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Importance of earthworm–seed interactions for the composition and structure of plant communities: A review

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ABSTRACT

Soil seed bank composition and dynamics are crucial elements for the understanding of plant population and community ecology. Earthworms are increasingly recognized as important dispersers and predators of seeds. Through direct and indirect effects they influence either positively or negatively the establishment and survival of seeds and seedlings.

Seedling establishment is affected by a variety of earthworm-mediated mechanisms, such as selective seed ingestion and digestion, acceleration or deceleration of germination, and seed transport. Earthworm casts deposited on the soil surface and the entrance of earthworm burrows often contain viable seeds and constitute important regeneration niches for plant seedlings and therefore likely favour specific seed traits. However, the role of earthworms as seed dispersers, mediators of seed bank dynamics and seed predators has not been considered in concert. The overall effect of earthworms on plant communities remains little understood. Most knowledge is based on laboratory studies on temperate species and future work has to explore the biological significance of earthworm–seed interactions under more natural conditions.

In this review we summarize the current knowledge on earthworm–seed interactions and discuss factors determining these interactions. We highlight that this interaction may be an underappreciated, yet major driving force for the dynamics of soil seed banks and plant communities which most likely have experienced co-evolutionary processes. Despite the experimental bias, we hypothesize that the knowledge gathered in the present review is of crucial relevance for restoration and conservation ecology. For instance, as earthworms emerge as successful and ubiquitous invaders in various ecosystems, the summarized information might serve as a basis for realistic estimations and modelling of consequences on native plant communities. We depict promising directions of future research and point to the need to consider above- and belowground interactions in order to mechanistically understand the driving forces of plant community assembly.

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1. Introduction

The processes that structure plant communities and maintain biodiversity have been a focus in community ecology (Connell, 1978; MacArthur and Wilson, 1967). Plant ecologists proposed three main processes or filters responsible for community assembly: (i) biogeographical constraints, e.g. due to limited dispersal, (ii) habitat

constraints and (iii) biotic interactions, such as facilitation, competition and predation (Belyea and Lancaster, 1999; Lortie et al., 2004). The balance between extinction/colonization events determines the regional species pool. At the local scale dispersal, habitat requirements and biotic interactions determine species diversity (Belyea and Lancaster, 1999), while at the patch scale biotic interactions at the neighbourhood level are most important (Lortie et al., 2004).

The composition and the dynamics of soil seed banks play a crucial role in the structure of plant populations and communities (Bekker et al., 1998). Seed banks are reserves of viable non-germinated seeds in the soil or at the soil surface (Thompson and Grime,

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1979). The capability of plant species to produce seeds remaining viable in the soil allows them to bridge temporally unsuitable habitat conditions for germination and establishment, spreading germination risk in time and conserving population genetic variation in the long term. At the community level, seed banks might co-determine the trajectory of secondary successions after large or small-scale disturbances (Pakeman and Small, 2005) or determine community composition and structure in open and highly disturbed habitats (Thompson et al., 1997). The soil seed bank also facilitates habitat restoration and conservation (Bakker et al., 1996; Van der Valk and Pederson, 1989). Thus, seed bank dynamics and its driving factors need to be considered for understanding vegetation dynamics and coexistence of plant species.

Animal activity is considered as one of the main agents burying seeds as well as bringing seeds back to the soil surface and affecting the contribution of the seed bank to plant recruitment (Willems and Huijsmans, 1994). In particular, mixing of soil layers (bioturbation) by soil macro-invertebrates such as earthworms significantly impacts seed bank dynamics (Eisenhauer et al., 2009b). Earthworms are considered to function as ecosystem engineers (Jones et al., 1994), as major driving forces for belowground processes, and thus are essential components of terrestrial ecosystems (Edwards and Bohlen, 1996; Lavelle et al., 2006). In non-acidic soils, earthworms often dominate the biomass of soil invertebrates. Due to their large body size, high consumption rates and burrowing activity, they are key ecosystem engineers forming the habitat of and resource availability for other soil biota (Anderson, 1988; Bal, 1982; Eisenhauer et al., 2009a; Lavelle et al., 1997; Lee, 1983). Earthworms interact with plants in both direct and indirect ways (Brown et al., 1999; Scheu, 2003). Indirect effects include changes in soil structure, aggregate stability, infiltration of water, aeration of deeper soil layers, nutrient mineralization, litter decomposition, and microbial and soil invertebrate biomass and community structure (Edwards and Bohlen, 1996; Eisenhauer et al., 2007; Lavelle et al., 2006; Lavelle and Spain, 2001). These changes have important consequences for plant communities (Scheu, 2003). Further, earthworms also modify plant growth *via* hormone-like effects, and *via* dispersion of plant growth stimulating microorganisms and of microorganisms antagonistic to root pathogens (reviewed in Brown, 1995; Scheu, 2003). Direct effects of earthworms on plants are root feeding and transport of plant seeds (Scheu, 2003). However, direct effects have received comparably little attention so far.

Effects of earthworms on seeds are likely to vary between earthworm species and functional groups, i.e. among epigeic, endogeic and anecic species (Bouché, 1977; Edwards and Bohlen, 1996). Epigeic species reside mainly in the upper organic soil layers, and cause limited mixing of mineral and organic layers. Endogeic species live in the upper mineral soil layers primarily consuming humified organic matter and forming horizontal non-permanent burrows. Anecic species typically are large earthworms

living in deep permanent vertical burrows up to 2 m deep, but predominantly feed on litter on the soil surface. Litter materials are translocated into deeper soil layers, but anecic species also transport mineral soil from deeper soil layers to the soil surface by casting (Bouché, 1977; Sims and Gerard, 1999). Recent studies indicate that earthworms from all ecological groups might significantly interact with seeds and thus are likely to impact plant community assembly (Asshoff et al., 2010; Eisenhauer et al., 2009a). However, most studies on earthworm–seed interactions have only considered anecic earthworm species of temperate regions.

