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1 Is earthworms' dispersal facilitated by the ecosystem engineering activities of conspecifics?

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Summary

In this work we documented the influence of earthworm's galleries on their speed of movements during dispersal events in the soil. We quantified, by using X-rays, the dispersal behaviour of earthworms in the soil. The observations were conducted in mesocosms in controlled conditions during 12 hours. Our experiments revealed that during a dispersal sequence of a batch of individuals of the species *Aporrectodea terrestris* (Savigny 1826): i) individuals used preferentially existing conspecifics galleries, ii) individual velocity increased after each dispersal event, and iii) the lag time before each dispersal event did not seem to be influenced by previous dispersers. Therefore, dispersal seems to be facilitated by conspecifics' activity, which strongly supports the hypothesis of a feedback between ecosystem engineers' activity and their dispersal speed.

Keywords: Cineradiography; X-ray Imagery; Conspecific facilitation; Dispersal behaviour; Earthworms activity; Ecosystem engineering.

Introduction

Earthworms have a profound influence on soil physical and chemical properties (Zhang and Schrader 1993; Blanchart et al. 1999). Consequently, they play a central role in soil functioning and in plant growth (Lee 1985; Edwards and Bohlen 1996; Scheu 2003). Their impacts on soil functioning and soil biota through the engineering of their physical environment have been the subject of a large number of studies. In contrast, there is little information available on the consequences of the potential feedback of these activities on their own life condition, although this is expected to play an important role in earthworm ecology and activity (Odling-Smee 1995; Mathieu et al. 2010). We now need to grasp these feedbacks in order to understand the driving factors of earthworm activity and spatial distribution. Here, we propose to explore the potential feedback between the construction of galleries and the dispersal speed of earthworms in the soil.

Dispersal is a central ecological process that allows both the colonization of new habitats and the exploitation of spatially and temporally variable resources (Ronce 2007). Active dispersal of animals (opposed to passive dispersal, where individuals are transported by an external agent) involves three successive behavioural stages: departure from a breeding site, crossing to a new place, and settlement (Clobert et al. 2001; 2009). A recurrent finding of evolutionary models is that dispersal rate depends on the balance between the costs and benefits of dispersal (Bowler and Benton 2005), which are strongly determined by environmental factors (e.g. habitat quality, habitat fragmentation, patch size, density, predation) and individual life traits (e.g. age, hormonal levels, (Bonte et al. 2006; Schtickzelle et al. 2006)). In consequence, strategies that reduce these costs, such as the capacity to use cues based on conspecifics and/or environmental conditions were selected over evolutionary times in many groups (Clobert et al. 2009). Such use of cues is not known in earthworms, but

previous studies suggest it might exist (Mathieu et al. 2010; Zirbes et al. 2010; 2012). It was noticed that the products of engineering activities, such as burrows, might be used as cues by earthworms to evaluate the state of the environment.

Based on these results, the existence of a feedback between earthworm activities and their dispersal behaviour was questioned. For instance, Mathieu et al (2010) showed that earthworm dispersal rate, during the departure stage, could be reduced when individuals were inoculated in a soil that was pre-used by conspecific individuals - which were no longer present - showing that earthworms can detect the former activity of conspecifics. Other studies showed that anecic earthworms use the galleries of conspecific individuals or of other species, but not specifically for dispersal (Capowiez 2000; Bastardie et al. 2003). These observations raise the question of the influence of earthworm activities on the speed of their movement during the second stage of dispersal (crossing stage).

In this work we specifically investigated the potential feedback between earthworms' activities and their dispersal rate by addressing three questions: i) do individuals use preferentially pre-existing conspecific galleries to disperse? ii) does dispersal velocity increase in a soil where conspecific already dispersed? and iii) is dispersal triggered by the departure of previous dispersers (like in a collective movement)? To answer these questions we developed a new technique based on X-rays imagery that allows to take pictures of earthworms in the soil, and to quantify their behaviour.

