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# Impact of soil engineering by two contrasting species of earthworms on their dispersal rates



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#### ABSTRACT

By burrowing galleries and producing casts, earthworms are constantly changing the structure and properties of the soils in which they are living. These changes modify the costs and benefits for earthworms to stay in the environment they modify. In this paper, we measured experimentally how dispersal behaviour of endogeic and anecic earthworms responds to the cumulative changes they made in soil characteristics. The influence of earthworm activities on dispersal was studied in standardised mesocosms by comparing the influence of soils modified or not modified by earthworm activities on earthworm dispersal rates.

The cumulative use of the soil by the earthworms strongly modified soil physical properties. The height of the soil decreased over time and the amount of aggregates smaller than 2 mm decreased in contrast to aggregates larger than 5 mm that increased. We found that: (i) earthworm activities significantly modified soil physical properties (such as bulk density, soil strength and soil aggregation) and decreased significantly the dispersal rates of the endogeic species, whatever the species that modified the soil; (ii) the decreasing in the dispersal proportion of the endogeic species suggests that the cost of engineering activities may be higher than the one of dispersal; (iii) the dispersal of the anecic species appeared to be not influenced by its own activities (intra-specific influences) or by the activities of the endogeic species (inter-specific influences). Overall these results suggest that the endogeic species is involved in a process of niche construction, which evolved jointly with its dispersal strategy.

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# 1. Introduction

Active dispersal of animals is a central ecological process that allows habitat colonization and the exploitation of resources that vary in time and space (Ronce, 2007). It is therefore regarded as a key process that determines species distribution from the local to the biogeographical scale (Hengeveld and Hemerik, 2002; Eijsackers, 2010, 2011; Mathieu and Davies, 2014). As a consequence, the study of dispersal has become a major field of research in ecology (Nathan, 2003). As of the direct relationship between dispersal behaviour and fitness, a wealth of literature has focused on the evolution and

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consequences of dispersal capacities. A central issue is the need to determine the conditions that induce dispersal (Matthysen, 2012). Dispersal behaviour involves the departure from a breeding site, moving to a new place, and settlement, and can occur at any life stage, at any spatial scales above the individual range and within more or less heterogeneous landscapes (Clobert et al., 2009). A recurrent finding of evolutionary models is that dispersal rates are mainly determined by a balance between dispersal costs and benefits (Bowler and Benton, 2005) that depend on environmental factors (e.g. habitat quality, habitat fragmentation, patch size, density, predation) (Bonte et al., 2012). We can therefore hypothesise that organisms that modify their physical and chemical environment through their activities, the so-called ecosystem engineers (Jones et al., 1994), modify the costs and benefits of their own dispersal. Through the modifications they impose to their environment they could therefore modify their own dispersal rates.

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If engineers improve the quality of their environment, we can expect that they should benefit from reducing their dispersal rates from patches they have engineered (i.e. they stay longer in engineered habitat). This would constitute a positive feedback (Mathieu et al., 2010). Conversely, if engineers decrease the quality of their environment they should benefit from increasing their dispersal rates from these patches (Caro et al., 2013a). This would constitute a negative feedback. Therefore, documenting the impact of habitat changes imposed by engineers on their own dispersal rates should help showing whether there is a negative or positive feedback between the engineer and its habitat, and it should give simultaneously key information on the dynamics of both engineer population and its habitat.

Feedback between organisms and their environment has been studied in plants (Kulmatiski et al., 2008), where they have been shown to be influential for plant demography and spatial distribution, species successions and coexistence patterns (Barot and Gignoux, 2004). Some models also confirm that feedback between ecosystem engineers and their environment may affect their demography and distribution and that this feedback is affected by the mobility of the engineers (Barot et al., 2007; Raynaud et al., 2013). Here we tested if earthworm active dispersal may be influenced by earthworm-mediated engineering activities. Such a mechanism has been, to our knowledge, poorly studied and is likely to affect the strength of the feedback between the engineer and its environment and to influence its spatial distribution.