While indirect effects of earthworms on plant growth have been extensively studied (Brown et al., 2004; Scheu, 2003) and their direct effects on seeds have been acknowledged for many years (McRill and Sagar, 1973; Pearce et al., 1994), detailed research on the consequences of earthworm–seed interactions is scarce and has received more attention only recently. However, there is increasing evidence that earthworm–seed interactions are likely to essentially impact on plant community composition. Therefore, in this review, we focus on the role of direct and indirect interactions between earthworms and seeds, and on the consequences of these interactions for the composition, structure and temporal dynamics of plant communities. By compiling the scattered literature on earthworm–seed interactions we aim to make plant ecologists aware of the underappreciated role of earthworms in shaping plant community structure. Moreover, we point to the urgent need for further studies under more natural conditions. Four major topics are presented: (i) the effect of earthworms on seeds (ii), the role of seeds for earthworm nutrition, (iii) the consequences of earthworm–seed interactions for plant community assembly, and (iv) identifying promising future research directions.

2. Impacts of earthworms on seeds

There is a multitude of mechanisms through which earthworms affect the fate of seeds. Earthworms affect four out of seven plant life stages directly (Fig. 1; Eisenhauer and Scheu, 2008): seed survival on the soil surface (Grant, 1983; Thompson et al., 1994), seed survival in the soil (Thompson et al., 1994), germination (Ayanlaja et al., 2001) and seedling establishment (Eisenhauer and Scheu, 2008; Eisenhauer et al., 2008b; Lee, 1985; Milcu et al., 2006). These effects impact in both positive and negative ways the distribution, survival, establishment, growth and production of seeds (Eisenhauer et al., 2008a, 2009a; Laossi et al., 2010). In this section, we discuss the different mechanisms through which earthworms influence seeds: seed translocation and burial, seed selection and ingestion, seed digestion, mucus secretion and maternal effects.

2.1. Seed translocation and burial

Translocation of seeds into deeper soil layers by earthworms is recognized to play an important role in vertical seed movement

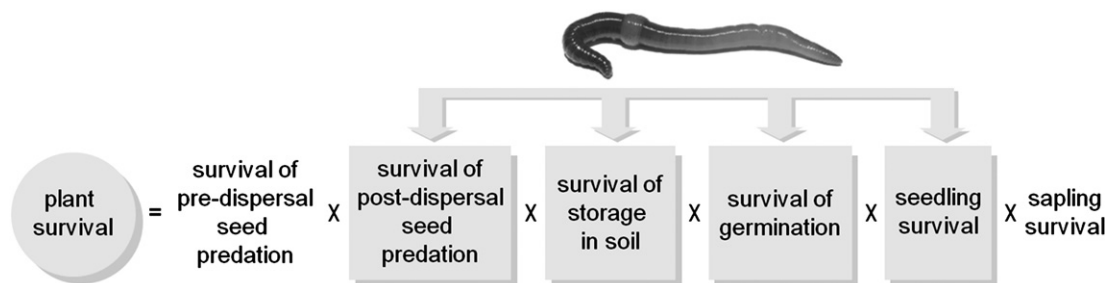


Fig. 1. Plant survival as a function of the survival of different early plant life stages (modified after Moles and Westoby, 2006). Life stages directly influenced by earthworms are highlighted with grey boxes (see text for more details). Modified after Eisenhauer and Scheu (2008).

(Decaëns et al., 2003; Eisenhauer et al., 2008a; Grant, 1983; Laossi et al., 2010; Milcu et al., 2006; Regnier et al., 2008; Willems and Huijsmans, 1994). Compared to seeds in the soil seed bank, those on the soil surface are more easily detected by surface foraging organisms, and thus are more vulnerable to predation by seed predators, such as birds, rodents and insects (Azcarate and Peco, 2003; Heithaus, 1981). In general, large seeds (>2 mm) are more at risk of being consumed by seed predators than small seeds (Brown and Heske, 1990), partly due to the greater difficulty of becoming buried in the soil. On the other hand, large seeds improve seedling nutrition; seedlings germinating from large seeds therefore better survive periods of resource shortage imposed by drought and shade (Westoby et al., 1996). In perennial communities, seed predation may destroy more than 95% of the seeds produced (Thompson, 1992). Therefore, the soil seed bank is considered to function as a predator-free (or reduced) spatial niche.

Seed burial might also reduce exposure to harsh environmental conditions (Thompson et al., 1994; Van Der Reest and Rogaar, 1988; Willems and Huijsmans, 1994). The soil seed bank, therefore functions as a refuge for surviving unfavourable environmental conditions such as fire, drought and frost (Cohen, 1966) and prevents germination of seeds during these unfavourable periods. Seeds of many species survive better in the soil seed bank than on the soil surface and remain dormant for long periods. Seeds translocated into deep soil layers by earthworms (seeds ingested or pulled into the burrow and buried) therefore contribute to the formation of a persistent seed bank (Thompson et al., 1993). However, when buried below a critical depth, seeds may fail to emerge and this depth is generally related to the seed size (Thompson et al., 1994; Traba et al., 2004). Precisely, large seeds, often characterized by few requirements for germination, may germinate in the soil and fail to emerge at the soil surface. Conversely, small seeds, needing light or large temperature fluctuations for germination, will simply fail to germinate (Milberg et al., 2000). Regnier et al. (2008) found, in a field experiment conducted to determine how *Lumbricus terrestris* affected *Ambrosia trifida* seed burial and seedling recruitment, that *L. terrestris* collected and buried over 90% of *A. trifida* seeds placed on the soil surface. Interestingly, *A. trifida* seeds were highly variable in size, ranging from 3 to 14 mm in length but the authors did not detect any earthworm-mediated differences in the speed of burial depending on seed size. However, small seeds were buried by *L. terrestris* deeper into the soil than large seeds and thereby germinated less. Thompson et al. (1994) showed that virtually all seeds found in earthworm casts weighed <0.3 mg, underlining the observations of McRill (1974) who found small seeds disproportionately more frequent in earthworm casts than in bulk soil. These results corroborate the decline in seed size with soil depth (Regnier et al., 2008) and suggest that this in part is due to the selective action of earthworms.

