Are dispersal behaviours of earthworms related to their functional group?

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ABSTRACT

Dispersal plays a key role in the dynamics of ecological communities as it strongly determines the potential of individuals to colonize new habitats. Understanding and predicting species dispersal behaviour is therefore central to any effort at managing or even understanding the formation of communities. In this context, it is essential to understand the influence of environmental and biotic determinants of dispersal. In this work, we assessed these questions using earthworms as model organisms.

We assessed the dispersal behaviour of six earthworm species belonging to two different functional groups (i.e. three anecics and three endogeics) in response to three key environmental factors: habitat quality, intraspecific density, and environment homogeneity. We found that habitat quality significantly influenced the dispersal rates of all species. Intraspecific density increased the dispersal rate of the three anecic species but only of one endogeic species. In a homogeneous environment, anecics dispersed further and in greater proportion than the majority of endogeics. Moreover, few anecic species have shown a tendency to follow conspecifics. Overall, anecic species seemed to have a higher active dispersal inclination than most endogeic ones. We found a high variability of our results within each functional groups, which suggests that this classification cannot be used to explain or predict the dispersal behaviour of earthworms.

1. Introduction

The link between biodiversity and ecosystem functioning is a central issue in ecology (Loreau et al., 2001; Duffy, 2002; Hooper et al., 2005). Previous studies pointed out the richness of functional groups − groups of species with similar functional traits (Blaum et al., 2011) − as being of particular importance for ecosystem functioning (Hector et al., 1999; Schwartz et al., 2000). Moreover, the mobility of animal species may result in complex relationships between functional group richness and ecosystem functioning. Predicting the spatial distribution of individuals hence appears as a requirement to manage populations of ecosystem engineers, in order to maintain the ecosystem services they deliver (Clobert et al., 2001; Petchey and Gaston, 2002). Given the variety of animals, it is necessary to search for general rules that predict their spatial distribution. A central point to address in this issue is the magnitude of the link between functional groups and dispersal behaviours.

Dispersal is a central ecological process that allows colonization of new habitats and exploitation of spatially and temporally variable resources (Ronce, 2007). Active dispersal of animals (opposed to passive dispersal, where individuals could be transported by an external agent and has not necessarily a cost for individual) is the result of three successive behavioural stages (following the definition given by Clobert et al., 2001, 2009). It involves the departure from a breeding site, crossing to a new place, and settlement. It 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). It is assumed to depend on the balance between the costs and benefits of dispersal (Bowler and Benton, 2005; Bonte et al., 2012), which are strongly determined by both environmental conditions (e.g. habitat quality, habitat fragmentation, patch size, density, predation) and individual life traits (e.g. age, hormonal levels; (Bonte et al., 2006; Schtickzelle et al., 2006)). Ecosystem engineers, such as earthworms, are species that can modify physically their surrounding environment in a specific way (Jones et al., 1994). These modifications could therefore interact with population density and drive complex dispersal behaviours. As species belonging to a given functional groups are expected to modify their environment in a similar way, it could also be expected to find a concordance between functional classification and dispersal behaviours.

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Earthworms provide a good model to assess the concordance between functional groups and dispersal behaviours. Indeed, earthworm species can be classified in contrasted groups, based on their traits, ecology and functional role regarding soil processes (Bouché, 1972, 1977). Besides, earthworms are of primary importance for ecosystem functioning as they modify the availability of resources for other organisms through physical and chemical changes in their surrounding soil environment (Jones et al., 1994, 2010; Lavelle et al., 2006). The most used functional classification of earthworms (Bouché, 1972, 1977) distinguishes epigeics, anecics and endogeics, based on morphological (e.g. size and pigmentation) and ecological features (soil stratum where individuals are active, food diet). Earthworm ecological preferences and impact on the environment have been largely documented (Bohlen and Edwards, 1995; Brown, 1995; Blanchart et al., 1999), as well as their burrowing behaviour (Capowiez, 2000; Bastardie et al., 2003). However the diversity of their dispersal features has been overlooked and still needs to be documented for most species and functional groups (Mathieu et al., 2010).

