Habitat quality, conspecific density, and habitat pre-use affect the dispersal behaviour of two earthworm species, *Aporrectodea icterica* and *Dendrobaena veneta*, in a mesocosm experiment

Jérôme Mathieu [a,*], Sébastien Barot [a], Manuel Blouin [b], Gael Caro [a], Thibaud Decaëns [c], Florence Dubs [a], Lise Dupont [b], Pascal Jouquet [d], Philippe Nai [a]

[a] UPMC Univ Paris 06 – IRD, UMR Bioemco, 32 av. H. Varagnat, 93143 Bondy, France
[b] Université Paris-Est, UMR Bioemco, 61 avenue du Général De Gaulle, 94010 Créteil cedex, France
[c] Laboratoire d'Ecologie, EA 1293 ECODIV, FED SCALE, UFR Sciences et Techniques, Université de Rouen, 76821 Mont Saint Aignan cedex, France
[d] IRD – IMWI, UMR Bioemco, SFRI, Dong Ngac, Tu Liem, Hanoï, Viet Nam

ARTICLE INFO

ABSTRACT

Dispersal capacity is a life-history trait that may have profound consequences for earthworm populations: it influences population dynamics, species persistence and distribution and community structure. It also determines the level of gene flow between populations and affects processes such as local adaptation, speciation and the evolution of life-history traits. It may play a great role in soil functioning by determining the spatial distribution of ecosystem engineers such as earthworms. Dispersal is an evolutionary outcome of the behaviour in response to the ecological constraints of the species. Hence different dispersal behaviour is expected from the different ecological types of earthworms. Nevertheless the dispersal behaviour of earthworms has been little documented.

In this work we test a series of basic mechanisms that are fundamental and complementary to understand earthworms dispersal behaviour. We focus on the dispersal triggered by environmental conditions, a fundamental process usually termed "conditional dependent dispersal". We show experimentally in mesocosms that in one week: 1) earthworm dispersal can be triggered by low habitat quality, either through soil quality or the presence/absence of litter. 2) Earthworms can be subject to positive density dependent dispersal, that is the rate of dispersal increases when density increases; and 3) earthworm dispersal can be reduced by the pre-use of the soil by conspecific individuals that are no longer present.

Our results suggest that earthworms may be more mobile than expected from previous estimations, and that they present high capacities of habitat selection. In the light of our findings we elaborate a behavioural scenario of earthworm foraging, and propose several priority working directions.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Dispersal is a central ecological process that has overwhelmingly important implications at multiple organization scales (Clobert et al., 2001). It directly affects the dynamics and persistence of populations, the distribution and abundance of species, the structure of natural communities and may influence ecosystem functioning through movements of keystone species and/or ecological engineers (Cuddington and Hastings, 2004). It is therefore a key parameter to explain species distribution from a local to

a biogeographical scale (Hengeveld and Hemerik, 2002). As a consequence, the study of dispersal has become a major field in ecology (Nathan, 2003). Because of the direct relationship between dispersal behaviour and fitness, a wealth of literature focused on the evolution and consequences of dispersal capacity, mainly in the framework of Optimal Foraging (Charnov, 1976), of the Ideal Free Distribution (Fretwell and Lucas, 1970; Krivan et al., 2008), of the Metapopulation Theory (Hanski and Gilpin, 1997), and of the Metacommunity theory (Holyolak et al., 2005). A central point that emerges in all these works is the necessity to determine the conditions that induce dispersal behaviours. They have been described for a large body of organisms, especially the easily sampled ones such as plants, birds, insects and fishes (Nathan, 2001). Some fundamental factors seem to operate on all organisms,

* Corresponding author. Tel.: +33 (0)1 48 02 59 65.
E-mail address: jerome.mathieu@snv.jussieu.fr (J. Mathieu).

such as habitat quality and population density. However it was also pointed out that specific dispersal mechanisms evolved among some taxa as products of particular ecological conditions. Consequently specific studies are required to understand properly the movements of any target taxonomical group.

Soil organisms face very specific ecological conditions compared to aboveground and aquatic organisms which have been the biological models for most dispersal studies (Nathan, 2001). They likely evolved original dispersal strategies due to the solidity, opacity and high spatio-temporal heterogeneity of the soil as well as the low energetic value of the soil organic matter they feed on. Despite these specificities, very few studies focused on underground soil fauna dispersal behaviour. For instance, although earthworms play a critical role in soil and ecosystem functioning (Lavelle and Spain, 2001), their dispersal behaviour still remain little investigated.

Studying earthworm dispersal would probably bring interesting new insights into the general framework of dispersal ecology. For instance, in a set of related species with contrasted ecology (such as endogeics, anecics and epigeics for earthworms), different dispersal behaviour is expected according to the ecological type of the species, but this point has not been addressed. In addition, it would provide basic information to improve field techniques of earthworm inoculation that aim to restore soils and increase crop production (e.g. Senapati et al., 1999). It would also help to explain the patterns of earthworms invasions in several regions (Tiunov et al., 2006). Finally, earthworms are potential dispersal vectors for parasites (Field and Michiels, 2006), plant and human pathogens (Toyota and Kimura, 1994; Williams et al., 2006), nematodes (Shapiro et al., 1995), ectomyccorhizal fungi (Reddell and Spain, 1991) and viable plant seeds (Decaëns et al., 2003). Therefore earthworm dispersal may have numerous consequences in agriculture and ecosystem functioning.