2.2. Seed selection and ingestion

Earthworms selectively feed on seeds with seed selection depending on seed size (Eisenhauer et al., 2009a; Shumway and Koide, 1994), shape (Eisenhauer et al., 2009a; McRill and Sagar, 1973) and surface structure (Shumway and Koide, 1994). Seed size is certainly the most important seed trait that influences their fate in response to earthworm ingestion. It influences both ingestion and digestion of plant seeds by anecic and endogeic earthworm species (Eisenhauer et al., 2009a). Most studies have used seed length as an indicator of seed size but other characteristics, such as seed surface and seed volume, might have a higher explanatory power than seed length (Eisenhauer et al., 2009a). Small seeds (<2 mm length) are more likely to be ingested by *L. terrestris* than larger seeds (Eisenhauer et al., 2009a;

Grant, 1983; Shumway and Koide, 1994). Indeed, seeds >3 mm are too big to be swallowed by most earthworm species of temperate regions (Shumway and Koide, 1994; Zaller and Saxler, 2007). Size selection depends on earthworm species (Eisenhauer et al., 2009a) since these animals vary significantly in body size from a few centimetres in epigeic species to 30 cm in anecic species such as *L. terrestris*. Surprisingly, however, little is known on species-specific effects of earthworms on seeds. Recently, Eisenhauer et al. (2009a) investigated the effect of four endogeic earthworms on seed ingestion. They found that small endogeic earthworms (*Aporrectodea rosea* and *Allolobophora chlorotica*) ingested small seeds (<1.4 mm width) in low numbers, whereas large endogeic species (*Octolasion tyrtaeum* and *Aporrectodea caliginosa*) ingested seeds of all six investigated grassland plant species. However, although in this experiment the body size of *O. tyrtaeum* exceeded that of *A. caliginosa*, seed ingestion was considerably higher in *A. caliginosa*, suggesting that seed ingestion not only depends on earthworm body size but also on earthworm species-specific feeding habits.

Although seed size is one of the main seed traits influencing their fate, other traits such as seed shape, texture and taste/smell might also be essential in determining seed selection by earthworms. Indeed, Willems and Huijsmans (1994) demonstrated that the selection of seeds by *L. terrestris* is linked to the taste or smell of the seeds; among the ten species studied seeds of aromatic species (*Origanum vulgare*, *Carex flacca* and *Daucus carota*) were most preferred. The results suggest that earthworms use chemical cues to select more palatable seeds (Grant, 1983; Willems and Huijsmans, 1994). Zaller and Saxler (2007) offered seeds from ten grassland species (three grasses, four non-leguminous forbs and three leguminous forbs) to *L. terrestris*. They found that *L. terrestris* generally preferred seeds of non-leguminous (*Taraxacum officinale*, *Sanguisorba officinalis*) and leguminous forbs (*Trifolium repens*) over seeds of grasses (see also Eisenhauer et al., 2010). Thus, other seed traits, such as nutritional value, coat thickness, shape, texture and taste, should be explored in future studies in order to gain a better understanding of factors determining seed selection by earthworms. Laboratory choice experiments might therefore represent a helpful tool in order to extract the most relevant seed traits.

2.3. Seed digestion

In the majority of documented cases, passage through the earthworm gut decreased the percentage of seed germination (Decaëns et al., 2003; Grant, 1983; McRill and Sagar, 1973). Seeds may suffer physical damage, due to earthworm gizzard contraction and chemical damage by enzymes produced by earthworms and gut-associated microorganisms (Lattaud et al., 1998; Urbasek, 1990). Decaëns et al. (2003) showed that seeds deposited in casts of *Martiodrilus* sp. lost between 70 and 97% of their germinability.

The passage through the earthworm gut especially reduces the germination rate of small seeds (Aira and Pearce, 2009; Laossi et al., 2009; Milcu et al., 2006), likely resulting in decreased germination rates. Eisenhauer et al. (2010) also reported seed digestion by *L. terrestris* to be negatively correlated with seed size. Grant (1983) suggested that most of the “lost” seeds during the gut passage, had been destroyed by earthworm gizzard contraction and enzyme activity, and this would be more likely in small than in large seeds. This more pronounced decrease in germination rate in small seeds could also be due to a lower resistance of small seeds against physical and chemical forces acting in earthworm guts, linked to seed coat characteristics. These assumptions should be tested and validated. Lastly, digestion of seeds by endogeic earthworm species has been found to be independent of seed size (Eisenhauer et al., 2009a). Contrary to seed ingestion, seed

digestion did not depend on earthworm body size (Eisenhauer et al., 2010; Eisenhauer et al., 2009a).

2.4. Secretion of mucus

The effects of mucus secretion by earthworms on the germination of seeds have only recently been investigated. Eisenhauer et al. (2009a) showed that the germination of *Medicago varia* seeds was increased by 12% in presence of *L. terrestris* mucus. However, they found that plant seed germination was primarily decreased by earthworm mucus, the germination of seeds of *Phleum pratense* being reduced by the mucus of *A. caliginosa* and *L. terrestris* by 9% and 8%, respectively, and that of *Plantago lanceolata* by the mucus of *A. caliginosa* by 15%. The positive effect of earthworm mucus could be ascribed to rhizogenic substances, indol-derived substances, measured on cutaneous excretions (El Harti et al., 2001). The predominating negative effect might however be due to high concentrations of ammonium in earthworm mucus that might induce seed dormancy and/or delay germination (Satchell, 1967). In fact, the contrasted effect of mucus on seed germination might depend on seed coat characteristics. Indeed, *M. varia* has hard-coated seeds but the other two species do not. Thus, earthworm mucus might reduce germination of seeds with low protection (thin seed coat), but facilitate germination of seeds with a thick coat. Future studies should elucidate the mechanisms underlying the effect of earthworm mucus on germination by considering morphological seed characteristics.