In this work, we tested the correspondence between earthworm functional groups and dispersal behaviours. We experimentally compared the dispersal behaviour of six species belonging to the functional groups anecics and endogeics, which are believed to have the strongest impact on soil functioning (Bouché, 1972, 1977). For each species, we tested the impact of three factors assumed to be important drivers of animal dispersal: habitat quality, conspecific density, and also the dispersal patterns in homogenous environment.

2. Materials and methods

2.1. Biological models

We used three endogeic species − Aporrectodea icterica (Savigny 1826), Aporrectodea caliginosa (Savigny 1826) and Allolobophora chlorotica (Savigny 1826) − and three anecic species − Aporrectodea giardi (Ribaucourt, 1901), Aporrectodea longa (Ude 1886) and Lumbricus terrestris (Linnaeus 1758) − which are all usually well represented in natural assemblages in North-Western France (Decaëns et al., 2008). Earthworms were collected in a forest in North-Western France (49°27′N, 1°4′E) and were reared in suitable soil (see Section 2.2) at low density (1.5 individuals per litre of soil, according to Mathieu et al. (2010), at 15 °C during the day and 10 °C at night. All individuals were used only once and were adult during the experiments.

2.2. Soils

Two types of soil were used for the experiments: an unsuitable and a suitable soil. The suitable soil (Table 1) was sampled in a grassland of the IRD research centre (48°54′E, 2°29′N) which hosts large earthworm populations. The unsuitable soil consisted of a very sandy soil with low pH (Table 1) collected in an area deprived of earthworms in the forest of Fontainebleau (48°24′N, 2°44′E). The suitable soil was from a brunisol and the unsuitable soil from a luvisol (based on the world reference base for soils, FAO). Both soils were air dried, sieved at 2 mm and rewetted manually at 25% of humidity (on a massic basis − soil water content was set by drying the soil at 105 °C during 48 h).

2.3. Experiments

We used separate standardized experimental devices (mesocosms) to study the influence of three different environmental factors on dispersal behaviours: (1) Intraspecific Density (ID); (2)

Table 1
Selected properties of the soil substrate used in the experiments.

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}

Habitat Quality (HQ); (3) Homogenous Environment (HE). These treatments were chosen to address three key mechanisms shaping the spatial distribution of populations: intraspecific competition, habitat choice and spread capabilities.

The influence of intraspecific density on dispersal (Experiment ID) was studied in mesocosms that consisted of a dispersal corridor of 100 cm long, 20 cm wide and 20 cm high (Mathieu et al., 2010), which was composed of three equal sections (Fig. 1): (1) the "inoculation" section, which was filled with suitable soil; (2) the intermediate "crossing" section, composed of unsuitable soil; (3) the "arrival" section composed of suitable soil. Soil densities were 1 ± 0.1 g cm^{-3} in each section of the mesocosm. This setup allows to reproduce the three stages of dispersal: departure, crossing and settlement in a suitable site (Clobert et al., 2009). In this context, we consider that the rates of individuals leaving to the inoculation section are dispersal rates. Moreover, the unsuitable soil in the crossing section was designed to represent a physical barrier generating dispersal costs. It allowed distinguishing between mechanisms of diffusion (random movements with potentially returns in the starting point) from active dispersal (Clobert et al., 2009) and to prevent to U-turns movements (Caro et al., 2012). To assess the effect of intraspecific density on dispersal rate, we inoculated earthworms at four densities (i.e. the numbers of worms inoculated in the first section): 1, 10, 20 or 30 individuals of the same species in the ID experiment. We ensured that all individuals were inoculated in the first section by waiting that each individual entered in the soil, which took on average 10 min after inoculation.