Earthworms are considered as key ecosystem engineers in the soil system (Lavelle et al., 2006). It has been shown that dispersal rates of Aporrectodea icterica can be reduced by the activities of conspecifics, whereas its dispersal rates increase with conspecific densities, as other earthworm species (Mathieu et al., 2010; Caro et al., 2013a). These apparently contradictory results suggest the existence of complex feedbacks between soil quality, engineering activities, and dispersal. In the field, communities of earthworms can indirectly interact through modifications of their common habitat, i.e. the soil. It is therefore necessary to evaluate the influence of interspecific interactions through earthworm activities on their dispersal rates. Earthworms often have patchy distributions (Richard et al., 2012). Such distributions are characterized by high earthworm densities in some patches, which consequently locally increases intensity of soil use by earthworms. According to our rationale and previous observations (Mathieu et al., 2010; Caro et al., 2013a), dispersal rates of earthworms should be impacted by the high density in these patches. Testing for such an effect and determining its influences is necessary to understand and predict earthworm dynamics and their spatial distribution.

To tackle the issue of the impact of habitat use by soil earthworms on their own dispersal, an experiment was established to determine how earthworm intra- and inter-specific activities affect soil properties and in turn dispersal rates. We characterized the soil physical, chemical and biological changes induced by the activities of two earthworm species, *Aporrectodea giardi* and *A. icterica* (Bouché, 1972, 1977). In the rest of the paper, we refer to earthworm activities as engineering activities. Further, we investigate how these changes influence the dispersal behaviour of each species.

# 2. Materials and methods

#### 2.1. Earthworms

To observe the dispersal behaviour of an earthworm species in response to (i) its own activity or (ii) to the activity of another species, we used two species that co-exist in natural conditions:

A. giardi (Ribaucourt 1901) and A. icterica (Savigny 1826). These two species differ by their size and feeding behaviour. A. giardi is the largest one with a length ranging 130–170 mm and a weight of  $3.3 \pm 0.9$  g; it is an anecic species, i.e. feeding on surface litter. A. icterica is approximately to folds smaller with 70–90 mm length and three folds lighter with a weight of  $1.2 \pm 0.25$  g; moreover it is an endogeic species feeding on organo-mineral soil. Adults of both species were sampled in grasslands in the centre of France (48.6167 N, 1.6833 E). They were reared in a pasture soil maintained at 15 °C during the day and 10 °C at night, we used horse dung to feed them. For the experiment, each individual was used only once.

# 2.2. Soils

We used two different soil types (Mathieu et al., 2010; Caro et al., 2013a): (1) a sandy soil collected in the forest of Fontainebleau (48.413287 N, 2.748245 E) that represented an "unsuitable" habitat for earthworms as it contained no earthworm in field conditions in relation with adverse physical and chemical characteristics (pH 3.8, organic carbon content = 0.85% and C:N ratio = 25.8); (2) a loamy soil collected in a grassland (48.91431 N, 2.484806 E) that represented a "suitable" habitat as it contained both species in natural conditions in relation with favourable soil characteristics (pH 7.5, organic carbon content = 3.91% and C:N ratio = 17). More information on these soils can be found in (Mathieu et al., 2010; Caro et al., 2013a). We collected 800 kg of the unsuitable and 1600 kg of the suitable soils both were air-dried for 4 days. The total 2.4 t of soil was sieved at 2 mm and this fine soil was rewetted to 0.25 g water  $g^{-1}$  dry soil.

#### 2.3. Experimental design

The experiment had two main steps: firstly the fine soil was first engineered by one of the two species; secondly we observed the effect of the engineered soil on the dispersal rates of the both species.

# 2.3.1. Soil engineering by the earthworms (step 1.1)

Only the suitable soil was used. It was put in 5L containers (33 cm long, 15 cm wide and 10 cm high) with an initial bulk density of  $1 \text{ g/cm}^3$ ; horse dung was uniformly added at the surface (150  $\pm$  1 g in each container). A total of 180 containers were prepared (Fig. 1, step 1):

- *N*=20 containers used at T0 (10 for each earthworm species);
- 160 containers at the other durations; i.e. 40 containers used at each of the 4 durations (1, 2, 4 and 6 weeks): N=10 being inoculated with A. giardi, N=10 inoculated with A. icterica and N=20 without worms used as controls.