2.5. Earthworm casts and burrows

Biostructures formed by earthworms impact seedling establishment via a number of mechanisms (Eisenhauer et al., 2008b; Shumway and Koide, 1994; Thompson et al., 1994). First, the region of burrow entrance is deprived of plants which facilitates seed germination (Fig. 2a) and seedling growth (Fig. 2b). These gaps with no or reduced competition with other plant are particularly important in dense herbaceous plant communities. Second, earthworm casts likely represent nutrient-rich (e.g. nitrogen-rich) regeneration niches for seeds (Eisenhauer and Scheu, 2008; Milcu et al., 2006) and might improve seed germination and seedling growth. Although earthworm burrows and casts are regarded as microsites of elevated nutrient availability and microbial activity (Eisenhauer et al., 2007; Maraun et al., 1999), evidence is inconsistent (Eisenhauer et al., 2009b; Straube et al., 2009). Third, casts comprise stable aggregates, rich in ammonium and resistant to gas and water infiltration (Blanchart et al., 2004; Decaëns, 2000), conditions known to maintain seed dormancy or delay germination (Grant, 1983). However, it has also been demonstrated that earthworm casts may accelerate seed germination by increasing water permeability of the seed surface (Tomati et al., 1988) and by breaking seed dormancy (Ayanlaja et al., 2001). Decaëns et al. (2003) estimated that about 40% of viable seeds emerge out of intact casts whereas the remaining 60% require further cast fragmentation to emerge, due to the high physical stability of casts. Smith et al. (2005) explored the distribution of seeds of weeds of annual crops and reported distinct differences between earthworm casts and the soil seed bank of the upper 5 cm, suggesting that earthworms contribute to the redistribution of weed seeds in arable and other systems, thereby affecting plant species assembly and community dynamics (Eisenhauer et al., 2008b; Milcu et al., 2006; Regnier et al., 2008).

2.6. Maternal effects

The phenotype of plant individuals is determined not only by their genotype and environment but also by maternal effects, i.e.

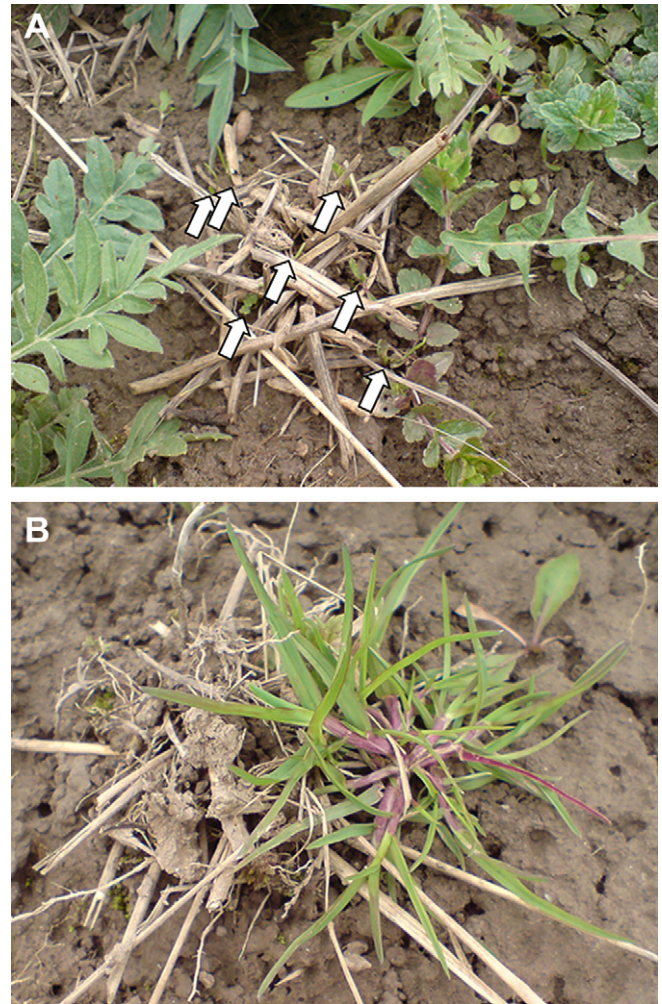


Fig. 2. Photographs of exemplary *Lumbricus terrestris* middens with several plant seedlings (indicated by arrows) on the field site of the Jena Experiment. Photo by N. Eisenhauer. Modified after Eisenhauer et al. (2008b).

the direct contribution of the maternal phenotype to the phenotype of its offspring. Indeed, the tissues immediately surrounding the developing embryo and the endosperm are all maternal. These tissues, the integuments of the ovule and the wall of the ovary, eventually form the seed coat and the fruit, and accessory seed structures, such as hairs, awns and barbs, are important determinants of seed dormancy, dispersal and germination traits (Roach and Wulff, 1987), thereby affecting later stages of plant life.

Since earthworms influence plant growth (Brown et al., 2004; Scheu, 2003), they generally increase their productivity and improve their mineral nutrition; thus, earthworms are likely to modify seed properties and subsequently trigger maternal effects. For example, earthworms have been shown to modify seed nutrient concentration (Baskin and Baskin, 2001; Noguera et al., 2010) and seed size (Poveda et al., 2005b). Such traits are known to influence seed germination and seedling growth (Baskin and Baskin, 2001). Recently, Laossi et al. (2010) investigated, in a greenhouse experiment, maternal effects on seed germination and seedling growth of three grassland plant species (*Veronica persica*, *Poa annua* and *Cerastium glomeratum*) induced by *A. caliginosa* and *L. terrestris*. Through maternal effects *A. caliginosa* enhanced seed germination (+74% for *V. persica* and +32% for *P. annua*) and seedling growth (+23% for *C. glomeratum* and +27% for *P. annua*) while *L. terrestris* reduced seed germination in *V. persica* (–17%). In some cases, the

increase in the germination rate of seeds produced in the presence of earthworms could be explained by a significant reduction in seed nitrogen concentration. These results suggest that the strength and direction of earthworm-induced maternal effects strongly vary with plant and earthworm species.

A number of issues still need to be investigated in this context: Do earthworm-mediated maternal effects persist after the seedling stage (Miao and Bazzaz, 1990)? Does interspecific competition between seedlings modulate such maternal effects? Do these maternal effects persist in the third generation (Alexander and Wulff, 1985; Miao et al., 1991)? Are earthworm-induced maternal effects adaptive and allow young plants to be better adapted to earthworm-mediated changes in soil properties? Thus, earthworm-induced maternal effects are little explored and offer a novel and promising field for future studies.