To study the influence of habitat quality on dispersal (Experiment HQ), we used the same mesocosm design with unsuitable soil in the inoculation section (Fig. 1). For each species, we inoculated 10 individuals. Both experiments (ID & HQ) lasted seven days and were replicated 5 times under the same conditions of temperature (15 °C during the day and 10 °C at night) and light as breeding. At the end of the experiment, we counted all individuals in each section.

In the HE experiment (dispersal in a homogeneously suitable environment), we observed the dispersal in larger mesocosms of 300 cm long, 20 cm wide and 20 cm high (Fig. 1), filled exclusively with suitable soil at a bulk density of 1 ± 0.1 g cm^{-3}. This allowed documenting the natural spread of individuals while removing the effect of heterogeneity. In order to identify the location of individuals in the mesocosms, we defined 13 regular sections of 23 cm long, which we named according to their distance to the central section. For each species, 10 individuals were inoculated in the central section (i.e. section 0) at the beginning of each experiment. We limited the time of each experiment to 24 h in order to prevent U-turns by individuals reaching the end of the mesocosm. Each experiment was replicated 4 times under the same conditions of temperature and light as for breeding. At the end of the experiment, we counted all individuals in each section.
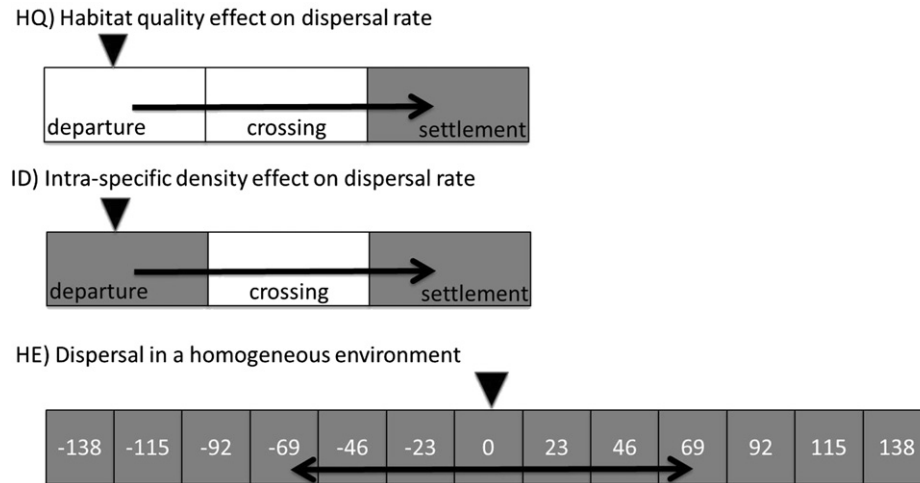
Fig. 1. Experimental designs of the dispersal studies: HQ) Habitat Quality effect on dispersal rate; ID) Intraspecific Density effect on dispersal rate; HE) dispersal in a Homogeneous Environment; White area = unsuitable soil; Grey area = suitable soil; triangles = exact location where earthworms were introduced (inoculation points).

In order to identify the influence of the body size on the dispersal responses, all individuals were weighed individually before and after each experiment. We found no significant effect of individual biomass on the dispersal behaviour (p-value > 0.05, Linear Model), and we also found that body size did not change significantly between the beginning and the end of the experiments (p-value > 0.05, Linear Model). In consequence, body size was not considered in further statistical analyses.

2.4. Dispersal quantification and statistical analyses

In ID and HQ experiments, we defined the dispersal rate as the proportion of individuals that moved from the inoculation section to the third section. For the ID experiment, we used a General Linear Model (GLM) with a binomial family to compare the dispersal rates at each density level.