The layout of the 180 containers was spatially randomized. In the inoculated containers, we introduced 30 adult individuals, i.e. 6 individuals  $L^{-1}$ . This earthworm densities used may be high in comparison to field conditions, however such densities where required for the soil to be significantly engineered within a short time. In the field, earthworms may engineer the soil for months but, for practical reasons, such duration was not possible for the pre-experiment.

# 2.3.2. Removing earthworms (step 1.2)

At the end of the engineering period, we weighted the mass of the remaining dung. Then, earthworms were removed without disturbing the soil physical structure and without altering earthworm health: the plastic containers were dived in a hot water bath ( $60 \,^{\circ}$ C). While the soil temperature was slowly increasing, the earthworms came at the surface and were caught manually and weighed individually. The controls containers were similarly dived in the hot

water bath. After all earthworms were caught, soil height in the container was measured to calculate the new soil bulk density and we measured the mechanical resistance to penetration (see below). Finally, the soil material was translocated to the mesocosms without disturbing its physical structure.

# 2.3.3. Setting up dispersal mesocoms (step 2.1)

The mesocosms consisted in a dispersal corridor (100 cm long, 15 cm wide and 10 cm high), divided in three equal sections (Fig. 1, step 2): (1) the "inoculation section" filled with the soil engineered by the earthworms for various durations; (2) the "crossing section" composed of unsuitable soil; (3) the "arrival section" composed of suitable soil sieved at 2 mm. The crossing section was determinant because it represented a physical barrier that generated dispersal costs, and thus allowed only active dispersal and avoided diffusion (i.e. random movements with possible returns to the starting point) (Caro et al., 2012).

We added 10 earthworms in the inoculation section containing the engineered or the control soil (Fig. 1, step 2). We made four combinations to test intra-and inter-specific influences:

- intra specific influences: *A. icterica* individuals in the soil engineered by *A. icterica* (II) and *A. giardi* in the soil engineered by *A. giardi* (GG).
- inter specific influences: *A. giardi* in the soil engineered by *A. icterica* (GI) and *A. icterica* in the soil engineered by *A. giardi* (IG) (Fig. 1).

For each treatment, we made N = 5 replicates and N = 5 controls.

#### 2.3.4. Measurement of the dispersal rate (step 2.2)

After seven days, each of the three sections was physically isolated from the others, and in each section the earthworms were counted and weighed individually and the dispersal rate (% disp.) was calculated as the proportion of individuals that reached the arrival section. We measured the physical and chemical characteristics of the soil from the inoculation section.

# 2.4. Measurements of soil physical and chemical properties

Bulk density was calculated as the weight of the soil in the container divided by its volume. Soil strength was quantified with a penetrometer consisting of a 3 mm rod mounted on a mobile base and connected to a pressure sensor. The rod was pushed into the soil with a constant velocity  $(0.067 \text{ mm s}^{-1})$ ; the penetration resistance was measured at regular intervals (0.1 mm) for the entire soil height. In each container, an average resistance profile was calculated by transect of 5 replicates along each container. The slope of the linear regression between penetration resistance and depth was considered as the soil strength (Rc). We measured the aggregate size distribution by passing an aliquot of 1 kg of air-dried soil through a set of sieves (10, 5 and 2 mm mesh sizes). The soil remaining on each sieve was weighed to obtain the proportions of aggregates >10 mm, 10-5 mm, 5-2 mm and <2 mm. Soil water content was calculated by estimating the mass loss observed after drying a 100 g aliquot of soil for 48 h at 105 °C.

pH was measured on a suspension of 10g of air-dried soil in 50 ml water (ISO 10390:2005). C and N contents were measured by dry combustion (ISO 10694:1995; ISO 13878:1998), P was quantified by the Olsen method (ISO 11263:1994).

