

1 **Importance of earthworm – seed interactions for the structure**
2 **and composition of plant communities: a review**

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1 **Abstract**

2 Soil seed bank composition and dynamics are crucial elements for the understanding of plant
3 population and community ecology. Among animal species earthworms are increasingly
4 recognized as important dispersers and predators of seeds. Through direct and indirect effects,
5 they influence either positively or negatively establishment and survival of seeds and
6 seedlings.

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

17 In this review we summarize the current knowledge on earthworm – seed interactions and
18 discuss factors determining these interactions. We shed light on the consequences of
19 earthworm-mediated impacts on soil seed banks, plant community dynamics and evolution.
20 Special attention is paid to promising future research directions and consequences for
21 restoration and conservation ecology. We conclude that earthworm – seed interactions likely
22 represent a crucial multitrophic interaction shaping plant community composition.

23

24 **Key-words:** plant recruitment, seed translocation, seed predation, germination, regeneration
25 niche, soil fauna.

1 **1. Introduction**

2 The relative importance of processes that structure plant communities and maintain
3 biodiversity have been a focus in community ecology (Connell, 1978; MacArthur and Wilson,
4 1967). Plant ecologists have proposed three main processes or filters responsible for
5 community assembly: (i) biogeographical constraints, e.g. due to limited dispersal, (ii) habitat
6 constraints and (iii) biotic interactions, such as facilitation, competition and predation (Belyea
7 and Lancaster, 1999; Lortie et al., 2004). The balance between extinction/colonisation events
8 determines the regional species pool. At the local scale dispersal, habitat characteristics and
9 biotic interactions determine species diversity (Belyea and Lancaster, 1999), while at the
10 patch scale biotic interactions at the neighbourhood level are most important (Lortie et al.,
11 2004).

12 The composition and dynamics of soil seed banks play a crucial role in the structuring of
13 plant populations and communities (Bekker et al., 1998). Seed banks are reserves of viable
14 non-germinated seeds in the soil or at the soil surface (Thompson and Grime, 1979). The
15 capability of plant species to produce seeds remaining viable in the soil allows them to bridge
16 temporally unsuitable habitat conditions for germination and establishment, spreading
17 germination risk in time and conserving population genetic variation in the long term. At the
18 community level, seed banks might co-determine the trajectory of secondary succession after
19 large or small-scale disturbances (Pakeman and Small, 2005) or determine community
20 composition and structure in open and highly disturbed habitats (Thompson et al., 1997). The
21 soil seed bank also facilitates habitat restoration and conservations (Bakker et al., 1996; van
22 der Valk and Pederson, 1989). Thus, seed bank dynamics and its driving factors need to be
23 considered for understanding vegetation dynamics and coexistence of plant species.

24 Animal activity is considered as one of the main agents burying seeds as well as bringing
25 seeds back to the soil surface and affecting the contribution of the seed bank to plant

1 recruitment (Willems and Huijsmans, 1994). In particular,, mixing of soil layers (bioturbation)
2 by large soil macro-invertebrates such as earthworms significantly impacts seed bank
3 dynamics (Eisenhauer et al., 2009b). In non-acidic soils, they constitute the most important
4 soil invertebrates in terms of biomass. Due to their large body size, high consumption rates
5 and burrowing activities they are key ecosystem engineers strongly modifyong the habitat of
6 other soil biota (Anderson, 1988; Bal, 1982; Eisenhauer et al., 2009a; Lavelle et al., 1997; Lee,
7 1983). Earthworms interact with plants in both direct and indirect ways (Brown et al., 1999;
8 Scheu, 2003). Indirect effects include changes of soil structure, aggregate stability, infiltration
9 of water, aeration of deeper soil layers, nutrient mineralization, litter decomposition, and
10 microbial and soil invertebrate biomass and community structure (Edwards and Bohlen, 1996;
11 Eisenhauer et al., 2007; Lavelle et al., 2006; Lavelle and Spain, 2001). These changes have
12 important consequences for plant communities and potentially the aboveground food web
13 (Scheu, 2003). Further, earthworms modify plant growth *via* hormone-like effects, dispersal
14 of plant growth stimulating microorganisms and dispersal of microorganisms antagonistic to
15 root pathogens (reviewed in Brown, 1995; Scheu, 2003). Direct effects of earthworms on
16 plants are root feeding and transposal of plant seeds (Scheu, 2003). However, direct effects
17 have received comparably little attention so far.

18 Effects of earthworms on seeds vary with earthworm species and functional groups, i.e.
19 among epigeic, endogeic and anecic species (Bouché, 1977; Edwards and Bohlen, 1996).
20 Epigeic species reside mainly in the upper organic soil layers and cause limited mixing of
21 mineral and organic layers. Endogeic species live in the upper mineral soil layers primarily
22 consuming humified organic matter and forming horizontal non-permanent burrows. Anecic
23 species typically are large earthworms living in deep vertical burrows up to 2 m deep, but
24 predominantly feed on litter on the soil surface. Litter materials are translocated into deeper
25 soil layers, but anecic species also transport mineral soil from deeper soil layers to the soil

1 surface by casting (Bouché, 1977; Sims and Gerard, 1999). Recent studies indicate that
2 earthworms from all ecological groups might significantly interact with seeds and thus are
3 likely to impact plant community assembly (Asshoff et al., 2010; Eisenhauer et al., 2009a).
4 However, most studies on earthworm – seed interactions only considered anecic earthworm
5 species of temperate regions.

6 While effects of earthworms on plant growth have been extensively studied (-Scheu ,
7 Brown) their effect on seed dynamics have been acknowledged for many years (ref) but have
8 never been thoroughly studied. Therefore, in this review, we focus on the direct and indirect
9 interactions between earthworms and seeds, and on the consequences of these interactions for
10 the composition, structure and temporal dynamics of plant communities. By compiling the
11 scattered literature on earthworm – seed interactions we aim to get plant ecologists aware of
12 the underappreciated role of earthworms for plant community structure. Moreover, we point
13 to the urgent need for further studies under more natural conditions. Four major topics are
14 presented: (i) the effect of earthworms on seeds (ii), the role of seeds for earthworm nutrition,
15 (iii) consequences for plant community assembly, and (iv) identifying promising future
16 research topics.

17

18 **2. Impacts of earthworms on plant seeds**

19 There is a multitude of mechanisms through which earthworms affect the fate of seeds (Fig.
20 1; Milcu, 2005). Earthworms affect four out of seven plant life stages directly (Fig. 2;
21 Eisenhauer and Scheu, 2008): seed survival on the soil surface (Grant 1983, Thompson et al.
22 1994), seed survival in the soil (Thompson et al., 1994), germination (Ayanlaja et al., 2001)
23 and seedling establishment (Lee, 1985). These effects impact in both positive and negative
24 ways the distribution, survival, establishment, growth and production of seeds (Eisenhauer et
25 al., 2008a; Eisenhauer et al., 2009a; Laossi et al., 2010). We discuss below the different

1 mechanisms through which earthworms influence seeds: seed translocation and burial, seed
2 selection and ingestion, seed digestion, mucus secretion and maternal effects.