3. The role of plant seeds in earthworm nutrition

Beginning with Darwin (1881), earthworms have repeatedly been shown to accelerate the downward movement of seeds into the soil profile (Eisenhauer et al., 2008b; Grant, 1983; Milcu et al., 2006; Regnier et al., 2008) as well as the upward movement of buried seeds to the soil surface (Decaëns et al., 2003; Willems and Huijsmans, 1994). Selectivity in seed displacement and ingestion by earthworms prompted McRill (1974) to propose earthworm–seed interactions to generate selective pressures on both organisms. Considering the pronounced interactions between earthworms (as highlighted below), particularly anecic species and seeds, the question arises if and how earthworms benefit from ingesting seeds (Eisenhauer and Scheu, 2008). One possible explanation is that seeds and seedlings may contribute to earthworm nutrition (Eisenhauer et al., 2010; Eisenhauer and Scheu, 2008; Shumway and Koide, 1994).

Generally, the diet of earthworms primarily consists of dead organic materials in various stages of decay (Edwards and Bohlen, 1996; Lee, 1985). Thus, earthworms are supposed to consume poor-quality food material and compensate low assimilation by high consumption rates (Curry and Schmidt, 2007). This view is supported by studies using novel techniques such as stable isotope analysis (Briones et al., 2001, 1999; Hendrix et al., 1999; Schmidt et al., 1997; Uchida et al., 2004). Moreover, earthworms benefit from ingested soil microorganisms and gut microflora, on the one hand by the enzymes produced by these microorganisms, e.g. cellulases (Lattaud et al., 1998), and on the other by microorganisms themselves serving as a food source as suggested by fatty acid analysis (Sampedro et al., 2006). Seeds and seedlings may however represent a high-quality food source for earthworms (Eisenhauer et al., 2010).

3.1. Feeding on seeds and seedlings

Grant (1983) reported seed losses of ~30% during earthworm gut passage. McRill and Sagar (1973) and Eisenhauer et al. (2009a) reported even higher rates of seed loss during *L. terrestris* gut passage i.e. 20–100% and 34–83%, respectively, depending on plant species identity. Seeds “lost” during earthworm gut passage may be destroyed by earthworm gizzard contraction and enzyme activity (Grant, 1983). Sand particles presumably grind of seeds in the earthworm gut, as has been shown for litter material (Marhan and Scheu, 2005; Schulmann and Tiunov, 1999). Moreover, the activity of enzymes, such as cellulases provided by the ingested microflora (Lattaud et al., 1998), likely contributes to seed digestion. Despite high seed digestion rates, only few studies have considered that seeds might contribute to earthworm nutrition.

Shumway and Koide (1994) observed earthworms grazing on seedlings in laboratory experiments and concluded that seeds transported readily beneath the soil surface in its burrows germinated and increased the availability of food resources for *L. terrestris*. The authors discussed two mechanisms by which earthworms might benefit from the germination of seeds. First, germination may render digestible seeds that were initially protected by resistant coats and passed undigested through the earthworm gut. Other studies supported this argument by showing that the passage of seeds of several plant species through the earthworm gut increased their germination percentage, probably by damaging the seed coat and thus breaking seed dormancy (Eisenhauer et al., 2010). Moreover, earthworms might benefit from biochemical changes during germination, such as vitamin synthesis, which potentially provide important nutrients for earthworms feeding on seedlings (Shumway and Koide, 1994). In laboratory microcosm experiments *Lumbricus terrestris* has been followed to pull down little seedlings germinating on the soil surface (N. Eisenhauer, personal observation). This topic deserves further attention.

3.2. Earthworm nutrition and resulting feedbacks

The suggestions of Shumway and Koide (1994) that seeds and germinating seeds significantly contribute to earthworm nutrition have been supported recently. Eisenhauer and Scheu (2008) added grass, legume and herb seeds to grassland plant communities varying in plant species composition. Earthworms lost weight when grass seeds were added to grass communities and legume seeds to legume communities; however, they gained weight when grass seeds were added to legume communities and legume seeds to grass communities. The authors suggested that germination and growth of plant species are inhibited by plants of the same plant functional group in close vicinity due to intra-functional group competition (Fargione and Tilman, 2005), i.e. grass seeds germinate better in legume communities and legume seeds germinate better in grass communities. Assuming that earthworms benefit from germinating seeds, *L. terrestris* possibly benefited from increased germination of seeds in plant communities of different functional group affiliation. However, this assumption could not be endorsed with data on plant germination rates and remained speculative.

More direct evidence for seedlings contributing to earthworm (*L. terrestris*) nutrition comes from three recent laboratory experiments (Eisenhauer et al., 2010). Earthworms were shown to selectively ingest seedlings rich in nitrogen (legumes) with the ingestion being lethal for each of the plant species investigated. Earthworms preferentially ingested seedlings rather than seeds, supporting the suggestion of Shumway and Koide (1994) that plant seedlings contribute to earthworm nutrition.

In addition to the quality (nitrogen concentration) of plant seeds and seedlings, collection of seeds by earthworms has been proposed to be driven by the relative growth rate of seedlings as if there was a size of seedlings beyond which earthworms are unable to swallow them (Eisenhauer et al., 2010). In fact, stable isotope analysis indicated increased resource acquisition from legume seedlings growing at a slower rate than grass seedlings. However, preferential feeding on legume seedlings may also be due to high nitrogen concentration; further experiments are needed to disentangle the relative role of nitrogen concentration vs. growth rate of seedlings in the food selection of earthworms. Resource capture from seeds and seedlings may explain why anecic earthworms such as *L. terrestris* vigorously collect virtually any debris in the vicinity of their burrows, mixing them with the mineral soil and feeding on the mixed materials (Butt et al., 2003). Nevertheless, it should be noted that current knowledge is based on few laboratory

experiments and the biological significance of seeds and seedlings for earthworm nutrition remains unclear.

4. Consequences for plant communities

As documented above, ingestion, transport, digestion and damage of seeds during passage through earthworm gut have the potential to affect seed bank composition and dynamics, plant recruitment, plant interactions and spatial-temporal plant distribution. Thus, earthworms are likely to contribute to the filtering of species at the community scale and to affect plant community structure, composition and dynamics.

