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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.

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 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 ± 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 ± 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 5 L containers (33 cm long, 15 cm wide and 10 cm high) with an initial bulk density of 1 g/cm^3; horse dung was uniformly added at the surface (150 ± 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 °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