Materials and methods

We used the species *Aporrectodea terrestris* (Savigny 1826), more commonly called *Aporrectodea giardi* (Ribaucourt 1901), an anecic species (size: 130-170mm; mean weight: 3.3 ± 0.9 g), which lives in the soil and feeds on surface litter (Bouché 1972, 1977). Adult earthworms were collected in North of France (49°27'N, 1°4'E) and were kept in suitable soil (see below) at low density (1.5 individuals per litre of soil), at 15°C during the day and 10°C at night. All earthworms were used once and were adult during the experiments. To overcome the problem of transparency of worms to X-rays and to have an accurate tracking point, we tagged individuals subcutaneously with a rod of lead of 2mm. Tags do not affect the growth of earthworms (Butt and Lowe 2007). Preliminary tests comparing dispersal behaviour between tagged and control individuals (not tagged) showed no effect on dispersal response (unpublished data).

Two types of soil were used for the experiments: an unsuitable and a suitable soil. The unsuitable soil consisted in a very sandy soil with low pH (Table 1) collected in an area deprived of earthworms in the forest of Fontainebleau, France (48°24'N, 2°44'E). The suitable soil (Table 1) contained more organic matter and clay than the unsuitable soil and was sampled in a grassland of the IRD research centre of Bondy, France (48°54'E, 2°29'N). Both soils were air dried, sieved at 2mm and rewetted manually to 25% of humidity (on a massic basis). The preference of earthworms for the suitable compared to the unsuitable soil was tested in a previous experiment (Mathieu et al. 2010).

The experiments were conducted in mesocosms following the procedure developed in Mathieu et al. (2010). Mesocosms consisted of dispersal corridor of 100 cm long, 20 cm wide and 20 cm height. They were composed of three equal parts (Figure 1): (1) the inoculation section, which was filled with unsuitable soil; (2) the intermediate “crossing section”,

composed of unsuitable soil, (3) the arrival section composed of suitable soil. All soils were disposed at density of $1 \pm 0.1 \text{ g.cm}^{-3}$. This setup triggered dispersal as individuals tend to disperse from habitats of low quality (Mathieu et al. 2010). It allows reproducing the three stages of dispersal: departure, crossing and settlement in a suitable site (Clobert et al. 2009). Earthworms were filmed in the crossing section, which was thinned by 40% to allow earthworms detection by X-rays. Each experimental unit was closed over by a tarp, to keep humidity and to prevent worms to escape. The experiment was replicated 5 times with different experimental units and different individuals each day.

In each replicate, 10 individuals were inoculated at the same time in the inoculation section (Figure 1). In order to prevent any contact between individuals during the inoculation, we ensured that each individual was inoculated at a sufficient distance from the others (10 different locations distant from at least 5cm from each others), and we checked that all individuals entered in the ground (on average, five minutes).

The X-ray filming device was composed of a video fluoroscopy machine (Philips Diagnostic C generator with a Basler A 504 K with digital video camera recorder), which could not moved. The X-rays were generated at 1.6 mA and 54.0 kV, which allowed seeing the worms in the soil within a 20 cm radius. After inoculation of the 10 earthworms, snapshots of the first 20 cm (in length) of the crossing section were taken (Figure 1) every minute during 12 hours. Dispersal events occurred without any artificial stimulation, which could have disturbed the dispersal behaviour of earthworms. In consequence we observed at most 3 passages in each replicate.

The X-rays filming device allowed us to take pictures of earthworms and their galleries in the soil, and to measure their dispersal velocity as well as the lag time between subsequent passages of individuals within replicates. For each individual, we determined the entrance and exit time in the observed section (approximately 315 cm²), which was centered on the crossing section. The velocity (V) was determined by the ratio between the travelled distance and the time required to travel over the corresponding distance. The difference of time between the moment where a worm left the observed section and the moment the next conspecific entered was used to calculate the lag time between two crossing events. The ratio V_{n+1}/V_n between the velocity during the passage n+1 and during the passage n was used to quantify the relative change in the dispersal velocity. We evaluated the link between the different components of dispersal behaviour (movement speed and lag time between dispersal events) and the order of passage or to the presence/absence of gallery with a linear regression model. All analyses and graphs were performed with the software R (Ihaka and Gentleman 1996).

Results and discussion

Despite the low number of dispersal events, we can clearly see that after the first crossing event, a majority (84% in the second dispersal event and 100% in the third) of the new dispersers used a gallery already built, rather than burrowing a new one. One individual started a new gallery but ended up in an existing gallery.

