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

2

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23 Summary

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

35

36

37

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

40

41 Introduction

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

53

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

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

69

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

79

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

87

88 Materials and methods

89

90 We used the species *Aporrectodea terrestris* (Savigny 1826), more commonly called
91 *Aporrectodea giardi* (Ribaucourt 1901), an anecic species (size: 130-170mm; mean weight:
92 3.3 ± 0.9 g), which lives in the soil and feeds on surface litter (Bouché 1972, 1977). Adult
93 earthworms were collected in North of France (49°27'N, 1°4'E) and were kept in suitable soil
94 (see below) at low density (1.5 individuals per litre of soil), at 15°C during the day and 10°C
95 at night. All earthworms were used once and were adult during the experiments. To overcome
96 the problem of transparency of worms to X-rays and to have an accurate tracking point, we
97 tagged individuals subcutaneously with a rod of lead of 2mm. Tags do not affect the growth
98 of earthworms (Butt and Lowe 2007). Preliminary tests comparing dispersal behaviour
99 between tagged and control individuals (not tagged) showed no effect on dispersal response
100 (unpublished data).

101

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

110

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

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

123

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

129

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

138

139

140

141 The X-rays filming device allowed us to take pictures of earthworms and their
142 galleries in the soil, and to measure their dispersal velocity as well as the lag time between
143 subsequent passages of individuals within replicates. For each individual, we determined the
144 entrance and exit time in the observed section (approximately 315 cm²), which was centered
145 on the crossing section. The velocity (V) was determined by the ratio between the travelled
146 distance and the time required to travel over the corresponding distance. The difference of
147 time between the moment where a worm left the observed section and the moment the next
148 conspecific entered was used to calculate the lag time between two crossing events. The ratio
149 V_{n+1}/V_n between the velocity during the passage n+1 and during the passage n was used to
150 quantify the relative change in the dispersal velocity. We evaluated the link between the
151 different components of dispersal behaviour (movement speed and lag time between dispersal
152 events) and the order of passage or to the presence/absence of gallery with a linear regression
153 model. All analyses and graphs were performed with the software R (Ihaka and Gentleman
154 1996).

155

156 Results and discussion

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

161

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

165 gallery construction phase (see the attached accelerated video file about gallery construction),
166 the average velocity was $0.6 \pm 0.3 \text{ cm} \cdot \text{min}^{-1}$, which was the lowest speed observed. This result
167 can be related to the low colonization rate of non-inhabited or previously tilled plots usually
168 observed in the field (Butt et al. 1995; Nuutinen et al. 1997; 2006; Grigoropoulou and Butt
169 2010; Eijsackers 2011). Our observations of dispersal velocity are well above observations
170 made in earthworm-free soils (Eijsackers 2011), reporting colonization rate of $5\text{-}8 \text{ m} \cdot \text{year}^{-1}$ for
171 *Aporrectodea longa* and $1.5\text{-}4 \text{ m} \cdot \text{year}^{-1}$ for *Lumbricus terrestris*. however comparison
172 between our results in experimental device to these field observations must be done with
173 caution due to the differences in environmental conditions (spatial and temporal
174 heterogeneity, weather, interspecific interactions), in scale (1 m versus a few km) and in the
175 length of observation (12 hours versus years). However, our results provide new insights in
176 the understanding of dispersal mechanisms of earthworms. Indeed, our observations supply
177 evidences of the capabilities of earthworms to move faster than expected from field
178 observations.

179

180 Average velocity of second dispersal events was three times faster ($1.8 \pm 0.7 \text{ cm} \cdot \text{min}^{-1}$)
181 than during the first one. This result can be explained by the fact that moving in existing
182 galleries requires much less efforts than moving in a pristine soil, as no burrowing work is
183 required (Ehlers 1975; Edwards and Lofty 1980; Hirth et al. 1997). During the third passage,
184 earthworms exclusively used existing galleries, and the average velocity was then even higher
185 ($4.5 \pm 2.8 \text{ cm} \cdot \text{min}^{-1}$), than during the first and second dispersal events. This can hardly be
186 explained by a decrease of burrowing costs, because they are low during the second and third
187 dispersal events. This suggests that the observed increase in dispersal velocity along dispersal
188 sequence should be triggered by another mechanism. Non-selective detection of conspecific
189 activity, like detection of empty spaces in the soil, would result only in the preferred use of

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

197

198 The lag time between two consecutive passages was apparently not influenced by the
199 presence of galleries or the number of previous departures (p-value = 0.5, Linear Model).