# 2.5. Statistical analysis

We used ANOVA to analyse the effects of the earthworms on soil properties for most characteristics. For soil strength, an increase can result from increased bulk density or a change in soil structure due to engineering activity. Thus, we performed a Pearson correlation between the *Rc* values and soil height to determine whether soil strength was the result of earthworm



Fig. 1. Experimental design of the study. Step 1 corresponds to the engineering of the soil by earthworms; step 2 corresponds to the dispersal experiment per se.

activities or of a natural collapse with time. The absence of correlation indicated that soil strength resulted from earthworm activities.

To compare the dispersal rates across the engineering periods, we used a General Linear Model (GLM) with a binomial family. To determine which soil parameters significantly influenced earthworm dispersal rates, we performed a multiple linear regression between dispersal rates of both species and soil characteristics that were significantly affected by earthworm activity. With a stepwise procedure, the Akaike Information Criterion (AIC) was used to select the most relevant model (Burnham et al., 2011). Then we selected the variables that composed the model with the lowest AIC and analysed their influence on dispersal rates with non-linear regression, using the following equation:

$$D(X_i)_j = a_j \times \exp(-b_j \times X_i),$$

where:

- $D(X_i)_j$  represents the dispersal rate (%) of species j in response to the soil parameter X in the soil engineered by species i;
- a<sub>j</sub> represents the maximal dispersal rate (%) of species j in an un-engineered habitat;
- *b*<sub>j</sub> represents the influence of the soil parameter *X* engineered by species i on the dispersal rate of species j.

Note that i and j can represent the same species, so the approach allowed us to test both the intra- and inter-specific interactions mediated by earthworm activities. To quantify the influence of a soil parameter X on dispersal, we calculated the coefficient of determination between the dispersal rate and the soil parameter X. Then we assessed its significance by testing the differences between this coefficient of determination and a null model with random intercept only by using an ANOVA.

#### 3. Results

# 3.1. Soil properties

The activities of both species significantly affected the soil physical properties in the same way. Between TO and T6, bulk density

increased significantly by  $30.4\% \pm 14.7$  and by  $22.8\% \pm 6.6$  in presence of *A. giardi* and *A. icterica*, respectively (Fig. 3a). This increase was significantly higher with *A. giardi* than *A. icterica* during the first two weeks of the experiment, while no difference was observed for longer time periods (Fig. 3a).

Both species significantly increased the soil resistance over time. Over 6 weeks (T6), soil height was reduced by  $27\% \pm 12$  and by  $20\% \pm 7$  with *A. giardi* and *A. icterica* respectively (Fig. 2). Between T0 and T2, *A. giardi* compacted the soil more intensively than *A. icterica* (Fig. 3b) but after T4, a higher compaction was observed with *A. icterica* (Fig. 3b). Consequently, the *Rc* value reached a maximum of  $0.02 \pm 5.10^{-3}$ with *A. giardi*, whereas it increased steadily during the experiment with *A. icterica* (Fig. 3b). In the controls (without earthworms) and *A. giardi* treatments, soil penetration resistance was correlated to soil height (*p*-value < 0.01) contrarily to *A. icterica* (*p*-value > 0.05).

The both earthworm species consumed the horse dung at the soil surface. *A. giardi* (the anecic species) has consumed 100% of the horse dung after 2 weeks (T2) whereas *A. icterica* (the endogeic species) has consumed  $59\% \pm 6$  after 6 weeks (T6). It is noteworthy that a significant loss of weight was measured for *A. giardi*  $(-23\% \pm 3)$  after 4 weeks (T4), whereas no variation was observed for *A. icterica*. However, no relation between food consumption and weight loss, or soil properties or dispersal rates was found (*p*-value > 0.05).

Both earthworm species significantly influenced the soil aggregate size distribution (Fig. 3c and d). The proportion of 5–10 mm aggregates increased significantly by  $24\% \pm 3$  and by  $16\% \pm 3$  with *A. giardi* and *A. icterica* respectively (Fig. 3c). The proportions of aggregates <2 mm decreased significantly by  $30\% \pm 12$  and by  $19\% \pm 11$  with *A. giardi* and *A. icterica* respectively (Fig. 3d). No difference was observed for the 2–5 mm and >10 mm aggregate size classes. The earthworms did not affect the chemical properties that we measured (*p*-value > 0.05).