3

4 *2.1. Seed translocation and burial*

5 Translocation of seeds into deeper soil layers by earthworms is recognized to play an
6 important role in vertical seed movement (Decaens et al., 2003; Eisenhauer et al., 2008a;
7 Grant, 1983; Laossi et al., 2010; Milcu et al., 2006; Regnier et al., 2008; Willems and
8 Huijsmans, 1994). Compared to seeds in the soil seed bank, those on the soil surface are more
9 easily detected by surface foraging organisms, and thus are more vulnerable to predation by
10 seed predators, such as birds, rodents and insects (Azcarate and Peco, 2003; Heithaus, 1981).
11 In general, large seeds (>2 mm) are more at risk of being consumed by seed predators than
12 small seeds (Brown and Heske, 1990) partly due to the greater difficulty to become buried in
13 the soil. On the other hand, large seeds improve seedling nutrition; seedlings germinating
14 from large seeds therefore better survive periods of resource shortage imposed by drought and
15 shade (Westoby et al., 1996). In perennial communities, seed predation may destroy more
16 than 95% of the seeds produced (Thompson, 1992). Therefore, the soil seed bank is
17 considered to function as a predator free (or reduced) spatial niche.

18 Seed burial might also reduce exposure to a harsh environmental conditions (Thompson et
19 al., 1994; Van Der Reest and Rogaar, 1988; Willems and Huijsmans, 1994). The soil seed
20 bank, therefore functions as refuge for surviving unfavourable environmental conditions such
21 as fire, drought and frost (Cohen, 1966) and prevents germination of seeds. Seeds of many
22 species survive better in the soil seed bank than on the soil surface and remain dormant for
23 long periods. Seeds translocated into deep soil layers by earthworms (seed ingested or pulled
24 into the burrow and buried) therefore contribute to the formation of a persistent seed bank
25 (Thompson et al., 1993). However, buried below a critical depth seeds may fail to emerge and

1 this depth is generally related to the seed size (Thompson et al., 1994; Traba et al., 2004).
2 Precisely, large seeds, often characterized by few requirements for germination, may
3 germinate in the soil and fail to emerge at the soil surface. Conversely, small seeds, needing
4 light or large temperature fluctuations for germination, will simply fail to germinate. Regnier
5 et al. (2008) found, in a field experiment conducted to determine how *L. terrestris* affected *A.*
6 *trifida* seed burial and seedling recruitment, that *L. terrestris* collected and buried over 90% of
7 *A. trifida* seeds placed on the soil surface. Interestingly, *A. trifida* seeds were highly variable
8 in size, ranging from 3 to 14 mm in length but the authors did not detect any earthworm-
9 mediated differences in the speed of burial depending on seed size. However, small seeds
10 were buried by *L. terrestris* deeper into the soil than large seeds. Thompson et al. (1994)
11 showed that virtually all seeds found in earthworm casts weighed <0.3 mg underlining the
12 observations of McRill (1974) who found small seeds disproportionately frequent in
13 earthworm casts. These results corroborate the decline in seed size with soil depth (Regnier et
14 al., 2008) and suggest that this in part is due to the action of earthworms.

15

16 2.2. Seed selection and ingestion

17 Earthworms selectively feed on seeds with seed selection depending on seed size
18 (Eisenhauer et al., 2009a; Shumway and Koide, 1994), shape (Eisenhauer et al., 2009a;
19 McRill and Sagar, 1973) and surface structure (Shumway and Koide, 1994).

20 Seed size is certainly the most important seed trait that influences their fate. It influences
21 both ingestion and digestion of plant seeds by anecic and endogeic earthworm species
22 (Eisenhauer et al., 2009a). Most studies used seed length as indicator of seed size but other
23 characteristics, such as seed surface and seed volume, might have higher explanatory power
24 than seed length (Eisenhauer et al., 2009a). Small seeds (<2 mm length) are more likely to be
25 ingested by *L. terrestris* than larger seeds (Eisenhauer et al., 2009a; Grant, 1983; Shumway

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

14 Although seed size is one of the main seed traits influencing their fate, other traits such as
15 seed shape, texture and taste/smell might also be essential in determining seed selection by
16 earthworms. Indeed, Willems and Huijsmans (1994) demonstrated that the selection of seeds
17 by *L. terrestris* is linked to the taste or smell of the seeds; among the ten species studied seeds
18 of aromatic species (*Origanum vulgare*, *Carex flacca* and *Daucus carota*) were most
19 preferred. The results suggest that earthworms use chemical cues to select more palatable
20 seeds (Grant, 1983; Willems and Huijsmans, 1994). Zaller and Saxler (2007) offered seeds
21 from ten grasslands species (three grasses, four non-leguminous herbs and three leguminous
22 herbs) to *L. terrestris*. They found that *L. terrestris* generally preferred seeds of non-
23 leguminous (*Taraxacum officinale*, *Sanguisorba officinalis*) and leguminous species
24 (*Trifolium repens*) over seeds of grasses (see also Eisenhauer et al., 2010). Thus, other seed
25 traits, such as nutritional value, coat thickness, shape, texture and taste, should be explored in

1 future studies in order to gain a better understanding of factors determining seed selection by
2 earthworms. Laboratory studies might therefore represent a helpful tool in order to extract the
3 most relevant seed traits.

4

5 2.3. Seed digestion

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

12 The passage through the earthworm gut especially reduces the germination rate of small
13 seeds (Laossi et al., 2009b; Milcu et al., 2006), likely resulting in modified germination rates.
14 For example, germination rate of seeds of *Poa pratensis* (1.9 x 1 mm), *Trifolium repens* (1.2 x
15 1.2 mm) and *Bellis perennis* (1.2 x 0.2 mm) was reduced from 24 to 5%, 56 to 6% and 43 to
16 10%, respectively, whereas the reduction of germination of the larger seeds of *Viccia cracca*
17 (2.8 x 2.8 mm) and *Tragopogon pratensis* (12 x 1.3 mm) was only reduced from 47 to 37%
18 and 54 to 38%, respectively (Milcu et al., 2006). The more pronounced decrease in
19 germination in small seeds is likely to be due to lower resistance of small seeds against
20 physical and chemical forces in earthworm guts (McRill and Sagar, 1979; Grant, 1983) linked
21 to seed coat characteristics, such as e.g. hardness and impermeability. Indeed, Eisenhauer et al.
22 (2010) reported seed digestion by *L. terrestris* to be negatively correlated with seed size.
23 However, digestion of seeds by endogeic earthworm species has been found to be
24 independent of seed size (Eisenhauer et al., 2009a). Contrary to seed ingestion, seed digestion
25 did not depend on earthworm body size (Eisenhauer et al., 2010; Eisenhauer et al., 2009a).