4.1. Soil seed bank composition and spatial distribution

The amount of soil deposited to the soil surface by earthworm casts ranges from 2 to 250 t/ha per year (Edwards and Bohlen, 1996). In temperate regions the upper 15 cm of soil, containing most seeds of the seed bank, may be turned over completely every 10–20 years by earthworms (Edwards and Bohlen, 1996). Because seeds from different plant species vary in their susceptibility to the gut passage through earthworms, soil turnover by earthworms is likely to affect the composition of the soil seed bank and to modify seed bank attributes, such as seed persistence and survival, and seed bank dynamics. Indeed, Zaller and Saxler (2007) demonstrated that some plant species present in earthworm casts were not present in the standing vegetation, suggesting that earthworms transport seeds of past vegetation to the soil surface. A recent field study showed that both anecic and endogeic European earthworm species invading Canadian forest ecosystems affect the composition of the soil seed bank of native forests (Eisenhauer et al., 2009b). Earthworm effects depended on earthworm ecological group and plant functional group identity, suggesting unpredictable changes in soil seed bank and herbaceous plant community composition due to earthworm invasion. The underlying mechanisms of interactive effects of invasive earthworm species/ecological groups are poorly understood (Eisenhauer et al., 2009b) and deserve further attention.

Neither plants nor seeds are uniformly distributed in space (Thompson, 1986) and time. Generally, the seed bank is clumped at least at the horizontal scale of a few meters (Lortie et al., 2005; Rees et al., 1996). Heterogeneity of the soil seed bank may also result from the patchy distribution of earthworms (Milcu et al., 2006). Earthworms usually are spatially aggregated at a scale of a few meters (Margerie et al., 2001; Rossi et al., 1997), and casts are thus clumped at a spatial scale that correspond to the patterns observed for soil seed banks (Decaëns and Rossi, 2001; Rossi and Nuutinen, 2004).

4.2. Seed traits and plant strategies

Seed size is a key trait of plant species, determining both competitive and colonizing ability (Turnbull et al., 2004). Generally, seed mass of plant species is thought to result from a trade-off between producing few large seeds, each with low dispersal ability and high probability of successful establishment, versus producing many small seeds, with high dispersal ability and low probability of establishment (Moles and Westoby, 2006). This competition-colonization trade-off mediated by seed size is assumed to be an important driver of successional patterns in plant communities (but see Higgins and Cain, 2002; Pacala and Rees, 1998).

As a result, the selective ingestion and increased digestion of small seeds by earthworms presumably is of particular importance during early succession when annual species (generally with small seeds) predominate. Also, at least for annuals living in a matrix of

perennial plants, germination is crucial to the survival of all annuals (Rees and Long, 1992). Conversely to perennials, annual species cannot compensate the risk of seedling mortality by adult longevity (Dyer et al., 2000; Verdu and Traveset, 2005). Annual species are thus more likely to stay in the soil seed bank for a long period to delay germination and avoid unfavourable environmental conditions (Kluth and Bruelheide, 2005; Lortie et al., 2005), a strategy that might be facilitated by earthworm activity. Even if seed ingestion by earthworms damages a great number of seeds in their casts, a single facilitated seed (*via* breaking seed dormancy, stimulation of germination, reduced competition with other seeds, nutrient rich germination sites) might be enough to ensure the survival of this species in the community. Probably there is a trade-off between seed mortality in the earthworm gut and germination facilitation in earthworm casts. The net effect of these contrasting mechanisms is likely to depend on, for instance, earthworm digestive capability and seed traits. As indicated by two recent greenhouse experiments, the impacts of earthworms on seedling recruitment varies significantly with seed size, and this has important consequences for plant succession and assembly (Eisenhauer and Scheu, 2008; Milcu et al., 2006). Indeed, in the study by Milcu et al. (2006), they sowed small and large seeds of 6 species both in control (without *L. terrestris*) and in earthworms mesocosms. Earthworms reduced the number of plant individuals of small and large-seeded species, but this was less pronounced in large compared to small-seeded plants (Fig. 3). Therefore, within a plant community, large-seeded plants are less disadvantaged by earthworm activity than small-seeded plants. Probably, large-seeded plants experienced less predation by earthworms but were buried mostly in the upper 3–4 cm of the soil or benefited from higher nutrient supply in earthworm middens than in control soil.

A further important seed trait may be the growth rate of germinating seeds. As anecic earthworms may function as seed and seedling predators, seedlings could benefit from reaching a size refuge as fast as possible, i.e. being too large to get swallowed by earthworms (Eisenhauer et al., 2010). Particularly fast germination of grass seeds and seedlings with fast relative growth rates at least in part might have evolved to escape consumption by earthworms. However, this assumption needs to be investigated in more detail.

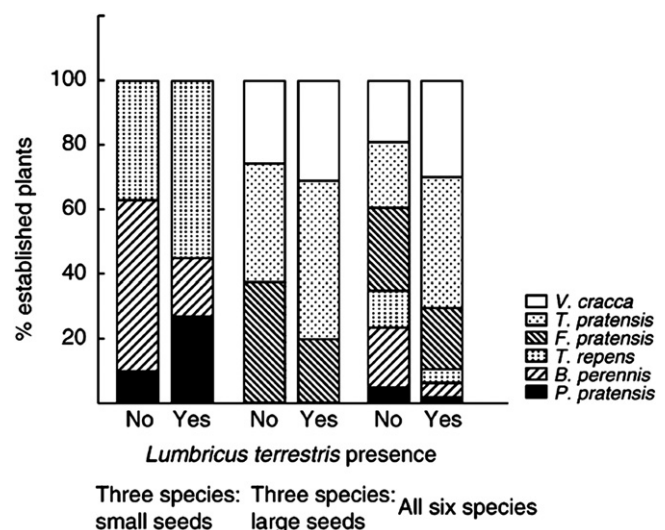


Fig. 3. Changes in plant species composition (percentage of established) as affected by presence of *Lumbricus terrestris* and seed size ($F = 9.00$, $P < 0.01$). *V. cracca* = *Vicia cracca*, *T. pratensis* = *Tragopogon pratensis*, *F. pratensis* = *Festuca pratensis*, *T. repens* = *Trifolium repens*, *B. perennis* = *Bellis perennis*, *P. pratensis* = *Poa pratensis*. Given in Milcu et al. (2006).