200 Therefore it seems that dispersal was not induced by the existence of galleries or by social
201 interactions during the departure of conspecifics, in contrast to previous observations
202 (Zirbes et al. 2010).

203

204 Conclusion

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

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

216

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323 Table

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

326

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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337 Figure captions

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

345

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

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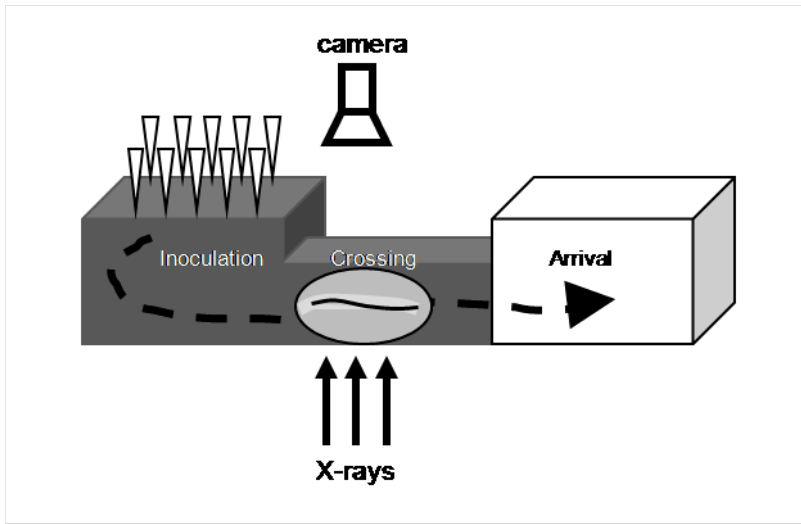
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362 Figures

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364 Figure 1



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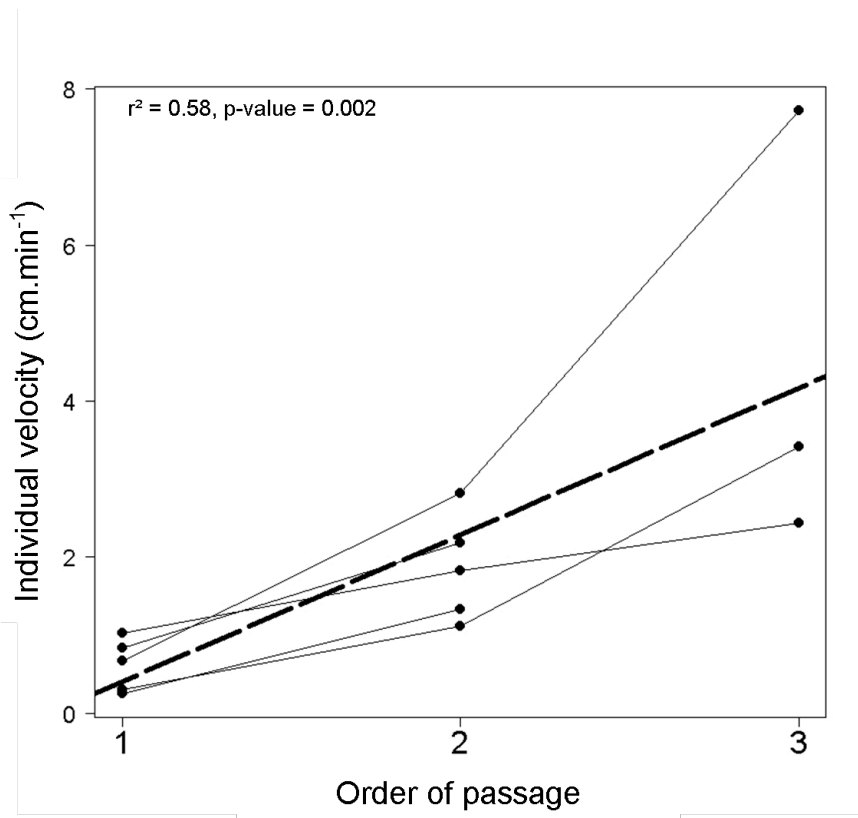
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381 Figure 2



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