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How good are epigeic earthworms at dispersing? An investigation to compare epigeic to endogeic and anecic groups

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ABSTRACT

Dispersal capacities can strongly determine an individual's ability to respond to changing environmental conditions, which would consequently influence the structure of natural communities. Nonetheless, we know little about the dispersal behaviour of soil organisms, despite some of these organisms, such as earthworms, have key roles in ecosystem functioning (e.g. organic matter decomposition). We expect that species exposed to frequent environmental changes would benefit from the capacity to escape from adverse environmental conditions and to disperse to settle in a more suitable habitat. In earthworms, we expect the epigeic group, which lives at or close to the soil surface, to have evolved higher dispersal capacities than the two other functional groups – anecic and endogeic, which live deeper in the soil. In this study, we investigated dispersal and diffusion behaviour of three species of epigeic earthworms (i.e. *Eisenia fetida*, *Eisenia andrei* and *Lumbricus rubellus*) and compared these behaviours with those of anecic and endogeic earthworms, whose behaviour has been previously measured through similar experiments. In accordance with our hypothesis, our study shows that dispersal behaviour of epigeic earthworms depends on habitat quality and population density, but that those responses vary among species and that it differs only to a limited extent from behaviour of anecic and endogeic earthworms.

1. Introduction

Dispersal is a central ecological process that allows colonization of new habitats and exploitation of spatially and temporally variable resources (Ronce, 2007). Active dispersal of animals (as opposed to passive dispersal, where individuals are transported by an external agent, and has not necessarily a cost for the disperser) is the result of three successive behavioural stages (following the definition given by Clobert et al., 2009, 2001). It involves the departure from a breeding site, crossing to a new place, and settlement (Clobert et al., 2009). It is thought to depend on the balance between the costs and benefits of dispersal (Bonte et al., 2012; Bowler and Benton, 2005), which are strongly determined by both environmental conditions (e.g. habitat quality, habitat fragmentation, patch size, density, predation; Bonte et al., 2006; Schtickzelle et al., 2006) and individual life traits (e.g. age, hormonal levels, movement abilities). Therefore, dispersal capacities are expected to strongly determine an individual's ability to respond to changing environmental conditions, which would consequently influence the dynamics and persistence of populations, the distribution and abundance of species, the structure of natural communities but also the functioning of ecosystems (Cuddington and Hastings, 2004). Nonetheless, we know little about the dispersal behaviour of soil organisms, even if some of these organisms, such as earthworms, play key roles in ecosystem functioning (Blouin et al., 2013).

Earthworms species are often classified into three functional groups based on their morphology, and their foraging behaviour (Bouché, 1977, 1972): endogeic earthworms live and feed in the soil, epigeic earthworms mainly live and feed on the leaf litter at the soil surface, anecic earthworms make vertical burrows in soil and feed on leaf litter which they drag into their burrows. Earthworms are of primary importance for ecosystem functioning because they modify the availability of resources for other organisms through physical and chemical changes in their surrounding soil environment (Jones et al., 2010, 1994; Rillig et al., 2016). As a consequence, they fulfil numerous soil-based ecosystem services (Blouin et al.,

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2013). While anecic earthworms, and to a lower extent endogeic and epigeic earthworms, are of particular importance for cropping systems (Bertrand et al., 2015; Van Groenigen et al., 2014), epigeic earthworms play a key role in organic matter decomposition in deciduous forests because of the ingestion of poorly decomposed litter (Manna et al., 2003) and the interactions they established with decomposer microorganisms (Gómez-Brandón et al., 2012; Monroy et al., 2008), which explains their use in vermicomposting (e.g. Suthar et al., 2008).

For these reasons, it is essential to identify the environmental factors that may influence earthworm prevalence and abundance in ecosystems (Curry, 1998; Palm et al., 2013), especially in the context of global changes. Indeed, anthropogenic activities, including urbanisation and agriculture, are responsible for considerable modifications of the natural environment through e.g. light, noise and chemical pollution, temperature modifications and habitat fragmentation. These changes may have considerable impact at the individual level and in terms of population dynamics and functioning (e.g. Dupont et al., 2015; Johnston et al., 2015; Orwin et al., 2015). To cope with these natural (e.g. soil heterogeneity, daily and seasonal cycles, etc.) or human-induced environmental constraints, high sensory capacities associated with acclimatization or dispersal abilities may have been naturally selected in earthworm species (e.g. Fisker et al., 2011; Spurgeon and Hopkin, 2000). Amongst other things, we expect species exposed to frequent environmental changes to benefit from a large tolerance range, meaning from high flexibilities (e.g. earthworms exposed to changing concentrations of pollutants should benefit from high flexibility in the synthesis of detoxification proteins; Lukkari et al., 2004) or from the capacity to escape from these detrimental environmental conditions and to disperse to settle in a more suitable habitat.