To test differences in dispersal responses to the density increasing among species, we fitted non-linear models on the dispersal rates in response to increasing intraspecific density:

$$D_k(d) = \mathrm{IDr}_k * d^2 / \left(\mathrm{IDs}_k^2 + d^2 \right)$$

where:

- $D_k(d)$ represent the dispersal rate of species k at density d;
- d represents the intraspecific density of the species;
- IDr_k represents the value at which the model reaches a plateau. It allows us to know the maximum dispersal rate of the species k in response to the intraspecific density increasing;
- IDs_k represents the inflection point of the model. It informs us on the density sensitivity of the species k.

We further used the estimated parameters, IDr_k and IDs_k, to perform pair-wise comparisons between functional groups with a Linear Model.

For the HQ experiment, we tested the influence of habitat quality on dispersal by comparing the observed dispersal rates to those obtained from a suitable environment, i.e. the ID experiment at a density of 10 individuals. Differences were tested using a GLM with a binomial family. To quantify earthworm sensitivity to habitat quality, we calculated the percentage of difference (HQs) between these two dispersal rates for each species: $\mathbf{HQs = (\textit{D}_{\textbf{unsuit},\textit{k}} - \textit{D}_{\textbf{suit},\textit{k}})/\textit{D}_{\textbf{unsuit},\textit{k}} * 100}$, where D_k represents the

dispersal rate from an unsuitable (unsuit) or a suitable (suit) environment of the species k. In this way, the HQs varies from 0 to 100 %; the HQs maximum value meaning that the dispersal of species k is almost only triggered by habitat quality. We used this index to compare the sensitivity of both functional groups to habitat quality with a Linear Model.

In the HE experiment, dispersal rate (HEr$_k$) was calculated as the proportion of individuals of a species k that left the central section (position 0; Fig. 1). We also computed the average distance crossed for each species (HEd$_k$) and a distribution index: $\mathbf{HEf_k = |(HEr_k \ left - HEr_k \ right)|}$, where: HEr$_k$ represents the dispersal rate at left or at right of starting section; Thus, HEf$_k$ varies from 0 (individuals equally distributed in each side) to 100 (all individuals in only one side) and gives an idea of the proportion of individuals that followed each other – the more HEf$_k$ is high, the more the species k have a high tendency in following conspecifics. We did not use a classic index of asymmetry because of boundary effects related to the mesocosms. In order to compare the species and functional group dispersal capabilities, we compared the mean distance crossed (HEd), the mean dispersal rates (HEr) and the tendency to follow conspecifics (HEf) with a Linear Model.

2.5. Dispersal behaviours synthesis

In order to synthesize these results, we constructed a table with the different species dispersal features: IDr$_k$ (maximum dispersal rate in response to intraspecific density), IDs$_k$ (sensitivity to intraspecifics density), HQs$_k$ (sensitivity to habitat quality), the HEd$_k$ (mean distance crossed in the homogeneous environment), HEr$_k$ (mean dispersal rate in the homogeneous environment) and HEf$_k$ (average tendency to follow conspecifics). Afterwards, we performed a Principal Component Analysis (PCA) on the centred and standardised table. This allowed depicting synthetically the link between ecological categories and dispersal behaviours. We retained 2 axes in the PCA, which accounted for 94.5% of the total inertia. To represent the dispersal strategy of each species, we plotted species on the PCA space with segment diagrams where each segment represents a dispersal parameter and the size of the segment represents the value of the parameter. This representation is similar to the standard correlation circle. All analyses were performed with the ADE-4 package from R (Ihaka and Gentleman, 1996; Thioulouse et al., 1997).

3. Results

3.1. Dispersal behaviours in detail

Intraspecific density was determinant in dispersal behaviours, except for *A. caliginosa* and *A. chlorotica*. For the other four species, when the density reached the threshold of 10 individuals, dispersal rates increased significantly (within each species, *p*-value < 0.05, binomial GLM; Fig. 2). Above the density of 10 individuals, the dispersal of *A. longa* and *L. terrestris* did not change significantly (within each species, *p*-value > 0.05, binomial GLM) whereas the dispersal of *A. icterica* and *A. giardi* significantly increased at 30 individuals per section (*p*-value < 0.05, binomial GLM; Fig. 2). Non-linear regressions showed that the sensitivity to intraspecific density was not strongly related to the dispersal threshold (here 10 and 30 individuals). For instance, *A. longa* had a value of IDs ten times lower than that of *A. giardi*. Although statistical analysis did not show any significant difference in the dispersal parameters among functional groups (IDr and IDs not significantly different), we observed that all anecics were density sensitive while among endogeics only *A. icterica* dispersed more at higher densities.