In this work we present the results of an experimental study that focused on three mechanisms that might lead to earthworm active dispersal. First we assessed whether habitat quality (soil properties or presence of litter on soil) may trigger earthworm dispersal. Many previous works on other organisms showed that low habitat quality generally induces active dispersal. Low resource availability, for instance, is known to increase intra-specific competition (Balkau and Feldman, 1973) of many groups. In a second step, we considered the role of earthworm density on their dispersal. Previous works showed that most terrestrial animals are prone to positive density dispersal (that is dispersal rate increases with increasing density, Matthysen, 2005). Nevertheless some species do not present this trend (Midtgaard, 1999; Bodasing et al., 2001) and some even show negative density dependence dispersal, i.e. a tendency to aggregate with conspecifics (Parrish and Edelstein-Keshet, 1999). These aspects have not been studied among earthworms, yet both kind of density dispersal may potentially occur among them. In a final experiment, we focused on the effects of the pre-use of the habitat by conspecifics. Among most organisms, former occupation of a habitat is generally considered to have negative consequences on an actual population because previous inhabitants may have consumed a significant part of the resources and may increase the new comers intra-specific competition (Charnov, 1976). However, as earthworms are ecosystem engineers (Jones et al., 1994), they may also modify the habitat in a way that will benefit new arrivals.

2. Materials and methods

Four separate experiments were carried out, each of them addressing a specific question related to dispersal mechanisms. Experimental units consisted of rectangular areas; 1 m long, 0.18 m

wide and 0.2 m high. The size of the mesocosms was estimated from data available (Edwards, 1998) and from preliminary experiments, so that they exceeded the estimated colonization rate in natural and artificial conditions for all species considered. Thus the mesocosms were large enough to give sufficient space for individuals, but also small enough, to make sure earthworms could cross the adverse section (see explanations below).

The experimental units were divided in three sections of identical dimensions (Fig. 1a): (1) An "inoculation section", where earthworms were systematically introduced. It was filled with "suitable" or "unsuitable" soil, depending on the experiment (see details below in specific sections); (2) An "adverse section" filled with the "unsuitable" soil; (3) A "target section" filled with the "suitable" soil. This disposition is classical in studies of dispersal (e.g. Boudjemadi et al., 1999). The adverse section is fundamental as it allows distinguishing dispersal behaviour (patch departure) from diffusion behaviour (random movements, Nathan et al., 2008). Indeed, the adverse section prevents earthworms reaching the target section by simple random movements. In the absence of this section, earthworms would diffuse in the mesocosms from the release section until finding the best location. This would constitute a case of diffusion and habitat selection, but not dispersal sensu stricto. In the presence of the adverse section, reaching the target section requires some kind of decision to leave the inoculation section and to cross an inhospitable one. Hence in this case the response depends on the dispersal behaviour of the earthworms, not
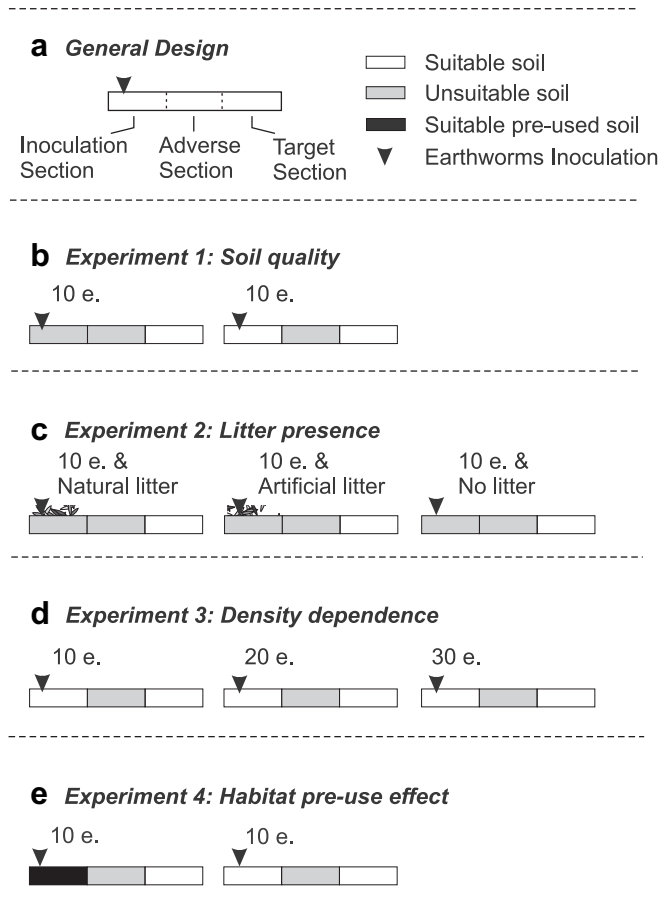

Fig. 1. Schematic representation of the experimental designs. The soil disposition in the mesocosms is symbolised by rectangles whose colours represent the nature of the soil substrate. The arrows indicate the section where earthworms (e.) were inoculated at the beginning of the experiments.

on the outcome of random movements. In consequence it is mandatory to separate the inoculation section from the target one by an adverse section. Inoculating the individuals in the middle of the mesocosms, without an adverse section, would give them equal access to the different soil types, and would constitute a case of pure habitat selection, with no dispersal process. In summary, the disposition with a release section and a target one separated by an adverse section is well adapted to properly test dispersal behaviour and to avoid confusion with diffusion and habitat selection.