Our results showed a striking increase of dispersal velocity due to previous earthworm's activities. We observed a significant increase of dispersal velocity along the sequence of dispersal events (linear regression $r^2=0.58$, $p\text{-value}=0.002$, Figure 2): during the

gallery construction phase (see the attached accelerated video file about gallery construction), the average velocity was $0.6 \pm 0.3 \text{ cm} \cdot \text{min}^{-1}$, which was the lowest speed observed. This result can be related to the low colonization rate of non-inhabited or previously tilled plots usually observed in the field (Butt et al. 1995; Nuutinen et al. 1997; 2006; Grigoropoulou and Butt 2010; Eijsackers 2011). Our observations of dispersal velocity are well above observations made in earthworm-free soils (Eijsackers 2011), reporting colonization rate of $5\text{-}8 \text{ m} \cdot \text{year}^{-1}$ for *Aporrectodea longa* and $1.5\text{-}4 \text{ m} \cdot \text{year}^{-1}$ for *Lumbricus terrestris*. however comparison between our results in experimental device to these field observations must be done with caution due to the differences in environmental conditions (spatial and temporal heterogeneity, weather, interspecific interactions), in scale (1 m versus a few km) and in the length of observation (12 hours versus years). However, our results provide new insights in the understanding of dispersal mechanisms of earthworms. Indeed, our observations supply evidences of the capabilities of earthworms to move faster than expected from field observations.

Average velocity of second dispersal events was three times faster ($1.8 \pm 0.7 \text{ cm} \cdot \text{min}^{-1}$) than during the first one. This result can be explained by the fact that moving in existing galleries requires much less efforts than moving in a pristine soil, as no burrowing work is required (Ehlers 1975; Edwards and Lofty 1980; Hirth et al. 1997). During the third passage, earthworms exclusively used existing galleries, and the average velocity was then even higher ($4.5 \pm 2.8 \text{ cm} \cdot \text{min}^{-1}$), than during the first and second dispersal events. This can hardly be explained by a decrease of burrowing costs, because they are low during the second and third dispersal events. This suggests that the observed increase in dispersal velocity along dispersal sequence should be triggered by another mechanism. Non-selective detection of conspecific activity, like detection of empty spaces in the soil, would result only in the preferred use of

conspecifics' galleries. It cannot explain the increase in speed between the second and third dispersal events. The most parsimonious explanation for this increase in speed is the retrieving of cues related to conspecifics' activity or presence, such as chemical cue (Schmidt Jr 1955; Ressler et al. 1968; Jiang et al. 1990). These cues could be non specific by-products of earthworms' transit in the galleries (like urea, faeces or the results of the interaction between mucus, microflora and soil on the walls of the galleries (Pan et al. 2010) or less likely, could be specific molecules like pheromones, like in ants (Dorigo et al. 1996).

The lag time between two consecutive passages was apparently not influenced by the presence of galleries or the number of previous departures (p-value = 0.5, Linear Model). Therefore it seems that dispersal was not induced by the existence of galleries or by social interactions during the departure of conspecifics, in contrast to previous observations (Zirbes et al. 2010).

Conclusion

Our results show that earthworm dispersal movements are much faster in areas previously engineered (i.e. burrowed) by conspecifics. Individuals selectively follow existing galleries rather than building new galleries, raising the question of the mechanisms involved in the localization of the galleries. This shows that earthworms' dispersal in soil is facilitated by their own activity, highlighting the existence of a feedback between engineering activities and dispersal velocity. It would be interesting to determine if this feedback is accidental (not specific, like autogenic engineers (Jones et al. 1994; Jouquet et al. 2006) or intended. Finally, our findings ask the question about the potential role of dispersal facilitation in community dynamic of earthworms, and the influences of this facilitation between different earthworm

species or ecological categories, especially regarding colonization pattern of new habitats (Uvarov 2009; Eijssackers 2011).

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323 Table

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325 Table 1: Selected properties of the used soils in the experiments.