Dispersal rate of earthworms inoculated in the unsuitable soil was in average 83% higher than in the suitable soil (within each species, *p*-value < 0.01, binomial GLM; Fig. 3). The most sensitive species to habitat quality were the two endogeics *A. chlorotica* and *A. caliginosa*, with HQs of 100% for each of them. Anecics were also sensitive to habitat quality, with HQs = +83 ± 8.5% in average. We found no significant differences in HQs among the two functional groups (*p*-value > 0.05, Linear Model).

In the homogeneous environment, all species dispersed from the inoculation section (Fig. 4). *A. icterica* moved significantly more than other species, either regarding the proportion of individuals that had dispersed (HEr), or the average distance crossed (HEd). Anecics dispersed significantly more than the two others

endogeics. Finally, the index HEf suggested that the dispersal direction of *A. giardi* was influenced by the previous passage of congeners (HEf$_{giardi}$ = 74.8) while *A. icterica* and *A. longa* seemed to avoid conspecifics (HEf$_{icterica}$ = 16.1 and HEf$_{longa}$ = 19.7) (Fig. 4).

3.2. Synthesis of dispersal behaviours

The first axis of the PCA accounted for 67.07% of the total variance and discriminated *A. chlorotica* and *A. caliginosa* (positive scores) from *A. icterica* (negative score; Fig. 5). It was highly associated with the maximum dispersal rate in response to intraspecific density (IDr), average distance crossed (HEd) and average dispersal rate (HEr) in a homogeneous environment, and, to a lesser extent, to the sensitivity to habitat quality (HQs) (Fig. 5). It was thus interpreted as a gradient in endogeics dispersal capabilities. The second axis accounted for 27.43% of the total variance and discriminated *L. terrestris* and *A. longa* (positive scores) from *A. giardi* (negative score) (Fig. 5). It was associated to the sensitivity to intraspecific density (IDs) and to the tendency to follow conspecifics (HEf) (Fig. 5) and was therefore interpreted as the influence of conspecifics on dispersal of anecic species.