The top of each experimental unit was covered by a nylon mesh for oxygenation and humidity conservation. Experiments were carried out in a glasshouse at the IRD Bondy centre, in France. Temperature was 18 °C during daylight and 15 °C during night, with 12 h of light per day and humidity was kept constant (soil humidity : 25% of dry weight). All experiments lasted one week and each treatment was replicated 6 times. We choose this period for two types of reasons. First, it appears to be relevant together with the size of our mesocosms in the light of the movement rates documented in the literature for earthworms (Mazaud and Bouché, 1980; Marinissen and Vandenbosch, 1992; Stein et al., 1992; Edwards and Bohlen, 1996). Second, we performed preliminary experiments that showed that earthworms are capable of crossing the mesocosms in one week.

2.1. Earthworm species

Earthworms are usually classified in three ecological categories: endogeic (that live and feed in the soil), anecic (that live in the soil but feed on surface litter) and epigeic (that live in and feed on surface litter) (Bouché, 1972). Due to their different ecologies, they face different constraints and might have evolved different dispersal strategies. We can expect epigeic species to be less sensitive to soil characteristics but more sensitive to the litter quality than endogeics. For this reason we used species of contrasted ecological categories: one endogeic: *Aporrectodea icterica* Savigny (1826) and one epigeic: *Dendrobaena veneta* Rosa (1886). The species names used herein conformed to the Fauna Europea web site (http://www.faunaeur.org/index.php).

A. icterica individuals were collected from the forest of Fontainebleau (48°24′N, 2°44′E). *D. veneta* individuals were purchased from a fishery shop. Earthworms were bred in the "suitable" soil at low density, at temperatures varying from 18 °C during the days to 15 °C at night. Earthworm individuals were used only once and replicates of each experiment were all performed simultaneously. All individuals were sub-adult at the time of the experiments.

2.2. Experiments

1) The influence of soil quality on endogeic dispersal was tested by comparing *A. icterica* displacements when 10 individuals were inoculated into "suitable" versus "unsuitable" soil (Fig. 1b).
2) The impact of litter cover, as shelter or as food resource, on epigeic dispersal was tested by comparing *D. veneta* movements after inoculating 10 individuals into three contrasted conditions: a) in "unsuitable" bare soil, b) in the same soil covered with *Tilia cordata* Miller (1768) leaf litter, and c) in the same soil covered with an artificial plastic litter (Fig. 1c).
3) Density dependence of endogeic dispersal was tested by introducing *A. icterica* at three different densities: 10, 20 or 30 individuals (respectively 166, 333 or 550 individuals m^{-2}) into the "suitable" soil (Fig. 1d). These density levels were representative of the natural levels observed for this species in the field (J. Mathieu, unpublished data)

4) The last experiment assessed the effect of former soil pre-use by conspecifics on endogeic dispersal rate. Ten specimens of *A. icterica* were inoculated (1) into the "suitable" soil that was previously processed by conspecific specimens, (i.e. the pre-used soil) or (2) into the same "suitable" soil but without pre-use (referred below as the "pristine soil") (Fig. 1e). The inoculation sections were prepared prior to the experiment: both soils were sieved one month before the experiment, and stored in boxes of the size of the inoculation sections. In the pre-used treatment, we inoculated 40 individuals of *A. icterica*. After one month they were removed by gently warming up the bottom of the boxes in a bain-marie. The soil for the pristine treatment was prepared in the same way but without earthworms.

2.3. Soils and litter

Two types of soil were used in the experiments to create habitats of different quality:

1) An "unsuitable" soil that was strongly avoided by earthworms during a previous preference test (Mathieu, unpublished data). This soil (Table 1) was sampled in a forest stand (48°24′N, 2°44′E, WGS84) dominated by *Quercus* sp. and *Carpinus betulus* and that contained very few earthworms.
2) A "suitable" soil that was largely preferred to the "unsuitable" soil in former preference tests. This soil (Table 1) was sampled in the park of the IRD Bondy centre (48°54′E, 2°29′N, WGS84), and contained more earthworms than the unsuitable soil.

Soils were sieved at 2 mm and re- humidified at respective field capacity by capillarity. They were adjacent in the three parts of the experimental units with no separation between them in order to allow earthworms to move freely from one section to the other. Removable partitions were used to avoid mixing of the section during their filling.

We also used two types of litter in the second experiment:

1) Leaves of *T. cordata* collected in the IRD Bondy park, at various decaying stages, up to one year old. This species was chosen because it is highly palatable to earthworms due do to its high Ca content (Reich et al., 2005).
2) A non-edible artificial litter to mimic the physical protection of natural litter but that could not be eaten. Artificial leaves were cut from thin (thickness: 5×10^{-4} m) plastic sheet and reproduced the shape of leaves at different decaying stages.

