorganisms (Decaëns et al. 1994, 2004; Curry et al. 2008; Bacher et al. 2018; Singh et al. 2021; Teutscherová et al. 2021b). Therefore, the impact of a higher stocking rate will depend on the balance between the negative effect of higher trampling and the positive effect of increased dung deposition and likely plant biomass production (Curry et al. 2008; Schon et al. 2017; Teutscherová et al. 2021b; Hoeffner et al. 2024). For example, Curry et al. (2008) described a higher earthworm abundance with an increasing stocking rate and N fertilization as a consequence of higher plant biomass and dung deposition counterbalancing the negative effects of higher soil trampling. In this sense, a correct grazing management that ensures an adequate period of rest for the grassland by rotational grazing seems to be a promising strategy to avoid the negative impacts on earthworm communities from high stocking rates (Teutscherová et al. 2021b). Otherwise, unsustainable grazing management can lead to plant community degradation, an increase in the areas of bare soil prone to erosion, soil structure degradation, and, finally, a lower earthworm abundance (Teague et al. 2011; Teutscherová et al. 2021b).

Intensified meadows, which are not directly grazed, can be mowed more frequently in comparison to extensively managed grasslands. A recent study showed a negative impact of mowing on earthworm abundance compared with no-mowing (Hyvönen et al. 2021) due to the forage biomass removal. In contrast, Hoeffner et al. (2024) found an increase in earthworm abundance and diversity in mowed compared with abandoned grasslands. The impact of mowing on earthworm communities is a priori lower than the impact of grazing due to the absence of physical disturbance by animal trampling (Schlaghamerský et al. 2007; Tälle et al. 2016). Yet, other studies have shown no differences between mowed and grazed grasslands, likely because less organic matter was incorporated into the soil (no dung deposition and forage removal from the plot) in the mowed than in the grazed system (Schon et al. 2010, 2017; Hoeffner et al. 2024). However, more frequent mowing may have negative impacts on soil earthworm communities by affecting the plant diversity or through soil compaction if the mowing is performed by machinery under suboptimal soil moisture conditions, although more studies should evaluate in detail the impact of mowing timing and frequency on soil earthworm communities.

3.2.5 Trends of Grassland Sustainable Intensification Strategies

Intensification of forage-based agriculture (in terms of increased plant biomass and animal productivity) can have detrimental effects on ecosystems unless appropriate measures to maintain or increase pasture (and soil) health are applied. The most commonly observed negative impacts include soil degradation, higher GHG emissions, plant community degradation (Dumont et al. 2018), and finally, a decrease in earthworm abundance and diversity (Birkhofer et al. 2008; Piotrowska et al. 2013; Manning et al. 2015; Siebert et al. 2019; Singh et al. 2021). It is, therefore, imperative to follow the agroecological framework adopting sustainable intensification practices to cover the increasing demand for livestock products while improving livelihoods and environmental co-benefits: land sparing; GHG mitigation; soil health and plant; and faunal biodiversity (Rao et al. 2015; zu Ermgassen et al. 2018; Dumont et al. 2018; Notenbaert et al. 2021). Only in that case, an abundant and diverse earthworm community that supports the sustainability of grasslands can be maintained (Decaëns et al. 1994; Birkhofer et al. 2008; Manning et al. 2015; Siebert et al. 2019; Vázquez et al. 2020; Singh et al. 2021; Teutscherová et al. 2021b).

In the tropical regions, a very common sustainable intensification strategy is the establishment of silvopastoral systems including improved grasses and legumes (both forages and shrubs/trees) combined with an intensive short-durational grazing period (Alfaro-Arguello et al. 2010; Rao et al. 2015; Lerner et al. 2017; zu Ermgassen et al. 2018; Notenbaert et al. 2021). These systems are characterized by a high plant biomass production, soil rich in N due to the presence of legumes, low or no input of synthesized fertilizers, high deposition of dung, and no soil disturbance in the form of tillage or periodical burning (Rao et al. 2015; Lerner et al. 2017; Notenbaert et al. 2021). The combination of these management practices can increase the stocking rates while reducing the negative environmental impacts of livestock production (Murgueitio et al. 2011; Ferguson et al. 2013; Lerner et al. 2017; Vázquez et al. 2020; de Freitas et al. 2020; Rodríguez et al. 2021a; Notenbaert et al. 2021). These diversified and well-managed systems enhance the earthworm abundance compared with grassland monocultures due to several reasons, including higher plant diversity and biomass production, higher spatial heterogeneity, the presence of legumes, higher dung deposition (as a consequence of the higher stocking rate), and the rotational management (Webster et al. 2019; Vázquez et al. 2020; Teutscherová et al. 2021b; Rodríguez et al. 2021a). This higher abundance of earthworms is linked to improved soil C storage, soil aggregation, and water infiltration, which confirms the sustainability of the systems and the important role of earthworms in soil health. However, the spatial heterogeneity of the paddock, as a result of tree presence, can also cause heterogeneity in the spatial distribution of earthworms. Vázquez et al. (2020) observed in a silvopastoral system that the continuous trampling of cattle under the rows of legume trees (better microclimatic conditions and more palatable food under the trees) leads to a decrease in earthworm abundance. This finding encourages a further evaluation of different silvopastoral arrangements with the aim of finding the most appropriate paddock design and management practices to optimize the sustainability of intensive short-durational grazing silvopastoral systems.