4.3. Earthworm effects on seed and seedlings interactions

Seed density and identity both positively and negatively affect germination and seedling emergence (Goldberg et al., 2001; Rebollo et al., 2001). At the microscale neighbouring seeds and seedlings affect survival of seedlings (Lortie and Turkington, 2002a,b; Turkington et al., 2005). Seedlings compete with each other for nutrients and space (Lortie and Turkington, 2002a) but seeds may also sense and influence other seeds (Murray, 1998) resulting in acceleration (Dyer et al., 2000) or reduction of seed emergence (Goldberg et al., 2001; Murray, 1998).

Earthworm activity is likely to change seed assemblages at the small scale, i.e. in casts deposited at the soil surface and in the surrounding of burrows (middens) where anecic species concentrate the debris they collect and mix it with mineral soil. Eisenhauer et al. (2008a) suggested that seedlings that emerge from *L. terrestris* middens benefit from lower intra- and interspecific root competition due to higher nutrient and water availability. It has been shown that a head start of as little as a few hours in seed germination may result in a “priority effect”, i.e. competitive dominance and increased growth and fecundity of the given plant (Fowler, 1984; Verdu and Traveset, 2005). Moreover, selective predation of seeds by earthworms is likely to change species composition and alter plant–plant interactions at the seedling stage. Disentangling the mechanisms involved is challenging since earthworms affect seedling survival and growth in numerous ways.

4.4. Disturbance and regeneration niches

Safe sites for seedling recruitment are rare in temperate semi-natural grasslands (Austrheim and Eriksson, 2003). Consequently, the creation of gaps and micro-disturbances are of key importance in enhancing plant establishment and community diversity by increasing niche dimensionality within local communities (Eisenhauer et al., 2008b; Harpole and Tilman, 2007). Such local heterogeneity affects the spread of species (Bergelson et al., 1993), influences seed and consequently plant density (Miller et al., 1994), the spatial distribution of plants (Houle, 1998) and competitive interactions (Stoll and Prati, 2001). In temperate grasslands, Grant (1983) found that 30% of seedlings germinated from earthworm casts. This indicates that earthworm casts and middens increase the spatial heterogeneity of grassland plant communities thereby forming an important regeneration niches *sensu* Grubb (1977). Indeed, earthworms enhance the sensitivity of plant communities to the establishment of weed species thereby also increasing the diversity of weeds (Eisenhauer et al., 2008b; Pearce et al., 1994).

The suitability of casts and middens as regeneration niches is likely to vary with cast characteristics (e.g., size, stability, age), earthworm species (Eisenhauer et al., 2008a) and plant community characteristics (Eisenhauer et al., 2008b). For example, Decaëns et al. (2003) found that in savannah grassland the numbers of seeds in casts deposited on the soil surface exceeded those deposited in the soil (but the number of viable seeds was about 3–40 times lower in casts than in soil). The number of viable seeds egested each year in surface casts was significantly higher at up to 10 million seeds $\text{ha}^{-1} \text{year}^{-1}$, compared to seed numbers reported by Willems and Huijsmans (1994) investigating *L. terrestris* in temperate pastures (890,000 seeds $\text{ha}^{-1} \text{year}^{-1}$). Smith et al. (2005) also found that cast production and seed density varied temporally and among crops. Both crop identity (corn, soybean and winter wheat) and management (monoculture or rotation of the three previous species) were investigated. For the whole experiment, weed seed densities were higher in earthworm casts than in samples collected from the soil surface and the seed bank. Earthworm cast production and germinable weed seed density were

higher in winter wheat (and mainly in monocultures) compared to corn or soybean crops. In addition, within winter wheat crops, differences in germinable weed seed densities in earthworm casts also differed in response to rotation.

5. Outlook

In this section, we highlight experimental biases of previous studies, discuss what we consider to be some of the most interesting topics for future research and, when possible, the promising experimental approaches.

5.1. Literature and experimental biases

Studies on interactions between earthworms and seeds and seedlings still are scarce. Reasons for this include (i) most studies investigate single crop/plant species, (ii) the difficulty of detecting and determining seed and seedling interactions, (iii) the lack of collaboration between plant ecologists and soil animal ecologists and (iv) the lack of knowledge on structure and fate of soil seed banks, the analogue of the hidden half of the plant soma, roots (Waisel et al., 2002).

Most previous studies on earthworm–seed interactions were published by soil ecologists in soil biology journals or general ecology journals and none in plant ecology journals (Fig. 4a). The