1

2 2.4. Secretion of mucus

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

18

19 2.5. Earthworm casts and burrows

20 Biostructures formed by earthworms impact seedling establishment *via* a number of
21 mechanisms (Eisenhauer et al., 2008b; Shumway and Koide, 1994; Thompson et al., 1994).
22 First, the region of burrow entrances of earthworms is deprived of plants which facilitates
23 seed germination (Fig. 3). These gaps with no or reduced competition with other plants are
24 particularly important in dense herbaceous plant systems. Second, earthworm casts likely
25 represent nutrient-rich regeneration niches for seeds (Eisenhauer and Scheu, 2008; Milcu et

1 al., 2006) and might improve seed germination and seedling growth by “fertilizing effects”.
2 Although earthworm burrows and casts are regarded as “hotspots” of nutrient availability
3 and microbial activity (Eisenhauer et al., 2007; Maraun et al., 1999), evidence is inconsistent
4 (Eisenhauer et al., 2009b; Straube et al., 2009). Third, casts comprise stable aggregates, rich
5 in ammonium and resistant to gas and water infiltration (Blanchart et al., 2004; Decaens,
6 2000), conditions known to maintain seed dormancy or delay germination (Grant, 1983).
7 However, it has also been demonstrated that earthworm casts accelerate seed germination by
8 increasing water permeability of the seed surface (Tomati et al., 1988) and by breaking seed
9 dormancy (Ayanlaja et al., 2001). Decaens et al. (2003) estimated that about 40% of viable
10 seeds emerge out of intact casts whereas the remaining 60% require further cast fragmentation
11 to emerge due to the high physical stability of casts. Smith et al. (2005) explored the
12 distribution of seeds of weeds of annual crops and reported distinct differences between
13 earthworm casts and the soil seed bank of the upper 5 cm suggesting that earthworms
14 contribute to the redistribution of seeds of weeds in arable and other systems thereby affecting
15 plant species assembly and community dynamics (Eisenhauer et al., 2008b; Milcu et al., 2006;
16 Regnier et al., 2008).

17

18 *2.6. Maternal effects*

19 The phenotype of plant individuals is determined not only by their genotype and
20 environment but also by maternal effects, i.e. the direct contribution of the maternal
21 phenotype to the phenotype of its offspring. Indeed, the tissues immediately surrounding the
22 developing embryo and endosperm are all maternal. These tissues, the integuments of the
23 ovule and the wall of the ovary, eventually form the seed coat and the fruit, and accessory
24 seed structures, such as the hairs, awns and barbs, are important determinants of seed

1 dormancy, dispersal and germination traits (Roach and Wulff, 1987) thereby affecting later
2 stages of plant life.

3 Since earthworms influence plant growth (ref)- they generally increase their biomass
4 accumulation and improve their mineral nutrition- they should also modify seed properties
5 and subsequently trigger maternal effects. For example, earthworms have been shown to
6 modify seed nutrient concentration (Baskin and Baskin, 2001; Noguera et al., 2010) and seed
7 size (Poveda et al., 2005b). Such traits are known to influence seed germination and seedling
8 growth (ref). Recently, Laossi et al. (2010) investigated, in a greenhouse experiment, maternal
9 effects on seed germination and seedling growth of three grassland plant species (*Veronica*
10 *persica*, *Poa annua* and *Cerastium glomeratum*) induced by *A. caliginosa* and *L. terrestris*.
11 Through maternal effects *A. caliginosa* enhanced seed germination (+74% for *V. persica* and
12 +32% for *P. annua*) and seedling growth (+23% for *C. glomeratum* and +27% for *P. annua*)
13 while *L. terrestris* reduced seed germination in *V. persica* (-17%). In some cases, the increase
14 in the germination rate of seeds produced in the presence of earthworms could be explained
15 by a significant reduction in seed nitrogen concentration. These results suggest that the
16 strength and direction of earthworm-induced maternal effects strongly vary with plant and
17 earthworm species.

18 A number of issues still need to be investigated in this context: Do earthworm-mediated
19 maternal effects persist after the seedling stage (Miao and Bazzaz, 1990)? Does interspecific
20 competition between seedlings modulate such maternal effects? Do these maternal effects
21 persist in the third generation (Alexander and Wulff, 1985; Miao et al., 1991)? Are
22 earthworm-induced maternal effects adaptive and allow young plants to be better adapted to
23 earthworm-mediated changes in soil properties?

24

25 **3. The role of plant seeds for earthworm nutrition**

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

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

21

22 *3.1. Feeding on seeds and seedlings*

23 Grant (1983) reported seed losses of ~30% during earthworm gut passage. McRill and
24 Sagar (1973) and Eisenhauer et al. (2009a) reported even higher rates of seed loss during the
25 gut passage through *L. terrestris*, i.e. 20 – 100% and 34 – 83%, respectively, depending on

1 plant species identity. “Lost” seeds during earthworm gut passage may be destroyed by
2 earthworm gizzard contraction and enzyme activity (Grant, 1983). Sand particles presumably
3 enforce grinding of seeds in the earthworm gut, as has been shown for litter material (Marhan
4 and Scheu, 2005; Schulmann and Tiunov, 1999). Moreover, the activity of enzymes, such as
5 cellulases provided by the ingested microflora (Lattaud et al., 1998), likely contributes to seed
6 digestion. Despite high seed digestion rates, only few studies considered that seeds might
7 contribute to earthworm nutrition.

8 Shumway and Koide (1994) observed earthworms grazing on seedlings in laboratory
9 experiments and concluded that seeds transported readily beneath the soil surface in its
10 burrows may increase the availability of food resources for *L. terrestris*. The authors
11 discussed two mechanisms by which earthworms might benefit from germination of seeds.
12 First, germination may render seeds digestible that were initially protected by resistant seed
13 coats and passed undigested through the earthworm gut. Other studies highlighted this
14 argument by showing that the passage of seeds through the earthworm gut increases the
15 germination percentage of seeds of several plant species by damaging the seed coat and thus
16 breaking seed dormancy (Eisenhauer et al., 2010) or stimulating seed germination. Second,
17 earthworms might benefit from biochemical changes during germination, such as vitamin
18 synthesis, which potentially provide important nutrients for earthworms feeding on these
19 seedlings (Shumway and Koide, 1994).