# 3.2. Dispersal rates

Soil engineering significantly decreased the dispersal rates of *A. icterica* when it did not influence the dispersal rate of *A. giardi* 



**Fig. 2.** Mean soil strength variation with soil height in the different treatments: (A) soil engineered by the anecic species (*Aporrectodea* giardi), (B) control for the anecic treatment, (C) soil engineered by the endogeic species (*Aporrectodea* icterica), (D) control for the endogeic treatment. Grey area = standard deviation.



**Fig. 3.** Dynamics of (A) bulk density, (B) *Rc* value, (C) proportion of 5–10 mm aggregates and (D) proportion of aggregates smaller than 2 mm, as affected by earthworm activities (mean  $\pm$  standard deviation, *N* = 10). Lines represent linear regression between soil properties and experimental duration; \* indicates significant difference between the treatments with the anecic (*Aporrectodea giardi*) and endogeic species (*Aporrectodea icterica*), at *p*-value < 0.05; \*\* indicates significant  $r^2$ .

(Fig. 4). Using the AIC criterion, we found a relation between dispersal rate and (i) soil penetration resistance (*Rc* value) and (II) the proportion of 5–10 mm aggregates. Dispersal rate for *A. icterica* decreased when individuals were inoculated in engineered soil (Figs. 5 and 6). In the "II" and "IG" treatments, dispersal rates were more strongly correlated to the proportion of 5–10 mm aggregates than to *Rc* ( $r^2 = -0.56$  and -0.42, respectively; Figs. 5 and 6). For *A. giardi's* dispersal rates, no relationship with soil physical properties was observed (Figs. 5 and 6) and no significant effect of chemical properties was observed.

# 4. Discussion

# 4.1. Earthworm activities influenced soil properties

Earthworms changed soil physical properties in a way that can be explained by burrowing and cast production (Lavelle et al., 2006; Capowiez et al., 2012). In the condition of the experiment, changes in soil structure solely due to physical processes, without earthworm activity, were insignificant (Fig. 3b and d). The earthworm activities impacted soil structure in a way that was



**Fig. 4.** Dispersal rates in response to the duration of the pre-experimental period of soil engineering by earthworms (*N*=5). The horizontal solid line represent the mean dispersal rate of all controls and the horizontal dashed lines represent standard deviation; \* indicates significant differences at *p*-value = 0.05 (GLM with binomial response) between the two juxtaposed barplots; lightly shaded barplots represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by *Aporrectodea icterica* and heavily shaded ones represent dispersal rate from a soil engineered by



**Fig. 5.** Correlations between earthworm dispersal rates and *Rc* values. Points = engineered treatment; cross = controls. Solid line = non linear regression by fitting *D*  $(X_i)_j = a_j \times \exp(-b_j \times X_j)$ . \*\*\* = significant difference between the fitted model and a null model using an ANOVA.

qualitatively and quantitatively similar to what was previously observed in the field (Blanchart et al., 1999; Frelich et al., 2006). In the engineered soil, the structural changes could thus be attributed to earthworm activities only, i.e. gallery burrowing and cast production. Despite the ecological differences between the two species (burrowing and feeding behaviours), some similarities were observed in the structural changes due to their activities: (i) a decrease in the total pore volume; (ii) a global soil compaction and; (iii) an increase in the proportion of large aggregates associated to a decrease in the proportion of small aggregates. The large aggregates were most probably resulting from the association of the smaller ones in the wall of the galleries and in the casts. Despite these similarities, an important difference can be observed in the mechanical resistance: the increase in soil resistance induced by *A. icterica* was almost twice more important than the one induced by *A. giardi* (Fig. 3b).

The absence of effect on soil chemical properties may be due to the short duration of our experiment, as also observed for carbon and nitrogen contents for periods greater than several months by Pashanasi et al. (1996) and Edwards (2004). The dung consumption



**Fig. 6.** Earthworm dispersal rates in response to the proportion of 5–10 mm aggregates. Points = engineered treatment; cross = controls. Solid line = non linear regression by fitting  $D(X_i)_j = a_j \times \exp(-b_j \times X_j)$ . \*\*\* = significant difference between the fitted model and a null model using an ANOVA.

resulted in the incorporation of dung in the soil. The absence of effect on soil properties and on dispersal rate suggests that in our case the incorporation of dung did not influence soil properties and earthworms dispersal. Nevertheless, it is possible that in the field, at least in some cases, earthworm impact on litter decomposition and on the incorporation of litter into the soil profile influences earthworm dispersal (Mathieu et al., 2010).