2.4. Statistical analyses

We defined the number of dispersing individuals as the number of individuals found in the target section at the end of the

Table 1
Selected properties of the soils used in the experiments. Unsuitable Soil = Soil avoided by the earthworms, Suitable Soil = Soil preferred by the earthworms.

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

experimental units. We analysed the link between the proportion of dispersers and the treatment with General Linear Models with Binomial response. All analyses were performed with R (R Development Core Team, 2007).

3. Results and discussion

3.1. Experiment 1&2: soil suitability and litter cover effects on dispersal

In the first experiment, 90% of the earthworms dispersed when inoculated into the unsuitable soil, whereas only 20% dispersed when inoculated into the suitable soil (Fig. 2). This striking difference shows that dispersal of *A. icterica* can be triggered by soil properties. In the second experiment, *D. veneta* responded dramatically to the presence of litter. When inoculated into bare ground, more than 80% of the individuals dispersed whereas only 26% dispersed when the inoculated section was covered by natural litter (Fig. 3). This significant difference shows that the presence of litter strongly influences the dispersal behaviour of this epigeic earthworm. Interestingly, less dispersal (34%) occurred in the presence of artificial litter than in bare ground (80%). The fact that both natural and artificial litter reduced dispersal suggests that the role of the litter as a shelter was more determinant than its role as a trophic resource.

A large body of observations already indicated that earthworms prefer habitats of high quality (in terms of food and environmental conditions) and that habitat quality actually affects earthworm fitness (Lowe and Butt, 2005). They also indicate that earthworms are able to select their habitat, and that they have food preferences (Westernarcher and Graff, 1987; Sanchez et al., 1997).

Our experiments highlight some kind of behavioural control in earthworm dispersal determinisms. Our results show that earthworm can disperse even if they are surrounded by an adverse environment, while there is no evidence of immediate benefits to disperse. This suggests that in the field, earthworms may avoid unsuitable environments and move until reaching a better habitat. Therefore earthworms should be more abundant in high quality habitats i.e. with high organic matter content, sufficient litter cover, or suitable soil properties. This prediction is generally verified for epigeic species (Westernarcher and Graff, 1987; Cannavacciuolo et al., 1998), but not always for endogeics (Valckx et al., 2009). Indeed, at small scales, typically plot scale of a few ha, the distribution of endogeic earthworms often display aggregative patterns forming patches with high densities (Margerie et al., 2001; Rossi, 2003), sometimes stable over periods of 2−3 years (Decaëns and Rossi, 2001; Jimenez et al., 2006). These patches are not consistently related to organic matter distribution (Rossi et al., 1997),
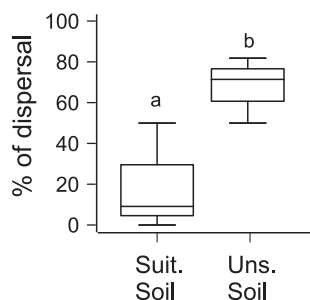

Fig. 3. Box plots comparisons of *D. veneta* dispersal rate in response to litter cover. Nat. = Natural litter; Art. = Artificial litter; different letters indicate significant differences at $p = 0.05$ (General Linear Models with Binomial response).

which suggests that soil properties other than organic matter may influence their location, and also that mechanisms other than habitat selection and dispersal from low quality habitats may be involved in the distribution of earthworms at the plot scale.

3.2. Experiment 3: density dependent dispersal

Dispersal rate of *A. icterica* increased with the density inoculated into the release section, with values significantly different between the lowest and highest density levels. Dispersal rate was 40% in treatments with 10 individuals inoculated, 45% with 20 individuals, and 69% in treatments with 30 individuals (Fig. 4). This endogeic species therefore seems to present a strong positive density dependent dispersal, a mechanism that has never been described in earthworm population studies, although it has been proposed to explain the punctual massive migration observed for some species (Reddy, 1980).

Positive density dependence in dispersal behaviour is supposed to be widespread in animals (see for instance Matthysen, 2005), and available examples include some soil organisms (see for instance Bengtsson et al., 1994). The most widely acknowledged hypothesis is that crowding increases intra-specific competition due to resource depletion, and that better fitness should be attained by dispersing from high-density sites (Murray, 1967; Waser, 1985). It was also noticed that positive density dispersal can avoid attracting predators in patches of high prey density (Wittenburger and Hunt, 1985), a phenomenon reported on earthworms (Macdonald, 1983). However, this behaviour can present serious evolutionary drawbacks, which may outweigh the benefits of positive density dispersal, especially among earthworms. In particular, emigration may induce local Allee effects (Stephens and Sutherland, 1999) which can seriously impede the growth and survival of populations. Many species of insects, birds

Fig. 2. Boxplot comparisons of *A. icterica* dispersal rate in response to soil properties. Suit. = Suitable soil; Uns. = Unsuitable soil; different letters indicate significant differences at $p = 0.05$ (General Linear Models with Binomial response).
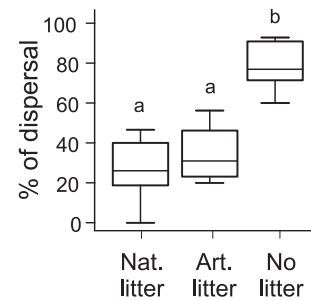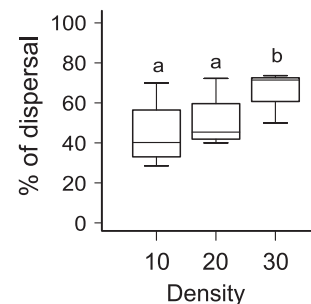