In the case of temperate regions, the sustainable intensification points toward the substitution of intensive meadows managed using high doses of fertilizers, high cutting frequency, and reduced plant diversity with extensively grazed grasslands with a high plant diversity (particularly legumes) and manure instead of synthesized fertilizers addition (Oberson et al. 2013; Manning et al. 2015; Dumont et al. 2018; Siebert et al. 2019). The adoption of those practices can enhance earthworm abundance due to the higher plant diversity and biomass production, the presence of legumes, the dung deposition, and the reduction or absence of synthesized fertilizers (Birkhofer et al. 2008; Singh et al. 2021). Similarly, the establishment or protection of silvopastoral systems, such as the Dehesa ecosystem, can enhance the abundance and diversity in earthworm communities (Moreno et al. 2016; Marsden et al. 2020).

Therefore, we consider that the sustainable intensification of grassland management could meet the increasing livestock production demands while enhancing earthworm communities compared with traditionally managed grasslands. Similarly, due to the sensitivity of earthworm communities to different management practices, the monitoring of earthworm communities may help to understand the sustainability of management practices, as we will discuss in the next section.

4 Earthworms as an Early Indicator of Grassland Management

The potential of earthworms to serve as bioindicators of the land use sustainability has been proposed by many researchers in the last decades (Paoletti et al. 1991; Muys and Granval 1997; Paoletti 1999; Tondoh et al. 2007; Pérès et al. 2011). In grasslands, multiple scientific studies have confirmed strong correlations between earthworm abundance and/or diversity and many important ecosystem services (see Sect. 2). Furthermore, there is strong evidence that earthworms are sensitive to different grassland management practices (see Sect. 3). This evidence, together with the low cost and relatively easy assessment, makes earthworms perfect candidates for being used as grassland health bioindicators. Some authors have already proposed earthworms to indicate the health status of pastures in Australia and New Zealand (King et al. 2007; Schon et al. 2022). Schon et al. (2022) proposed a specific assessment method and flowchart to provide a tool for farmers to assess the health status of their pastures based on the abundance and diversity of earthworms. This progressing trend of earthworm inclusion into ready-to-use methodology for farmers to assess the health status of their grasslands can be also observed in the visual soil evaluation methodologies (Ball et al. 2017) which are well studied in temperate grasslands. Recently, both visual assessment of soils and earthworm counting showed a great correlation also in the tropics (Colombian pastures), and in addition, both proved to be suitable for distinguishing among contrasting grazing management practices (Teutscherová et al. 2021a).

To be successfully used by farmers and agricultural services, the evaluation must be easily performed and include earthworm counting and only basic classification. In addition, flowcharts with different thresholds could help to assess the health status of grasslands. Furthermore, a recent database compiled hundreds of studies in earthworm communities from the last decades (Phillips et al. 2021), which could help to adapt this methodology to different climates, soils, or types of grasslands (pastures or meadows). In this sense, the development of a digital tool, such as an app for mobile phones, could boost the real application of earthworms as bioindicators of grassland health status. This app could help farmers assess the soil health status of their grasslands based on the observed abundance and type of earthworms in combination with edaphoclimatic and management parameters.

5 Outlook and Future Perspectives

With the increasing population and global demand for meat products, the importance of grasslands has become more apparent than ever. These grassland ecosystems are crucial for human livelihood because they (1) play a crucial role in livestock-based agriculture worldwide and (2) provide many ecosystem services related to soil, water, and air quality. The latter is largely facilitated by earthworms, which greatly affect grassland soil physical properties, nutrient availability, plant biomass production, and water and climate regulation. However, earthworm communities and their functionality are very sensitive to different grassland management practices as confirmed in many studies and summarized in this chapter. It is precisely their importance and sensitivity that make earthworms suitable candidates to assess the health status of grasslands and help to understand the potential impacts of grassland management on soil functioning. We advise considering the impacts on earthworm communities in grassland establishment, management, and other potential land-use changes (e.g., grassland establishment after forest clearance) to better predict the long-lasting impacts of such activities.

We suggest that future research should comprise both mechanistic studies in experimental plots and mesocosms and on-farm observations to increase our understanding of different management interactions, as the simultaneous application of techniques can have individually contrasting effects on earthworms. However, we recognize that the comparison of real farms (as opposed to strictly monitored and controlled experimental grasslands) brings some challenges in data quality and interpretation due to potential baseline confounding bias. In general, the evaluation of real farms is based on the comparison of adjacent farms with contrasting managements. These across-the-fence comparisons make it difficult to distinguish between the effects caused by the current management, the legacy of the previous management, and/or other potential micro-edaphoclimatic differences or confounding factors. This problem could be solved by sampling both farms in a time series and then comparing the development of earthworm communities over time under different management strategies. Another problem arises with the lack of independent replications because it is not realistic to find different farms that are replicating the exact same practices under the same conditions. Farmers generally adapt management practices to the local edaphoclimatic conditions and resource possibilities. Then with time series data, comparisons can be made between farms following management practices with the same inspiration, even though the management is not the same (i.e., rotational management practices vs continuous grazing, organic vs conventional, or silvopastures vs no-tree pastures). Despite these limitations, we consider that more real farm studies can help to better understand earthworm communities and their functionality in grasslands in a scenario of continuous changes in grassland management practices.

Finally, we encourage the development of accessible and easy methods to assess the earthworm community health status in grasslands similar to what the visual assessment has done for soil health (Ball et al. 2017). Such methods could be a tool for farmers and agricultural services to assess the impact of their management on the earthworm community and help them adjust their practices. These earthworm assessment methods, adapted to different regions and grasslands, can be developed based on the work performed in the last decades by thousands of scientists, farmers, and agronomists who have evaluated and studied earthworms in grasslands worldwide. Thus, it is time to further develop the potential of earthworms for healthier and more sustainable grasslands.

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