# 4.2. Earthworm dispersal rates changed along the use of the soil by earthworms

Dispersal rate of the endogeic species decreased significantly with the proportion of 5-10 mm aggregates and soil strength. With 10 individuals, dispersal occurs at a low rate from the inoculation section fulfilled with control soil (the not engineered one, Caro et al., 2013a), so that changes in soil properties could lead to changes in the dispersal rate. Such an earthworm density is thus particularly suitable to test the impact of soil engineering on dispersal, which is precisely our goal. We did not observe an increase in dispersal rate when soil had been strongly used. This suggests a significant feedback between the way this species physically engineers the soil and the drivers of its own dispersal rate: by modifying the soil, individuals inhibits the environmental stimuli generating dispersal movements. The absence of stimuli triggering dispersal should increase the density of soil engineers and further increases soil engineering. This engineering, i.e. changes in soil aggregation, might increase the habitat quality for earthworms (cues, casts or galleries presence). Indeed, the structures existing in engineered soil (for instance, galleries) might facilitate movement of earthworms and so reduce dispersal costs (Caro et al., 2012).

In the case of the anecic species, we found no response to soil engineering, irrespective of the two species that engineered the soil. We previously observed that the combination of both intra-specific and soil engineering effects influences significantly *A. giardi* dispersal across the time (Caro et al., 2013b). Here, no stimulating effect of soil engineering by a high density of conspecific earthworms on the *A. giardi* dispersal rates was observed. The comparison between the both studies suggested that only the combination of direct intra-specific interactions and soil engineering may affect the dispersal of *A. giardi*.

# 4.3. Niche construction mechanism in endogeic species?

A decrease in dispersal rate in response to habitat engineering may suggest an increase in habitat quality: the earthworms stay in the soil they have engineered only if they benefit from soil engineering. Our observations suggest the existence of such a feedback for the endogeic species (see also Mathieu et al., 2010). Dispersal rate is assumed to depend on the balance between the cost of remaining in one habitat and that of moving to another (Bonte et al., 2012). The high dispersal rate observed for the endogeic species when soil was poorly engineered suggests that in this case the cost of engineering activities may be higher than the cost of dispersal. However, this balance seemed to be gradually reversed when soil was further engineered, suggesting the existence of a trade-off between activities leading to soil engineering and dispersal (Bonte et al., 2012).

The positive feedback we hypothesised between the endogenic earthworm and its activities of ecosystem engineer might indicate a process of niche construction (Lewontin, 1978; Odling-Smee, 1988; Odling-Smee et al., 2013): evolution might have selected in earthworm (1) activities that allow them to change soil characteristics in a beneficial way and (2) a shift in their habitat and feeding preferences towards the modifications they impose to soils. This should lead to ecological and evolutionary feedbacks that are likely to be very influential for the whole ecology of ecosystem engineers (life-history, behaviour) (Erwin, 2008) and for ecosystem and soil properties (Raynaud et al., 2013). Our results thus suggest that dispersal and stimuli that trigger dispersal have evolved in close relation with engineering activities: decreasing dispersal in engineered soil should increase local earthworm densities and thus increases soil engineering. Such feedback may influence the selection pressure for particular dispersal strategies, as observed here. Importantly, such feedback should play an important role for the present population dynamics of earthworms, their spatial distribution, soil characteristic and heterogeneity in soil characteristics (Barot et al., 2007; Cuddington et al., 2009).

In conclusion, it would be interesting to document feedbacks between soil engineering and dispersal for other species of soil engineers in order to assess quantitatively and qualitatively the influence of these feedbacks on soil functioning and heterogeneity. These experiments contribute to a new research area merging the fields of dispersal and the ecology of ecosystem engineers.

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