The three functional groups of earthworms inhabit three different niches whose exposure to aboveground conditions increases from the endogeic group to the epigeic group. The aboveground environment is characterized by a high temporal and spatial heterogeneity. Therefore, epigeic earthworms have to face highly fluctuating environments (e.g. temperature and humidity changes) and are more directly exposed to soil inputs (e.g. pesticides, hydrocarbons, fertilizer, etc.), soil surface state (e.g. subsidence exerted by vehicles, ploughing or bioturbations) and predators. Consequently, we may expect epigeic earthworms to have evolved higher sensibility to surface conditions (i.e. quicker responses) and higher dispersal abilities (i.e. lower dispersal costs, associated with physiological and anatomical adaptations for low latency and high speed movements) than endogeic and anecic groups.

Habitat (i.e. soil and litter) structure (e.g. particle size distribution), composition (e.g. amount of organic carbon) and pH, both linked to bioavailability of chemicals in soils and earthworms' ability to move in the habitat, are expected to influence earthworm habitat preference (Lanno et al., 2004) and as a consequence dispersal behaviour. Moreover, the amount of food in the environment is often limited; therefore, food availability per individual is negatively correlated with population density (Curry, 1998). Alternatively, population density may affect soil physical and chemical properties (Jones et al., 2010, 1994; Rillig et al., 2016), which may lead to facilitating mechanisms (Caro et al., 2012; Mathieu et al., 2010). Nonetheless, to our knowledge, few studies have investigated the environmental factors that influence dispersal behaviour in earthworms. Caro et al. (2013, 2012) and Mathieu et al. (2010) showed that low soil quality increased dispersal rate of *Aporrectodea icterica*, *Allolobophora chlorotica*, *Aporrectodea caliginosa* (endogeic species) and of *Aporrectodea longa*, *Lumbricus terrestris* and *Aporrectodea giardi* (anecic species). Moreover, the absence of litter increased dispersal rate in *Dendrobaena venata*, an epigeic species (Mathieu et al., 2010). High intraspecific density also increased dispersal rate in those three anecic species and in *A. icterica* but not in *A. chlorotica* and *A. caliginosa*. Finally, while dispersal speed was increased by conspecifics through the use of existing galleries in *Aporrectodea giardi* (Caro et al., 2012), dispersal rate was reduced by the pre-use of soil in *A. icterica* (Mathieu et al., 2010). Previous studies on earthworm dispersal were mostly carried out on endogeic and on anecic groups (Caro et al., 2013, 2012) or on a single epigeic species (Mathieu et al., 2010). Therefore, we still know little about the dispersal behaviour of the epigeic group and whether it is different from the two other groups.

To investigate diffusion and dispersal behaviour of epigeic earthworms, we performed three different experiments on three epigeic species (i.e. *Eisenia fetida*, *Eisenia andrei* and *Lumbricus rubellus*), following the same experimental protocol as a previous experiment (Caro et al., 2013). We investigated diffusion behaviour in a homogeneous environment (experiment 1), to measure earthworm propensity to explore, their distance of exploration and their tendency to follow their conspecifics. We measured dispersal rate in response to habitat quality (experiment 2) or in response to population density (experiment 3). Then, we compared diffusion and dispersal behaviours of epigeic earthworms with that of the two other functional groups: anecics and endogeics, whose behaviours have been previously measured through similar experiments (Caro et al., 2013). We expected high specificity in epigeic dispersal behaviours because of their species-related selective pressures.

2. Methods

2.1. Subjects and housing

Free-living adult earthworms from three epigeic species – *Eisenia fetida*, *Eisenia andrei* and *Lumbricus rubellus* - were collected in November 2015 from several rural locations in Ile-de France, near Paris, France (between 48°69′N, 2°60′E and 48°74′N, 2°68′E). Earthworms were kept in acclimatizing mesocosms (12 cm × 10 cm x 8 cm) filled with suitable soil (see 2.2 Diffusion and dispersal mesocosm set-up) with a density of 10 earthworms per mesocosm, at a constant 17 °C. Before the start of the trials (section 2.3) earthworms were acclimatized for a period of at least 3 weeks, depending on their capture date and the trial dates, to remove potential stress effects of capture. Acclimatizing mesocosms were humidified and enriched with homogenized horse dropping twice a month. The species names used herein conformed to the Fauna Europaea web site.

2.2. Diffusion and dispersal mesocosm set-up

First, we investigated diffusion in a homogeneous environment (experiment 1). Then, two different environmental factors were tested on epigeic earthworm dispersal: population density (experiment 2) and habitat quality (experiment 3). The experiments' setting followed the protocol used by Caro et al. (2013). Diffusion behaviour in a homogeneous environment was tested in mesocosms (300 cm × 20 cm x 20 cm) that consisted of a suitable habitat. The suitable habitat consisted of grassland soil collected from a brunisol at the IRD research centre (48°54′N, 2°29′E), which hosts large earthworm populations. Because epigeic earthworms mainly inhabit litter, lime leaves (*Tilia vulgaris*) were added on the surface of the suitable soil. This litter is generally well consumed by earthworms (Hendriksen, 1990). This first experiment tested the natural spread of individuals while removing the effect of