4. Discussion

We observed that the distribution of endogeic species on the PCA plan can be explained by differences in dispersal capabilities, such as the distance crossed and the dispersal rate (Fig. 5). In this analysis, *A. icterica* had the highest dispersal basal rate among endogeics, while the other two species of this functional group only dispersed in response to strong environmental stimuli, such as unsuitable soil conditions (Figs. 2 and 3). The anecic species distribution on the PCA plan appeared to be strongly defined by differences in their sensitivity to conspecifics: they were the most sensitive species to intraspecific density (with a very low IDs value;
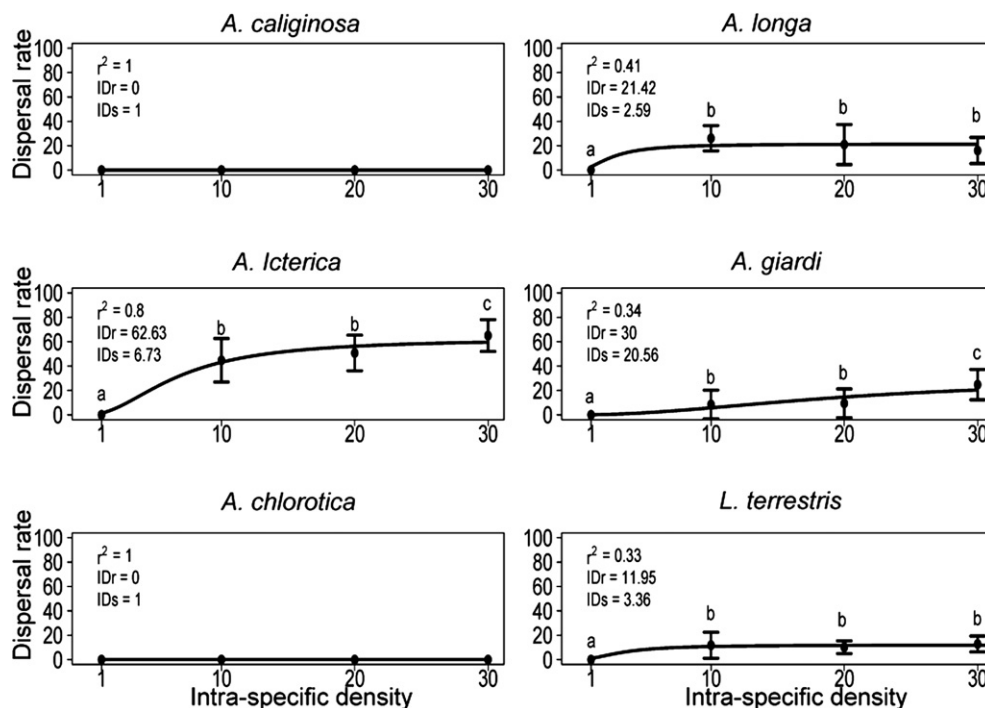

Fig. 2. Dispersal rate in response to the intraspecific density (mean ± standard deviation; *N* = 5). Different letters indicate significant differences at *p* = 0.05 (General Linear Models with a binomial family). The line represents the non-linear regression by fitting the equation $D_k(d) = IDr_k * d^2/(IDs_k^2 + d^2)$ on the dispersal data of the species *k*, where *d* represent the intraspecific density and $D(d)_k$, the dispersal rates of the species *k*. The IDr$_k$ and IDs$_k$ values represent the parameters of this function and the r_k^2 is the coefficient of determination between the curve fitted and the data from the species *k*.
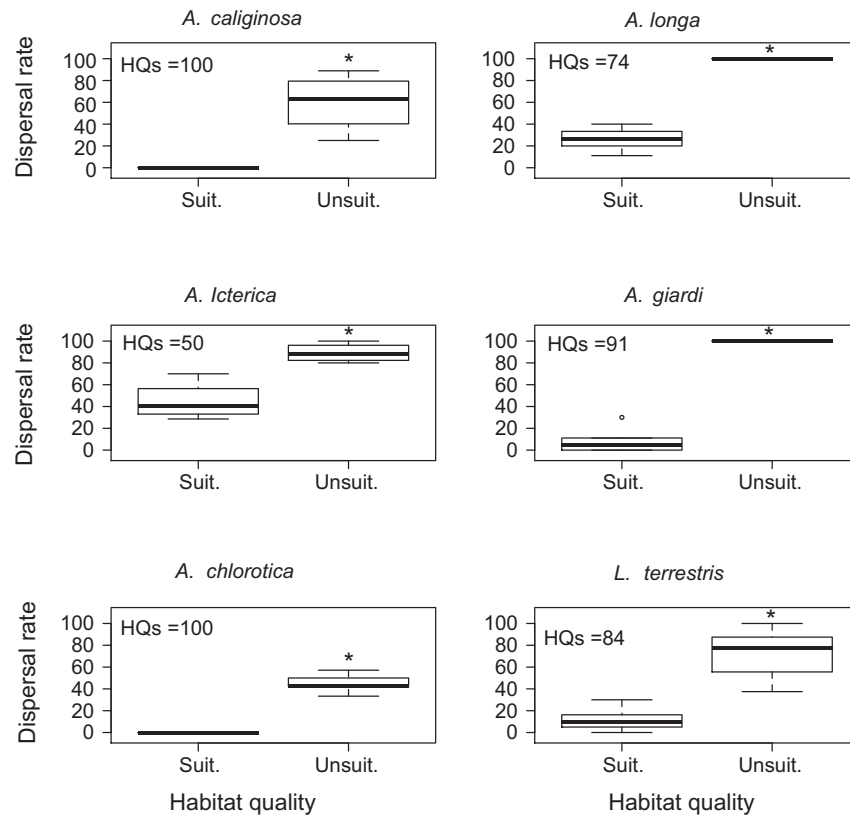
Fig. 3. Boxplot of dispersal rates in response to the habitat quality ($N = 5$); suit. = suitable; unsuit. = unsuitable; HQs = percentage of difference between the dispersal rates; * indicate significant differences at $p = 0.05$ (General Linear Models with Binomial response).