Fig. 4. Boxplot comparisons of *A. icterica* dispersal rate in response to earthworm density (number of individuals) inoculated into the soil. Different letters indicate significant differences at $p = 0.05$ (General Linear Models with Binomial response).

and mammals present negative density dependence, which often results from conspecific attraction (Danielson and Gaines, 1987; Stamps, 1991). The aggregation behaviour was already reported among the earthworm species Lumbricus terrestris (Linné, 1758), but the effect could not be distinguished from habitat selection (Butt et al., 2003). Indeed, in this experiment aggregation might come from a natural tendency to aggregate without a forcing by the heterogeneity of the environment, i.e. an aggregation behaviour, but also from individuals ending up in the patch of high quality after selecting the best habitat available (habitat selection).

3.3. Experiment 4: soil pre-use effect on dispersal

Soil pre-use strongly reduced the dispersal rate of earthworms: in pristine soil dispersal rate was 30%, whereas in pre-used soil no individuals dispersed (Fig. 5). This result shows that earthworm activities can have persistent effects which can be detected by new immigrants. This result may be explained by different mechanisms. First, the former inhabitants may have increased the quality of the habitat through soil engineering, i.e. the burrowing of galleries, which is a highly energy consuming activity. New comers would thus prefer soil with existing galleries, which would represent a readily suitable habitat colonisable with minimal burrowing cost. This hypothesis is supported by a recent work on earthworms behaviour (Felten and Emmerling, 2009). Second, former inhabitants may have enhanced trophic resource quality by activating decomposition processes through soil ingestion and mucus deposition, a mechanism previously coined "external rumen" (Lavelle, 1986). This kind of priming effect increases the availability of nutrients and carbon for the next consumers. Lastly, earthworms may have released attracting molecules in the soil. For instance, some anecic earthworms leave mucus on the ground which they use to locate their burrows (Nuutinen and Butt, 1997). This mucus may behave as a signal molecule which attracts conspecifics, a point which as never been tested, including on endogeics species, on which we worked.

This positive effect of soil pre-use can be considered as an original form of philopatry (i.e. the tendency to return to a specific environment or location) where the environment is the by-product of former individual activity. Such complex feedbacks between habitat quality, engineering activity, and dispersal have already been mentioned in theoretical works, but have rarely been demonstrated experimentally (see Cuddington and Hastings, 2004; Klironomos, 2002). Theoretically they can lead to the formation of patches of individuals through self-organization, without the forcing of any pre-existing heterogeneity in soil properties or interspecific interactions (Barot et al., 2007).
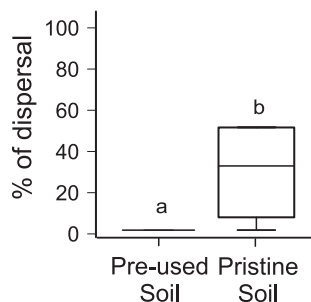

Fig. 5. Box plots comparisons of A. icterica dispersal rate in response to the former use of the soil substrate by conspecific individuals. Different letters indicate significant differences at $p = 0.05$ (General Linear Models with Binomial response).

3.4. Dispersal behaviour and earthworm spatial distribution

Dispersal patterns have profound effects on the distribution of species and community assemblage (Holyolak et al., 2005; Decaëns et al., 2008). Long Distance Dispersal (LDD) is a condition for the maintenance of metapopulations and metacommunites (Holyolak et al., 2005), and determines the capacity of species to colonize free habitats. At this scale, movements are likely dominated by passive dispersal mediated by external factors such as animals, wind, runoff and human activities. For instance earthworm cocoons may be transported in the fur of animals, in the soil of potted plants, or by being stuck in tractor wheels (Marinissen and Vandenbosch, 1992).

However passive dispersal alone is probably not sufficient to explain earthworm distributional patterns. Also active dispersal potentially plays an important role even at large scale. For instance the accumulation of many small stepping stone displacements can lead to large migration patterns or invasions (Nentwig, 2007). Many invasive species that were first introduced artificially in remote areas spread themselves by active dispersal (Lockwood et al., 2006). Some rare observations of introduction in previously earthworm-free habitats, such as polders, showed that earthworms are capable of colonising new areas at distances ranging from 4 (L. terrestris) to 14 m year^{-1} (Lumbricus rubellus Hoffmeister (1843)) (Mazaud and Bouché, 1980; Marinissen and Vandenbosch, 1992; Stein et al., 1992; Edwards and Bohlen, 1996). According to our experiments, A. icterica and D. veneta can travel distances of 0.5–0.9 m per week in mesosoms (26–47 m. year^{-1}) under conditions that trigger dispersal. Massive and spectacular migrations of earthworms are acknowledged to occur episodically (Reddy, 1980), but they probably don't occur very often.