20

21 *3.2. Earthworm nutrition and resulting feedbacks*

22 The suggestions of Shumway and Koide (1994) that seeds and germinating seedlings
23 significantly contribute to earthworm nutrition have been supported recently. (Eisenhauer and
24 Scheu, 2008) added grass, legume and herb seeds to grassland plant communities varying in
25 plant species composition. Earthworms lost weight when grass seeds were added to grass

1 communities and legume seeds to legume communities; however, they gained weight when
2 grass seeds were added to legume communities and legume seeds to grass communities (Fig.
3 4). The authors concluded that germination and growth of plant species are inhibited by plants
4 of the same plant functional group in close vicinity due to intra-functional group competition
5 (Fargione and Tilman, 2005), i.e. grass seeds germinate better in legume communities and
6 legume seeds germinate better in grass communities. Assuming that earthworms benefit from
7 germinating seeds, *L. terrestris* possibly benefited from increased germination of seeds in
8 plant communities of different functional group affiliation. However, this assumption could
9 not be endorsed with data on plant germination rates.

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

16 In addition to the quality (nitrogen concentration) of plant seeds and seedlings, collection
17 of seeds by earthworms has been proposed to be driven by the growth speed, i.e. the relative
18 growth rate, of seedlings as there likely is a 'size refuge' of seedlings beyond which
19 earthworms are unable to swallow seedlings (Eisenhauer et al., 2010). In fact, stable isotope
20 analysis indicated increased resource acquisition from legume seedlings growing slowly than
21 from grass seedlings growing quickly. However, preferential feeding on legume seedlings
22 may also be due to high nitrogen concentration; further experiments are needed to disentangle
23 the relative role of nitrogen concentration vs. speed of growth of seedlings in food selection of
24 earthworms. Resource capture from seeds and seedlings may explain why anecic earthworms
25 such as *L. terrestris* vigorously collect virtually any debris in the vicinity of their burrows,

1 mix them with mineral soil and feed on the mixed materials (Butt et al., 2003). Nevertheless,
2 it should be noted that current knowledge is based on few laboratory experiments and the
3 biological significance of seeds and seedlings for earthworm nutrition remains unclear.

4

5 **4. Consequences for plant communities**

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

11

12 *4.1. Soil seed bank composition and spatial distribution*

13 The amount of soil deposited on surface by earthworm casts ranges from 2 to 250 t/ha per
14 year (Edwards and Bohlen, 1996). In temperate regions the upper 15 cm of soil, containing
15 most seeds of the seed bank, may be turned over completely every 10–20 years by
16 earthworms (Edwards and Bohlen, 1996). Because seeds from different plant species vary in
17 their susceptibility to the gut passage through earthworms, soil turnover by earthworms is
18 likely to affect the composition of the soil seed bank and modify seed bank attributes, such as
19 seed persistence and survival, and seed bank dynamics. Indeed, Zaller and Saxler (2007)
20 demonstrated that some plant species present in casts are not present in the standing
21 vegetation, suggesting that earthworms transport seeds of the past vegetation to the soil
22 surface. A recent field study showed that both anecic and endogeic earthworm species
23 invading Canadian forest ecosystems affect the composition of the soil seed bank of native
24 forests (Eisenhauer et al., 2009b). Remarkably, the effects strongly depended on plant
25 functional group identity (Fig. 5), suggesting distinct changes in herbaceous plant community

1 composition after earthworm invasion and fundamental alternations of soil seed banks
2 induced by earthworms spread by man. However, the underlying mechanisms of interactive
3 effects of invasive earthworm species/ecological groups are poorly understood (Eisenhauer et
4 al., 2009b) and deserve further attention.

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

12

13 *4.2. Seed traits and plant strategies*

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

22 As a result, the selective ingestion and increased digestion of small seeds by earthworms
23 presumably is of particular importance during early succession when annual species
24 predominate. Also, at least for annuals living in a matrix of perennial plants, germination is
25 crucial for survival, performance and dynamics of annual species (Rees and Long, 1992).

1 Conversely to perennials, annual species cannot compensate the risk of seedling mortality by
2 adult longevity (Dyer et al., 2000; Verdu and Traveset, 2005). Annual species are thus more
3 likely to stay in soil seed bank for a long period to delay germination and avoid unfavourable
4 environmental conditions (Kluth and Bruelheide, 2005; Lortie et al., 2005), a strategy that
5 might be facilitated by earthworm activity. Even if seed ingestion by earthworms damages a
6 great number of seeds in casts, one facilitated seed (*via* breaking seed dormancy, stimulation
7 of germination, reduced competition with other seeds, nutrient rich germination sites) might
8 be enough to ensure the survival of this species in the community. Probably there is a trade-
9 off between seed mortality in the earthworm gut and germination facilitation in earthworm
10 casts. The net effect of these contrasting mechanisms is likely to depend on, for instance,
11 earthworm digestive capability and seed traits. Among these factors, seed size is likely to be
12 among the most important factors with earthworms favouring plants with larger seeds. As
13 indicated by two recent greenhouse experiments impacts of earthworms on seedling
14 recruitment vary significantly with seed size, and this has important consequences for plant
15 succession and assembly (Eisenhauer and Scheu, 2008; Milcu et al., 2006). Indeed, in the
16 study by Milcu et al. (2006), particularly plants with large seeds benefited from the presence
17 of earthworms (Fig. 6). Probably, large-seeded plants experience less predation by
18 earthworms. Although the number of established plants was lower in the presence of
19 earthworms in both studies, plants with intermediate-sized (Eisenhauer and Scheu, 2008) and
20 large-sized seeds (Milcu et al., 2006) built significantly more biomass, most likely due to
21 elevated nutrient supply in earthworm middens.

22 A further important seed trait is the speed of germination. As anecic earthworms may
23 function as seed and seedling predators, seedlings could benefit from reaching a size refuge as
24 fast as possible, i.e. being too large to get swallowed by earthworms (Eisenhauer et al., 2010).
25 Particularly fast germination of grass seeds and seedlings with fast relative growth rates at

1 least in part might have evolved to escape consumption by earthworms. Thus, the exploration
2 of potential co-evolutionary processes between earthworms and plants represents a novel and
3 fascinating field in ecological research.

4

5 *4.3. Earthworm effects on seed and seedlings interactions*

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

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

24

25 *4.4. Disturbance and regeneration niches*

1 Safe sites for seedling recruitment are rare in temperate semi-natural grasslands
2 (Austrheim and Eriksson, 2003). Consequently, the creation of gaps and micro-disturbances
3 are of key importance in enhancing plant establishment and community diversity by
4 increasing niche dimensionality within local communities (Eisenhauer et al., 2008b; Harpole
5 and Tilman, 2007). Such local heterogeneity affects the spread of species (Bergelson et al.,
6 1993), influence seed and consequently plant density (Miller et al., 1994), the spatial
7 distribution of plants (Houle, 1998) and competitive interactions (Stoll and Prati, 2001). In
8 temperate grasslands, Grant (1983) found 30% of seedlings germinating from earthworm
9 casts. This indicates that earthworm casts and middens increase the spatial heterogeneity of
10 grassland plant communities thereby forming an important regeneration niche *sensu* Grubb
11 (1977). Indeed, earthworms enhance the sensitivity of plant communities to the establishment
12 of weed species thereby also increasing the diversity of weeds (Eisenhauer et al., 2008b;
13 Pearce et al., 1994).