Fig. 2) and had a net tendency to follow their conspecifics (*L. terrestris* and *A. giardi* had an HEf index high; Fig. 4). Consequently, we did not observe any strong correspondence between earthworm functional groups and the groups of species identified by the PCA on the basis of their dispersal behaviours. This observation highlights the diversity of dispersal behaviours among species.

Some degree of functional redundancy is expected among species of a single functional group, and this implies that the disappearance of one or more of those species is not expected to affect ecosystem processes in a significant way because the remaining species can compensate for it (Naeem, 1998; Walker et al., 1999). In a context of increasing environmental disturbances, the
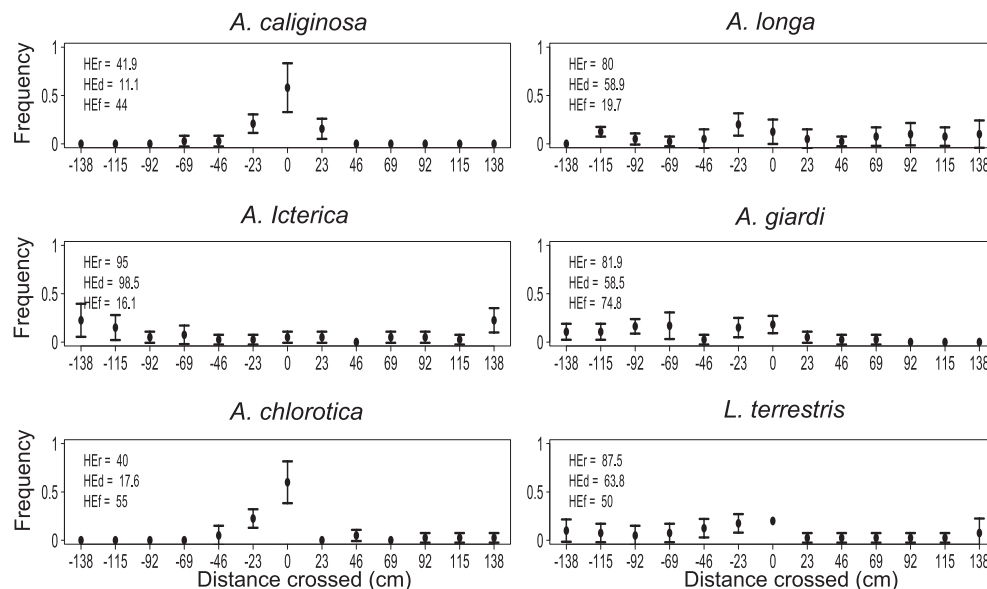

