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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.

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; Piearce 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

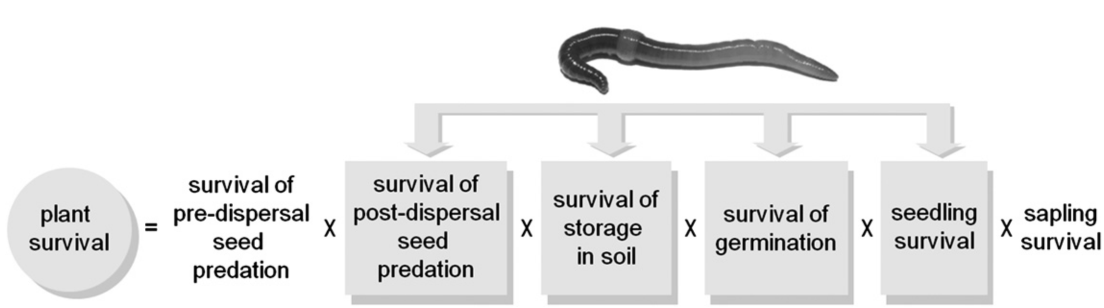

Fig. 1. Plant survival as a function of the survival of different early plant life stages (modified after Moles and Westoby, 2006). Life stages directly influenced by earthworms are highlighted with grey boxes (see text for more details). Modified after Eisenhauer and Scheu (2008).