14 The functioning of casts and middens as regeneration niche is likely to vary with cast
15 characteristics (e.g., size, solidity, age), earthworm species (Eisenhauer et al., 2008a) and
16 plant community characteristics (Eisenhauer et al., 2008b). For example, Decaëns et al. (2003)
17 found that in savannah grassland the number of seeds in casts deposited on the soil surface
18 exceeded those deposited in soil (but the number of viable seeds was about 3–40 times lower
19 in cast than in soil). The number of viable seeds excreted each year in surface casts was
20 significantly higher at up to 10 million seeds ha year⁻¹, compared to seed numbers reported by
21 Willems and Huijsmans (1994) investigating *L. terrestris* in temperate pastures (890,000
22 seeds ha⁻¹ year⁻¹). Smith et al. (2005) also found that cast production and seed density varied
23 temporally and among crops. Both crop identity (corn, soybean and winter wheat) and
24 management (monoculture or rotation of the three previous species) were investigated. For
25 the whole experiment, weed seed densities were higher in earthworm casts than in samples

1 collected from the soil surface and seed bank. Earthworm cast production and germinable
2 weed seed density were higher in winter wheat (and mainly in monocultures) compared to
3 corn or soybean crops. In addition, within winter wheat crops, differences in germinable weed
4 seed densities in earthworm casts also differed in response to rotation. As expected by the
5 authors, seed content of earthworm casts was related to cast size, with larger casts containing
6 more weed seeds.

7

8 **5. Outlook**

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

12

13 *5.1. Literature bias*

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

20 Most previous studies on earthworm - seed interactions were published by soil ecologists
21 in soil biology journals or general ecology journals and none in plant ecology journal (Fig. 7a).
22 The majority of studies (i) investigated temperate grassland systems in Europe and America,
23 and (ii) anecic earthworm species, mostly a single species, *L. terrestris* (Fig. 7b), (iii) have
24 been performed under laboratory conditions. This suggests that we should study seed-
25 earthworm interactions in much diverse situations, i.e. tropical systems and all ecological

1 earthworm groups (including endogeic and epigeic). Additionally, laboratory experiments are
2 short-term experiments usually focussing on the individual plant scale. However, to predict
3 the effect of earthworm - seed interactions on plant communities, experiments should
4 manipulate whole plant communities for several generations (see Laossi et al 2011) . Finally,
5 the effect of earthworms on seed fate should be compared to the influence of other factors
6 affecting seeds in the field to assess their importance as drivers of seed and seedling
7 performance (Brooker et al., 2005).

8

9 *5.2. Applying our understanding*

10 By modifying the characteristics of plant communities, interactions between earthworms
11 and seeds can also modify the stability of plant communities against plant invasion
12 (Eisenhauer et al., 2008b). Community stability can be described *via* a multitude of properties
13 including resistance and resilience (Mitchell et al., 2000). Earthworms might affect the
14 resistance of plant communities against invasions, i.e. colonisation of species not previously
15 present in the community *via* effects on seeds. As discussed above, the formation of
16 regeneration niches and the increase in the spatial heterogeneity within plant assemblages are
17 likely to alter the stability of ecosystems. Resilience of grassland communities might be
18 increased by translocation of seeds from the seed bank to soil surface. In a microcosm
19 experiment *L. terrestris* significantly increased the number of weeds, suggesting that
20 earthworms translocated seeds from deeper soil layers to the soil surface where they
21 germinated (Milcu et al., 2006). This indicates that the soil seed bank contributes to the
22 resilience of grassland communities *via* seed translocation by earthworms. In fact, seeds of
23 *Malva pusilla* and two *Verbascum* species were still alive after 120 years of burial (Telewski
24 and Zeevaart, 2002). Thus, seed burial by earthworms might contribute to increase
25 community resilience by increasing seed persistence. Decaëns et al. (2003) suggested that

1 earthworm casts might enhance the recovering of savannahs after fire events. Earthworm casts
2 may remain at the soil surface for more than one year thereby forming a pool of seeds ready
3 to germinate after disturbances (Decaens et al., 2003).

4 In face of the current rapid degradation of terrestrial ecosystems worldwide, there is an
5 increasing need for the development of novel, low-cost and efficient restoration techniques
6 for maintaining ecosystem function and services (e.g. Hobbs et al., 2006; Ormerod et al.,
7 2003). Earthworms may help in achieving these goals, e.g. in mitigating human impacts on
8 plant diversity by activating the seed bank of the former vegetation.

9 On the other hand, by altering seedbed conditions, exotic earthworms act as threat for
10 herbaceous plants in forests previously devoid of earthworms (Hale et al., 2006; Holdsworth
11 et al., 2007). A recent study showed that exotic earthworms alter seedling emergence from
12 forest seed banks and the composition of the established plant seedlings (Eisenhauer et al.,
13 2009b). This highlights the strong effects of invasive earthworms on aboveground ecosystem
14 characteristics and foreshadows fundamental changes of native ecosystems by earthworms
15 spread by humans.

16

17 *5.3. Implications for plant evolution*

18 Since earthworms influence the fate of seeds, they also influence the fitness of plant
19 species and should thus exert evolutionary pressures on plants. In habitats with high
20 earthworm densities there might be a strong selective pressure on seeds of herbaceous plants
21 to survive the passage through the earthworm gut and to germinate shortly after voiding of
22 casts (Decaens et al., 2003; Eisenhauer et al., 2008b; Grant, 1983). In particular, in alkaline
23 soils where earthworm densities are high this may have shaped plant evolution. Presumably,
24 certain plant species, such as annuals that produce small seeds resistant to digestion, depend
25 on regeneration niches formed by earthworms, while others developed the opposite strategy,

1 e.g. the production of large seeds or seeds of bad taste, thereby avoiding consumption by
2 earthworms.