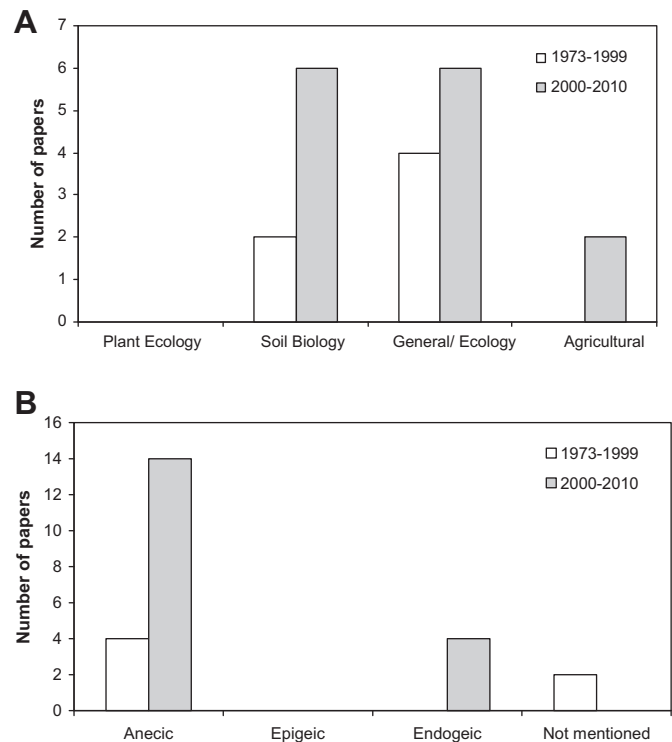


Fig. 4. Journals in which studies on effects of earthworms on seeds have been published (A), and earthworm groups used in these studies (B) in the periods 1973–1999 and 2000–2010. Soil biology journals include *Applied Soil Ecology*, *European Journal of Soil Biology*, *Pedobiologia*, *Soil Biology and Biochemistry*, and a book chapter; general/ (sinon Nature est un journal d'écologie...) ecology journals include *Acta Oecologica*, *Ecography*, *Ecosystems*, *Functional Ecology*, *Journal of Biological Education*, *Nature*, *Oikos*, *PLoS ONE*; Agricultural journals include *Agriculture*, *Ecosystems and Environment*. Authors and dates of publication of studies included in the survey are Aira and Pearce (2009), Asshoff et al. (2010), Decaëns et al. (2003), Eisenhauer et al. (2008a,b, 2010, 2009a,b), Eisenhauer and Scheu (2008), Grant (1983), Jimenez and Decaëns (2004), Laossi et al. (2009), McRill and Sagar (1973), Milcu et al. (2006), Pearce et al. (1994), Regnier et al. (2008), Shumway and Koide (1994), Smith et al. (2005), Thompson et al. (1994), Willems and Huijsmans (1994), Zaller and Saxler (2007).

majority of studies (i) investigated temperate grassland systems in Europe and America, and (ii) anecic earthworm species, mostly a single species, *L. terrestris* (Fig. 4b), (iii) have been performed under laboratory conditions. This suggests that we should study seed–earthworm interactions in many diverse situations, i.e. tropical systems and all ecological earthworm groups (including endogeic and epigeic). Additionally, laboratory experiments are short-term experiments usually focussing on the individual plant scale. However, to predict the effect of earthworm–seed interactions on plant communities, experiments should manipulate whole plant communities for several generations (Laossi et al., 2011). Finally, the effect of earthworms on seed fate should be compared to the influence of other factors affecting seeds in the field to assess their importance as drivers of seed and seedling performance (Brooker et al., 2005). It is likely that earthworms interact with other seed dispersers and predators in affecting plant community assembly.

5.2. Applying our understanding

By modifying the characteristics of plant communities, interactions between earthworms and seeds can also modify the stability of plant communities. Community stability can be described via a multitude of properties including resistance and resilience (Mitchell et al., 2000). Earthworms might affect the resistance of plant communities against invasions, i.e. colonisation of species not previously present in the community via effects on seeds (Eisenhauer et al., 2008b). As discussed above, the formation of regeneration niches and the increase of small-scale disturbances within plant assemblages are likely to increase invasibility and thus to alter the stability of ecosystems. The resilience of grassland communities might be increased by translocation of seeds from the seed bank to the soil surface. In a microcosm experiment *L. terrestris* significantly increased the number of weeds, suggesting that earthworms translocated seeds from deeper soil layers to the soil surface where they germinated (Milcu et al., 2006). *Seed banks might provide during decades a memory of the standing vegetation* (Baskin and Baskin, 2001). For example, seeds of *Malva pusilla* and two *Verbascum* species were still alive 120 years after burial (Telewski and Zeevaert, 2002). Thus, translocation of seeds to the soil surface might be of great interest to restore species when plants have disappeared from the soil surface. This indicates that the soil seed bank contributes to the resilience of grassland communities via seed translocation by earthworms. Moreover, seed burial by earthworms might contribute to increased community resilience by increasing seed persistence. Decaëns et al. (2003) also suggested that earthworm casts might enhance the recovery of savannahs after fire events. Earthworm casts may remain at the soil surface for more than one year thereby forming a pool of seeds ready to germinate after disturbances (Decaëns et al., 2003).

In face of the current rapid degradation of terrestrial ecosystems worldwide, there is an increasing need for the development of novel, low-cost and efficient restoration techniques for maintaining ecosystem functions and services (e.g. Hobbs et al., 2006; Ormerod et al., 2003). Earthworms may help to achieve these goals, e.g. in mitigating human impacts on plant diversity by activating the seed bank of former vegetation.

On the other hand, by altering seedbed conditions, exotic earthworms may act as threats for herbaceous plants in habitats previously devoid of earthworms (Hale et al., 2006; Holdsworth et al., 2007). A recent study indicated that exotic earthworms alter seedling emergence from forest seed banks in an earthworm species and plant functional group-specific way (Eisenhauer et al., 2009b). Although these findings suggest changes in the composition of herbaceous plant communities due to earthworm invasion,

the underlying mechanisms need further attention in order to predict the consequences for plant community structure.

5.3. Implications for plant evolution

Since earthworms influence the fate of seeds, they also influence the fitness of plant species and should thus exert selective pressures on plants. In habitats with high earthworm densities there might be a strong selective pressure on seeds of plants to survive the passage through the earthworm gut and to germinate shortly after voiding of casts (Decaëns et al., 2003; Eisenhauer et al., 2008b; Grant, 1983). The net impact of earthworms may significantly alter plant fitness as a result of a trade-off between seed destruction and facilitation of germination in casts. In particular in non-acidic soils where earthworm densities are high this may have shaped plant evolution. Presumably, certain plant species that produce small seeds resistant to digestion, depend on regeneration niches formed by earthworms (even if some seeds are too deeply buried to emerge), while others have developed the opposite strategy, e.g. the production of large seeds or seeds of bad taste, thereby avoiding consumption by earthworms. Thus, the exploration of potential co-evolutionary processes between earthworms and plants represents a novel and fascinating field in ecological research.

6. Conclusions

There is increasing evidence that interactions between earthworms and seeds are of primary importance for both earthworm performance and plant community structure. The present paper highlights the multitude of mechanisms through which earthworms and seeds interact and evaluates their consequences for plant community assembly. We conclude that earthworm–seed interactions are a major driving force for the dynamics of soil seed banks and plant communities which most likely have experienced co-evolutionary processes. Nevertheless, most knowledge is based on laboratory studies on temperate species and the biological significance of each mechanism discussed above needs to be explored. Although this topic certainly deserves further attention, we hypothesize that the knowledge gathered in the present review is of crucial relevance for restoration and conservation ecology. For instance, as earthworms emerge as successful and ubiquitous invaders in various ecosystems, the summarized information might serve as a basis for realistic estimations and modelling of consequences on native plant communities. We propose promising directions of future research and point to the need for more holistic studies considering above- and belowground multitrophic interactions in order to mechanistically understand the driving forces of plant community assembly.

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