At small scales, earthworms are known to form patches of high densities separated by areas of low densities (Rossi et al., 1997). The formation of these patches is a complex phenomenon resulting from local demographic processes associated with migration − emigration (both aspects of dispersal), interspecific interactions (competition versus ecological complementarity) and feedbacks between soil quality and earthworm engineering activity (Barot et al., 2007; Decaëns and Rossi, 2001; Rossi et al., 1997; Jimenez et al., 2006; Decaëns et al., 2009). In theory, their formation may arise from different processes, the most evident being an aggregation behaviour. However we observed rather positive density dispersal, meaning that earthworms avoid high densities. This implies that earthworms are relatively mobile at small scale, a condition under which patch formation was not expected in previous models, unless there was a strong influence of soil properties on demographic parameters (Barot et al., 2007). Under these circumstances patch formation appears as a subtle quantitative output of the balance between local demography and dispersal behaviour. Therefore in order to explain the formation of patches of earthworms, it is necessary to evaluate their movement range, their dispersal kernel as well as the variability of their demographic parameters in the field. In addition to these intra-specific mechanisms, interspecific interactions should also be considered. Competition, ecological complementarity and facilitation interactions may be in part responsible for spatial patterns observed in earthworm assemblages. For instance, interspecific competition has been described as a potential driving factor for the formation of patches dominated by specific species assemblages (Holyolak et al., 2005; Jimenez and Rossi, 2006; Decaëns et al., 2009), which is supported by experimental results that demonstrated antagonistic interactions between species pairs (Butt, 1998). Conversely, mutualistic, or at least reciprocal beneficial relationships can also lead to patch formation (Hoopes et al., 2005). For instance it was thought to explain the distribution of two African species in separate patches, where each species was

relying on the activity of the other to access soil organic matter (Blanchart et al., 1997).

From our result we can elaborate a first behavioural scenario of earthworm foraging: when they are either in a crowded or a low resource patch, they disperse until finding a suitable place, preferably formerly inhabited by conspecifics. After some time density increases in the suitable places, leading potentially to patch formation, and after some more time, density starts decreasing because of positive density dispersal.

3.5. Concluding remarks and perspectives

Our work clearly shows that earthworms are reactive to the quality of their environment, and that they can easily disperse from unsuitable conditions. The mechanisms we highlight bring significant information but they are not sufficient to explain patch formation in field conditions, and should thus be considered in tandem with field demographic studies.

Further work is required to understand how dispersal influences population and community dynamics. In particular, it is necessary to investigate if all species behave similarly in response to the same environmental conditions. Indeed, species, or even earthworm ecological categories, may present specific dispersal behaviours. The second point we need to focus on is the role of life stage. Indeed hatchlings, juveniles and adults may have very different behaviours and hence different dispersal options, as suggested by previous studies (Cannavacciuolo et al., 1998; Valckx et al., 2009). Lastly, the effects of interspecific interactions on dispersal behaviour should be considered. Species distribution in the field likely depends on this aspect. In order to model earthworm dispersal in a realistic way, we also needs to evaluate the mathematical shape of the dispersal kernel (dispersal curve) — the frequency distribution of the distances travelled by all individuals in a population —, which is a central feature of classical dispersal models (Kot et al., 1996; Neubert and Caswell, 2000). This could be done by taking advantage of recent techniques, such as earthworm tagging (Fujiwara et al., 2006; Butt and Lowe, 2007) and genetic approaches (Manel et al., 2003), allowing the study of individual movements at both small and large scales (Nathan, 2003).

Acknowledgements

References

Balkau, B.J., Feldman, M.W., 1973. Selection for migration modification. Genetics 74, 171–174.

Barot, S., Rossi, J.-P., Lavelle, P., 2007. Self-organization in a simple consumer-resource system, the example of earthworms. Soil Biology and Biochemistry 39.

Bengtsson, G., Hedlund, K., Rundgren, S., 1994. Food- and density-dependent dispersal: evidence from a soil collembolan. Journal of Animal Ecology 63, 513–520.

Blanchart, E., Lavelle, P., Braudeau, E., Bissonnais, Y., Valentin, C., 1997. Regulation of soil structure by geophagous earthworm activities in humid savannas of Côte d'Ivoire. Soil Biology & Biochemistry 29, 431–439.

Bodasing, M., Slotow, R., Crouch, T., 2001. The influence of group size on dispersal in the social spider Stergodyphus mimosarum (Aranae, Eresidae). The Journal of Arachnology 29, 56–63.

Bouché, M.B., 1972. Lombriciens de France. Ecologie et systématique. INRA, Paris, 671 pp.

Boudjemadi, K., Lecomte, J., Clobert, J., 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. Journal of Animal Ecology 68, 1207–1224.

Butt, K.R., 1998. Interactions between selected earthworm species: a preliminary, laboratory-based study. Applied Soil Ecology 9, 75–79.

Butt, K.R., Lowe, C.N., 2007. A viable technique for tagging earthworms using visible implant elastomer. Applied Soil Ecology 35, 454–457.

Butt, K.R., Nuutinen, V., Siren, T., 2003. Resource distribution and surface activity of adult Lumbricus terrestris L. in an experimental system. Pedobiologia 47, 548–553.