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Soil Properties (Unit)	Unsuitable	
	Soil	Suitable Soil
Clay (%)	4.7	15.7
Silt (%)	18.5	13.4
Sand (%)	76.8	70.9
Organic C (g kg ⁻¹)	8.5	28.1
Total N (g kg ⁻¹)	0.33	2.61
C:N	25.8	10.8
Organic Matter (g kg ⁻¹)	14.6	48.6
pH	3.8	7.5
CEC (Metson) (cmol kg ⁻¹)	2.9	11.7

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Figure captions

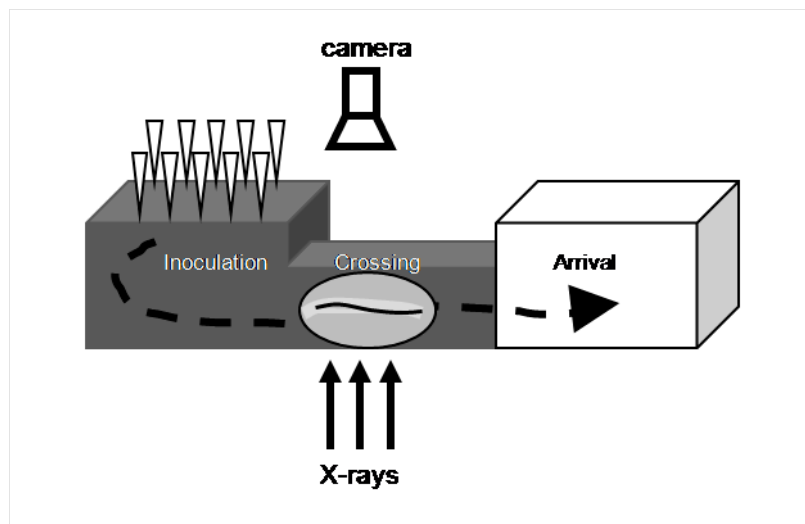
Figure 1: Experimental design of the study (100 cm long; 20 cm wide; 20 cm height, 8cm height for the thinned section); Grey area = unsuitable soil; White area = suitable soil. The clearest circle represents the observed area. Each triangle represents an inoculation point, where a single earthworm was introduced. Arrows represent the section observed by X-rays, which have been captured by a camera. A dashed arrow symbolizes the direction of movement.

Figure 2: Individuals' dispersal velocity ($\text{cm} \cdot \text{min}^{-1}$) according to their rank of passage during the dispersal sequence. A line links earthworms belonging to the same mesocosm. The dashed line represents the linear regression.

362 Figures

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364 Figure 1



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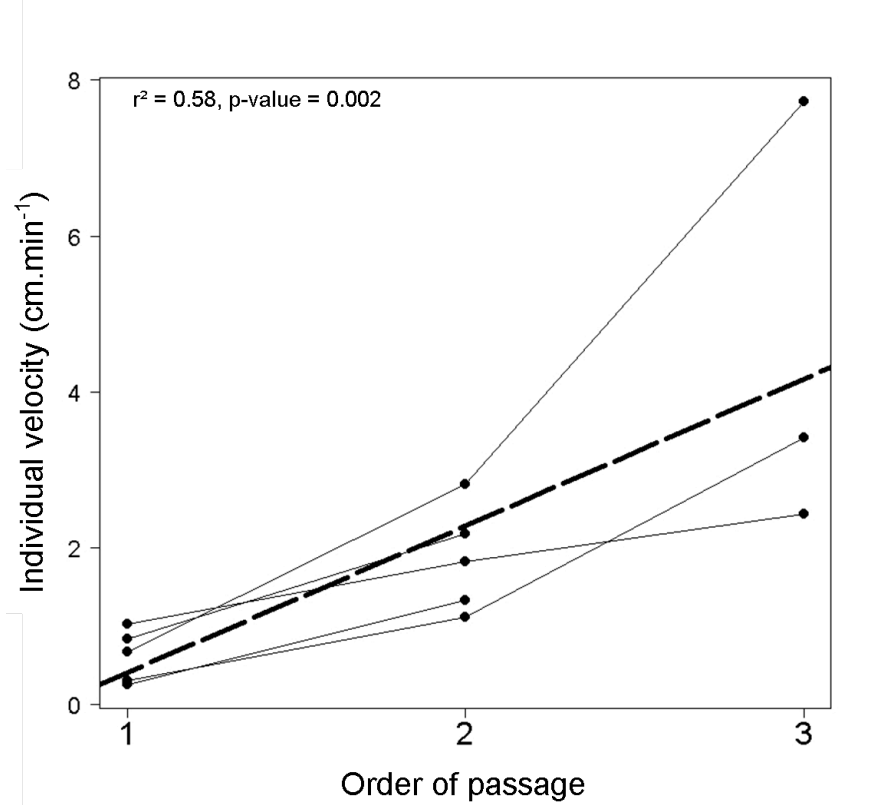
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381 Figure 2



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