3

4 **6. Conclusions**

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

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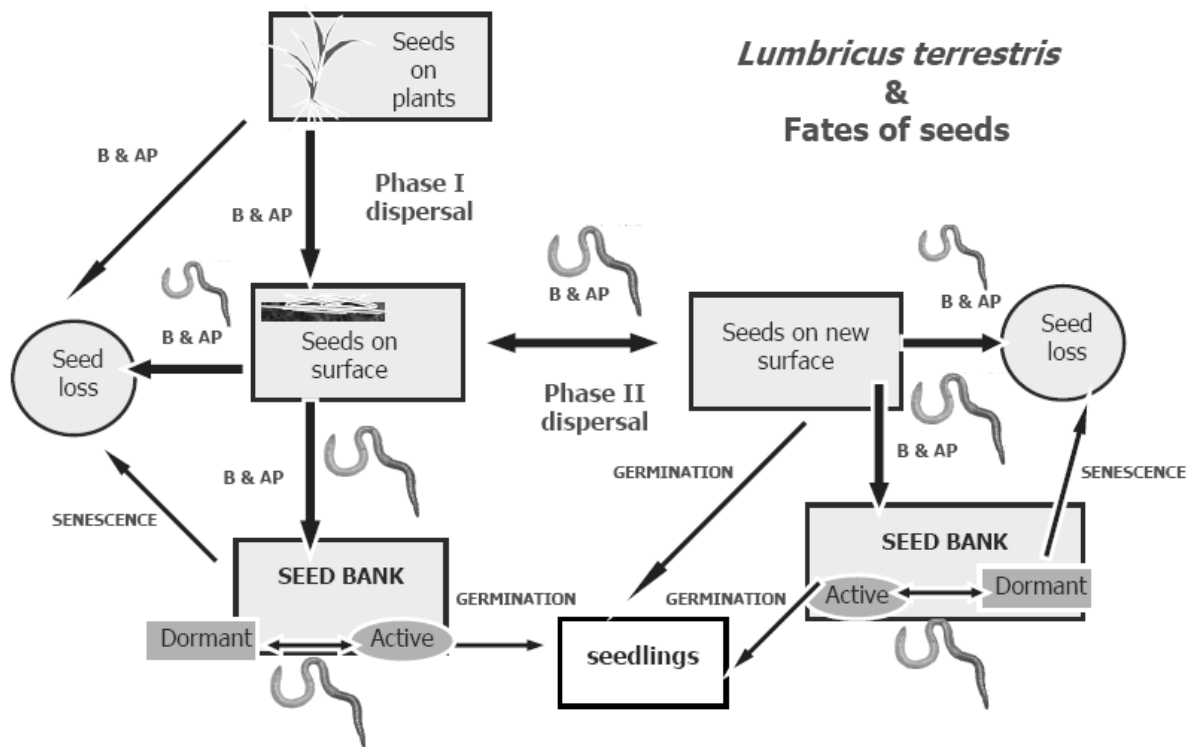
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1 **Figures**

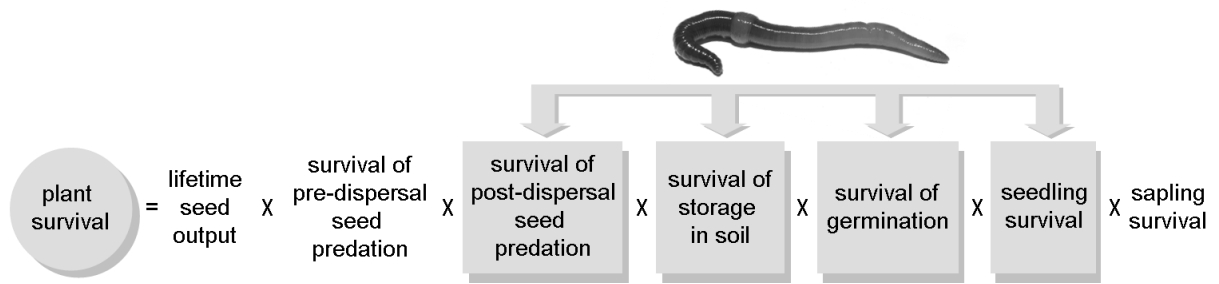
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4 **Fig. 1.** Conceptual framework of the movements and fates of seeds. Seeds can be affected by
5 biotic processes (B) or abiotic processes (AP). As part of the biotic processes (B) earthworms
6 point to the stages where *Lumbricus terrestris* interact with seeds. Modified after Chambers
7 and MacMahon (1994) in Milcu (2005).

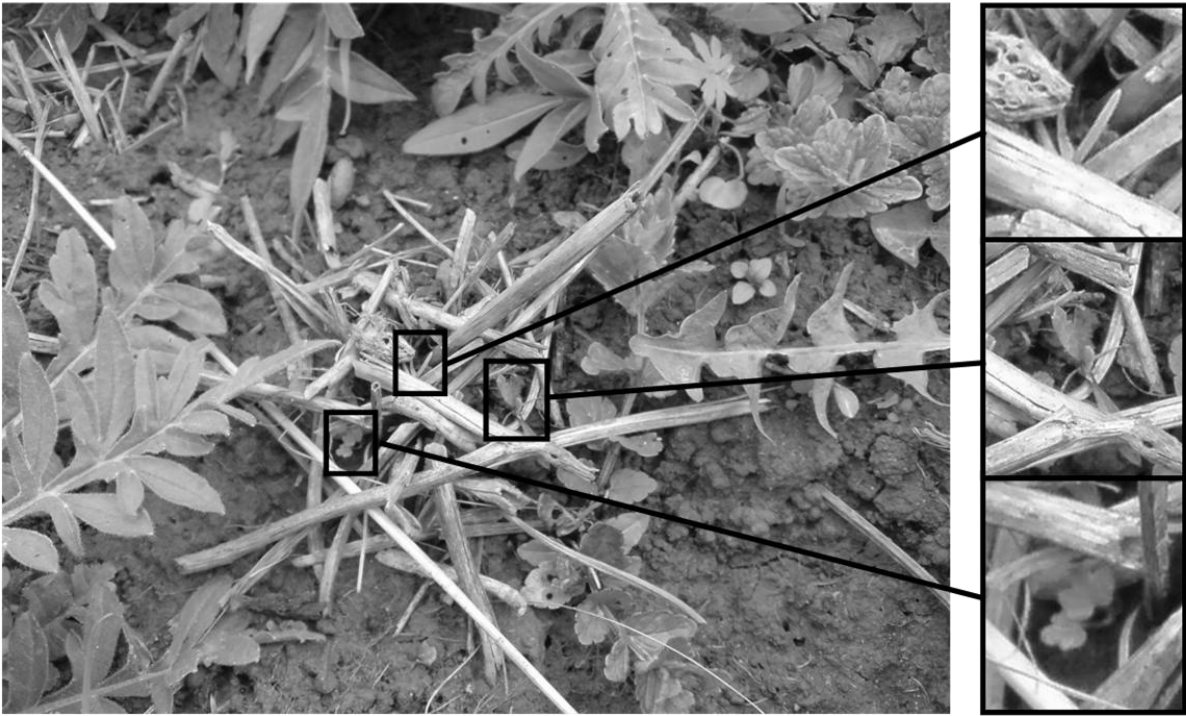
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3 **Fig. 2.** Plant survival as a function of the survival of different plant life stages with emphasis
 4 on life stages directly influenced by earthworms. Modified after Moles and Westoby (2006) in
 5 Eisenhauer and Scheu (2008).