Cannavacciuolo, M., Bellido, A., Cluzeau, D., Gascuel, C., Trehen, P., 1998. A geostatistical approach to the study of earthworm distribution in grassland. Applied Soil Ecology 9, 345–349.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9, 129–136.

Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D., 2001. Dispersal. Oxford University Press, New York, 452 pp.

Cuddington, K., Hastings, A., 2004. Invasive engineers. Ecological Modelling 178, 335–347.

Danielson, B.J., Gaines, M.S., 1987. The influences of conspecific and heterospecific residents on colonization. Ecology 68, 1778–1784.

Decaëns, T., Jiménez, J.J., Rossi, J.P., 2009. A null model analysis of the spatio-temporal distribution of earthworm species assemblages in Colombian grasslands. Journal of Tropical Ecology 25, 415–427.

Decaëns, T., Margerie, P., Aubert, M., Hedde, M., Bureau, F., 2008. Assembly rules of earthworm communities at the regional scale. Applied Soil Ecology 39, 321–335.

Decaëns, T., Mariani, L., Betancourt, N., Jimenez, J.J., 2003. Earthworm effects on permanent soil seed banks in Colombian grasslands. Acta Oecologica 24, 175–185.

Decaëns, T., Rossi, J.-P., 2001. Spatio-temporal structure of earthworm community and soil heterogeneity in a tropical pasture. Ecography 24, 671–682.

Edwards, C.A., 1998. Earthworm Ecology. St. Lucie Press, LEWIS/Boca Raton/Boston/London/New York/Washington, D.C, 389 pp.

Edwards, C.A., Bohlen, P.J., 1996. Biology and Ecology of Earthworms. Chapman and Hall, London, 426 pp.

Felten, D., Emmerling, C., 2009. Earthworm burrowing behaviour in 2D terraria with single- and multi-species assemblages. Biology and Fertility of Soils 45, 789–797.

Field, S.G., Michiels, N.K., 2006. Does the acephaline gregarine Monocystis sp. modify the surface behaviour of its earthworm host Lumbricus terrestris? Soil Biology & Biochemistry 38, 1334–1339.

Fretwell, S.D., Lucas, H.L., 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19, 13–36.

Fujiwara, M., Anderson, K.E., Neubert, M.G., Caswell, H., 2006. On the estimation of dispersal kernels from individual mark-recapture data. Environmental and Ecological Statistics 13, 183–197.

Hanski, I., Gilpin, M., 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, London, UK, 512 pp.

Hengeveld, R., Hemerik, L., 2002. Biogeography and dispersal. In: Bullock, J.M., et al. (Eds.), Dispersal Ecology. Blackwell, Malden, USA, pp. 303–324.

Holyolak, M., Leibold, M.A., Holt, R.D., 2005. Metacommunities. Spatial Dynamics and Ecological Communities. The University of Chicago Press, Chicago/London, 513 pp.

Hoopes, M.F., Holt, R.D., Holyoak, M., 2005. The effects of spatial processes on two species interactions. In: Holyoak, M. (Ed.), Metacommunities. Spatial Dynamics and Ecological Commnities. The University of Chicago Press, Chicago/London, pp. 35–67.

Jimenez, J.J., Decaëns, T., Rossi, J.-P., 2006. Stability of the spatio-temporal distribution and niche overlap in Neotropical earthworm assemblages. Acta Oecologica 30, 299–311.

Jimenez, J.J., Rossi, J.-P., 2006. Spatial dissociation between two endogeic earthworms in the Colombian "Llanos" European Journal of Soil Biology 42, S218–S224.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Klironomos, J.N., 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature 417, 67–70.

Kot, M., Lewis, M., van den Driessche, P., 1996. Dispersal data and the spread of invading organisms. Ecology 77, 2027–2042.

Krivan, V., Cressman, R., Schneider, C., 2008. The ideal free distribution: a review and synthesis of the game-theoretic perspective. Theoretical Population Biology 73, 403–425.

Lavelle, P., 1986. Associations mutualistes avec la microflore du sol et richesse spécifique sous les tropiques: l'hypothèse du premier maillon. Comptes rendus de l'Académie des Sciences série III — Sciences de la vie — Life Sciences T. 302 (Sér. III), 11–14.

Lavelle, P., Spain, A.V., 2001. Soil Ecology. Kluwer Scientific Publications, Amsterdam, 654 pp.

Lockwood, J., Hoopes, M., Marchetti, M., 2006. Invasion Ecology. Wiley-Blackwell, 312 pp.

Lowe, C.N., Butt, K.R., 2005. Culture techniques for soil dwelling earthworms: a review. Pedobiologia 49, 401–413.

Macdonald, D.W., 1983. Predation on earthworms by terrestrial vertebrates. In: Satchell, J.E. (Ed.), Earthworm Ecology: From Darwin to Vermiculture. Chapman & Hall, London.

Manel, S., Schwartz, M.K., Luikart, G., Taberlet, P., 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology & Evolution 18, 189–197.

Margerie, P., Decaëns, T., Bureau, F., Alard, D., 2001. Spatial distribution of earthworm species assemblages in a chalky slope of the Seine Valley (Normandy, France). European Journal of Soil Science 37, 291–296.