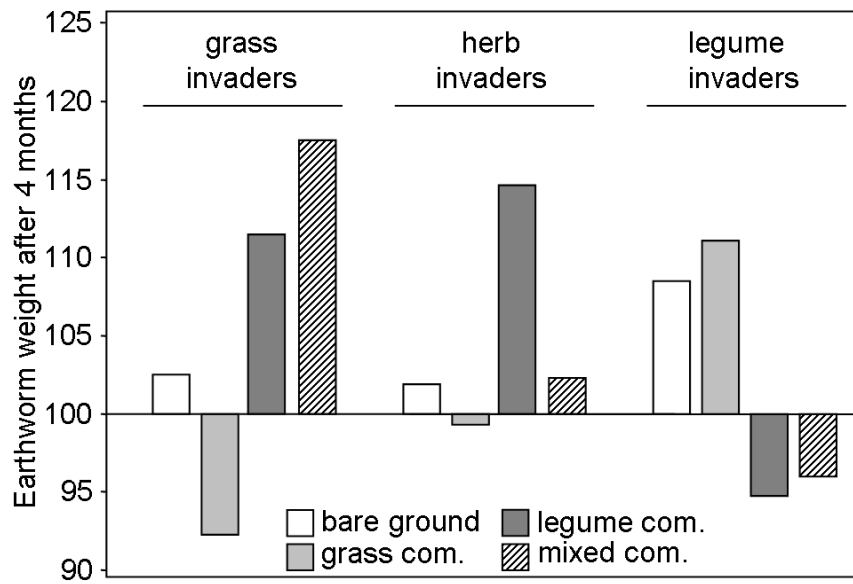
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2 **Fig. 3.** Photograph of one exemplary *Lumbricus terrestris* midden with three plant seedlings

3 on the field site of the Jena Experiment. Photo by N. Eisenhauer. Given in Eisenhauer et al.

4 (2008b).

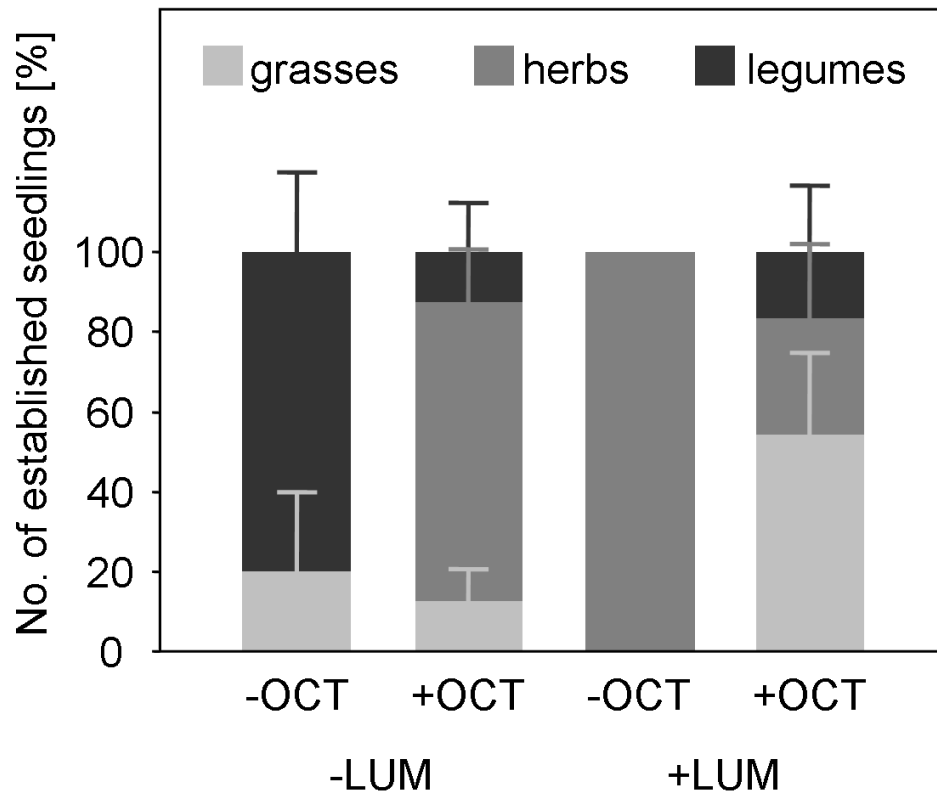
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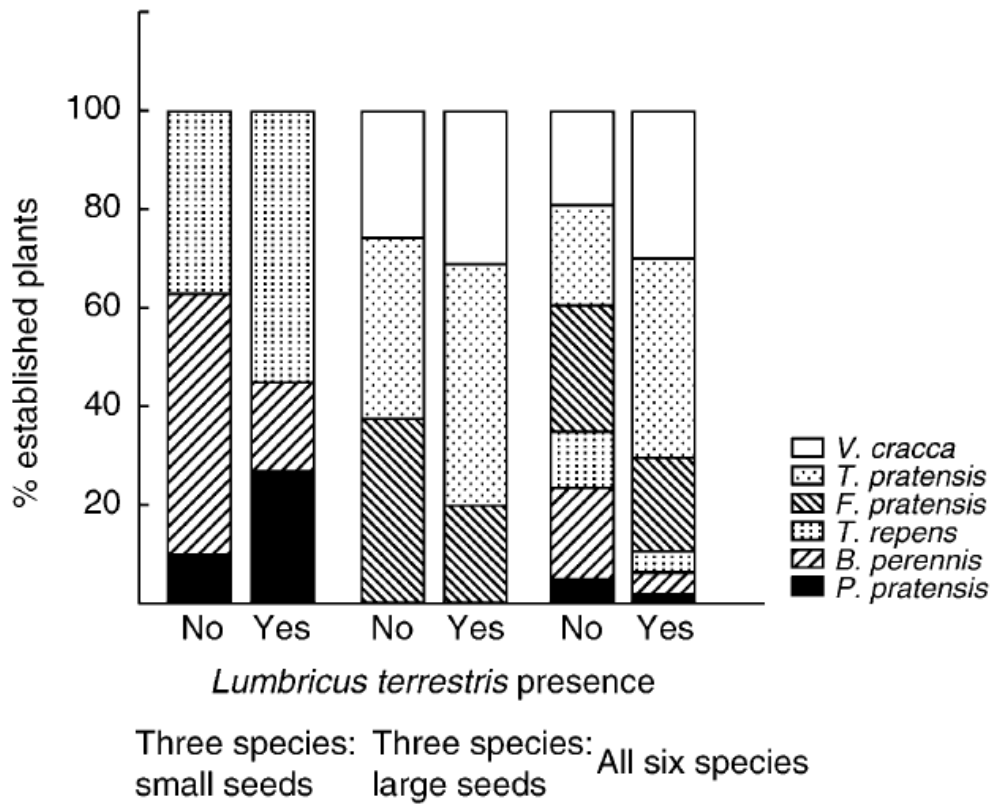
2 **Fig. 4.** Changes in body fresh weight of *Lumbricus terrestris* during the experiment (% of
3 initial) as affected by the resident plant community (PC; bare ground, grass community,
4 legume community and mixed community) and the functional group of the invading plant
5 species (FG; grass, legume and herb invaders; significant PC x FG interaction, $F_{6,37}=3.41$,
6 $P=0.009$). Given in Eisenhauer and Scheu (2008).