Marinissen, J.C.Y., Vandenbosch, F., 1992. Colonization of new habitats by earthworms. Oecologia 91, 371–376.

Matthysen, E., 2005. Density-dependent dispersal in birds and mammals. Ecography 28, 403–416.

Mazaud, D., Bouché, M.B., 1980. Introduction en surpopulations et migrations de lombriciens marqués. In: Proc. VII International Colloquium of Soil Zoology. EPA, Washington, pp. 687–701.

Midtgaard, F., 1999. Is dispersal density-dependent in carabid beetles? A field experiment with *Harpalys rufipes* (Degeer) and *Pterostichus niger* (Schaller)(Col. Carabidae). Journal of Applied Entomology 123, 9–12.

Murray, B.G.J., 1967. Dispersal in vertebrates. Ecology 48, 975–978.

Nathan, R., 2001. The challenges of studying dispersal. Trends in Ecology & Evolution 16, 491–493.

Nathan, R., 2003. Seeking the secrets of dispersal. Trends in Ecology & Evolution 18, 275–276.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105, 19052–19059.

Nentwig, W., 2007. Biological Invasions. Springer, Berlin, 423 pp.

Neubert, M.G., Caswell, H., 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81, 1613–1628.

Nuutinen, V., Butt, K.R., 1997. The mating behaviour of the earthworm *Lumbricus terrestris* L. (Oligochaeta: Lumbricidae). Journal of Zoology, London 242, 783–798.

Parrish, J.K., Edelstein-Keshet, L., 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science 284, 99–101.

R Development Core Team, 2007. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reddell, P., Spain, A.V., 1991. Earthworms as vectors of viable propagules of mycorrhizal fungi. Soil Biology & Biochemistry 23, 767–774.

Reddy, M.V., 1980. Mass migration and mortality of Amynthas (= *Pheritima*) *alexandri* (beddard) (Megascolecidae: oligochaeta). Current Science 49, 606.

Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.A., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecology Letters 8, 811–818.

Rossi, J.-P., 2003. Clusters in earthworm spatial distribution. Pedobiologia 47, 490–496.

Rossi, J.-P., Lavelle, P., Albrecht, A., 1997. Relationships between spatial pattern of the endogeic earthworm *Polypheretima elongata* and soil heterogeneity. Soil Biology and Biochemistry 29, 485–488.

Sanchez, E.G., Muñoz, B., Garvin, M.H., Jesus, J.B., Diaz Cosin, D.J., 1997. Ecological preferences of some earthworm species in southwest Spain. Soil Biology & Biochemistry 29, 313–316.

Senapati, B.K., Lavelle, P., Giri, S., Pashanasi, B., Alegre, J., Decaëns, T., Jimenez, J.J., Albrecht, A., Blanchart, E., Mahieux, M., Rousseaux, L., Thomas, R., Panigrahi, P., Venkatachalam, M., 1999. Soil earthworm technologies for tropical agroecosystems. In: Lavelle, P. (Ed.), The Management of Earthworms in Tropical Agroecosytems. CAB International, Wallingford, UK, pp. 189–227.

Shapiro, D.I., Tylka, G.L., Berry, E.C., Lewis, L.C., 1995. Effects of Earthworms on the dispersal of *Steinernema* spp. Journal of Nematology 27, 21–28.

Stamps, J., 1991. The effect on conspecifics on habitat selection in territorial species. Behavioural Ecology and Sociobiology 28, 29–36.

Stein, A., Bekker, R.M., Blom, J.H.C., Rogaar, H., 1992. Spatial variability of earthworm populations in a permanent polder grassland. Biology and Fertility of Soils 14, 260–266.

Stephens, P.A., Sutherland, W.J., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology & Evolution 14, 401–405.

Tiunov, A.V., Hale, C.M., Holdsworth, A.R., Vsevolodova-Perel, T.S., 2006. Invasion patterns of Lumbricidae into previously earthworm-free areas of northeastern Europe and the western great lakes region of North America. Biological Invasions 8, 1223–1234.

Toyota, K., Kimura, M., 1994. Earthworms disseminate a soil-borne plant pathogen, *Fusarium oxysporum* f. sp. *raphani*. Biology and Fertility of Soils 18, 32–36.

Valckx, J., Cockx, L., Wauters, J., Van Meirvenne, M., Govers, G., Hermy, M., Muys, B., 2009. Within-field spatial distribution of earthworm populations related to species interactions and soil apparent electrical conductivity. Applied Soil Ecology 41, 315–328.

Waser, P.M., 1985. Does competition drive dispersal? Ecology 66, 1170–1175.

Westernarcher, E., Graff, O., 1987. Orientation behaviour of earthworms (*Lumbricidae*) towards different crops. Biology and Fertility of Soils 3, 131–133.

Williams, A.P., Roberts, P., Avery, L.M., Killham, K., Jones, D.L., 2006. Earthworms as vectors of *Escherichia coli* 0157:H7 in soil and vermicomposts. FEMS Microbiology Ecology 58, 54–64.

Wittenburger, J.F., Hunt, G.L., 1985. The Adaptive Significance of Coloniality in Birds Avian Biology. Academic Press, New York, USA, pp. 1–78.