7



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 2 **Fig. 5.** Variations in the proportion of the number of established seedlings belonging to the
 3 plant functional groups grasses, herbs, and legumes as affected by the presence of *Lumbricus*
 4 *terrestris* (-LUM = without and +LUM = with) and *Octolasion tyrtaeum* (-OCT = without and
 5 +OCT = with; interaction between LUM x OCT: $F_{1,17; \text{grasses}}=2.63$, $P>0.05$, $F_{1,17; \text{herbs}}=17.77$,
 6 $P<0.001$, $F_{1,17; \text{legumes}}=4.84$, $P<0.05$). Means with standard error. Given in Eisenhauer et al.
 7 (2009b).

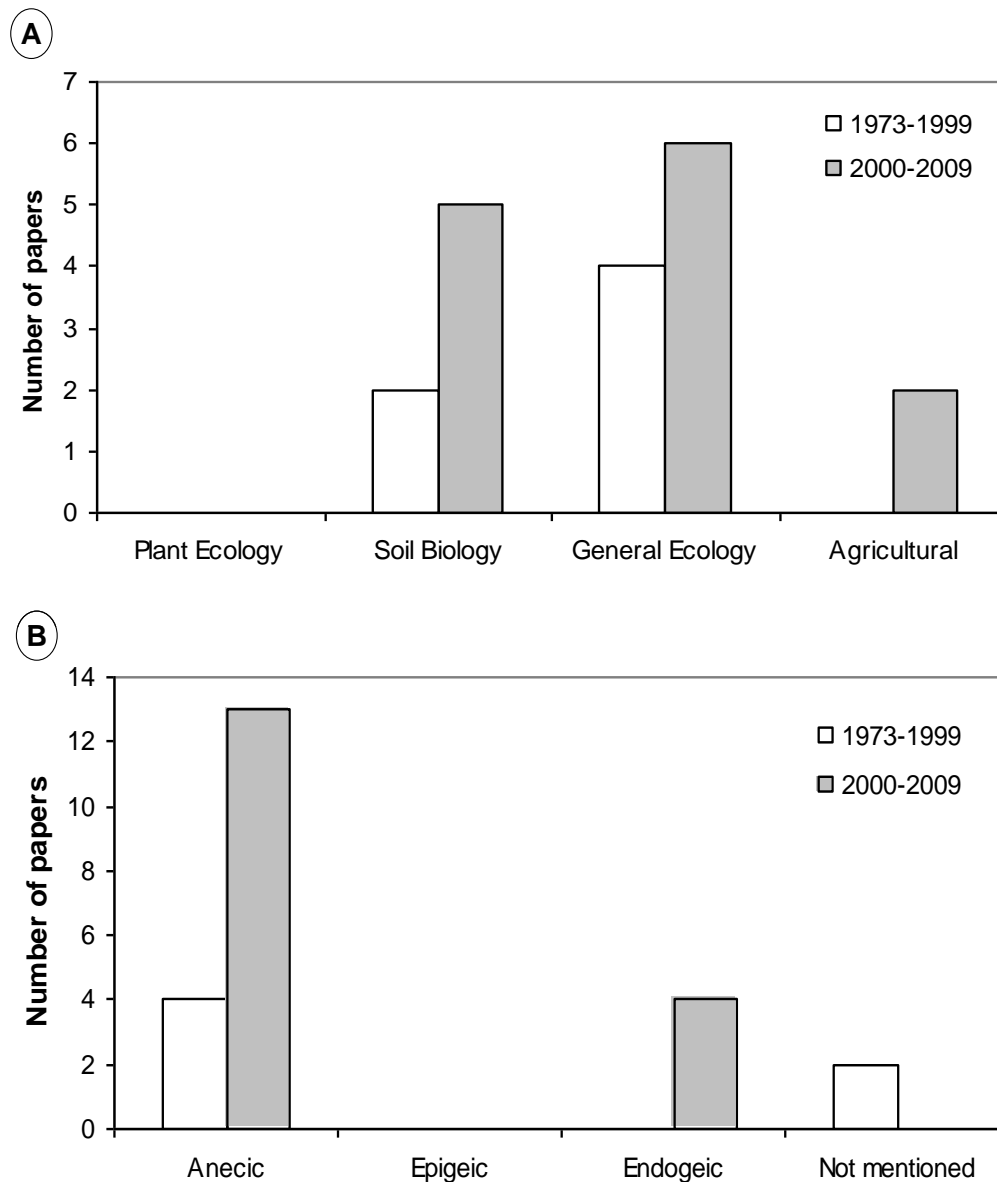
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2 **Fig. 6.** Changes in plant species composition (percentage of established) as affected by
 3 presence of *Lumbricus terrestris* and seed size ($F=9.00$, $P<0.01$). *V. cracca* = *Vicia cracca*, *T.*
 4 *pratensis* = *Tragopogon pratensis*, *F. pratensis* = *Festuca pratensis*, *T. repens* = *Trifolium*
 5 *repens*, *B. perennis* = *Bellis perennis*, *P. pratensis* = *Poa pratensis*. Given in Milcu et al.
 6 (2006).

7



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3 **Fig. 7.** Journals in which studies on effects of earthworms on seeds were published (a), and
 4 earthworm groups used in these studies (b) in the periods of 1973-1999 and 2000-2009. Soil
 5 biology journals include *Applied Soil Ecology*, *European Journal of Soil Biology*,
 6 *Pedobiologia*, *Soil Biology and Biochemistry*, and a book chapter; General ecology journals
 7 include *Acta Oecologica*, *Ecography*, *Ecosystems*, *Functional Ecology*, *Journal of Biological*
 8 *Education*, *Nature*, *Oikos*, *PLoS ONE*; and Agricultural journals include *Agriculture*,
 9 *Ecosystems & Environment*.

1 Authors and date of publication of studies included in the survey are Aira and Pearce, 2009;
2 Asshoff et al., 2010; Decaëns et al., 2003; Eisenhauer et al., 2008a; Eisenhauer et al., 2008b;
3 Eisenhauer et al., 2010; Eisenhauer et al., 2009a; Eisenhauer et al., 2009b; Eisenhauer and
4 Scheu 2008; Grant, 1984; Jimenez and Decaëns, 2004; Laossi et al., 2009; Mc Rill and Sagar,
5 1973; Milcu et al., 2006; Pearce et al. 1994; Regnier et al., 2008; Shumway and Koide, 1994;
6 Smith et al., 2005; Thompson et al., 1994; Willems and Huijsmans,1994; Zaller and Saxler,
7 2007.