Fig. 4. Distribution of individuals according to the distance to the inoculation section ($N = 4$). We represented the mean proportion of individuals in each part of the mesocosm (mean ± standard deviation). HEr = mean dispersal rate; HEd = mean distance crossed; HEf = tendency to follow conspecifics.
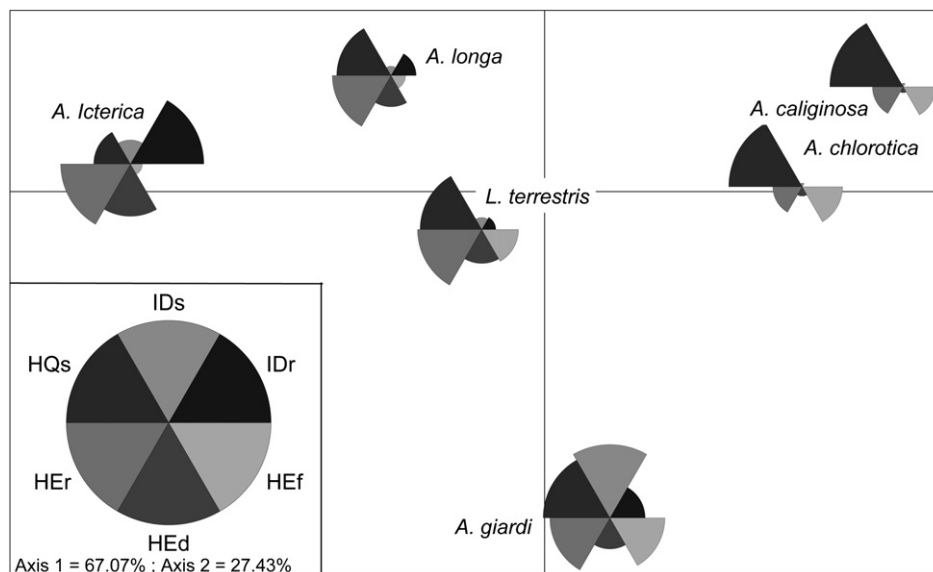
Fig. 5. Ordination of the species according to their dispersal behaviours in the plane defined by the axis 1 and 2 of the PCA. The position of the species is represented by their name associated to a segmented diagram where each segment represents a dispersal parameter and the size of the segment is proportional to the value of the parameter. IDr = maximum dispersal rate in response to the intra-specific density; IDs = sensibility to the intra-specifics density; HQs = sensitivity to the habitat quality; HEd = mean distance crossed in the homogeneous environment; HEr = mean dispersal rate in the homogeneous environment; HEf = average tendency to follow conspecifics.

presence of a pool of species responding differently to the same perturbation may allow the maintenance of the diversity of their functions. The diversity in dispersal behaviours observed in our study may for instance facilitate the maintenance of a group by different mechanisms of dispersal and different potentials for colonizing disturbed habitats (Walker, 1992, 1995; Diaz and Cabido, 2001).

Several studies reported a negative influence of high intraspecific densities on the growth rate and maturation of both endogeic and anecic earthworms (Eriksen-Hamel and Whalen, 2007; Uvarov, 2009). In addition, anecics are usually negatively impacted by endogeics, whereas the presence of anecics is often considered as beneficial to endogeics (Uvarov, 2009). From an evolutionary point of view, the fact that anecics seem negatively influenced by both intra- (based on our observations; Fig. 2) and interspecific density (Uvarov, 2009) suggests that they may have evolved greater dispersal capabilities than most endogeic species in order to minimize these negative interactions (Clobert et al., 2001). In comparison, it seems that endogeics such as *A. caliginosa* evolved weak dispersal abilities (Uvarov, 2009). Our results suggest that endogeics could have high capacities to take advantage of the burrowing activities of other species, a hypothesis supported by previous studies (Capowiez, 2000; Jégou et al., 2001; Uvarov, 2009). This could explain in part the low dispersal rates observed in *A. chlorotica* and *A. caliginosa*.

The fact that anecic species present a higher active dispersal capabilities than the majority of endogeics, in the specific context of our experiment, suggests that they could be the first colonizers of new habitats, paving the way for other species through the building of a network of re-usable galleries (Butt et al., 1999; Capowiez, 2000; Caro et al., 2012). However, this assumption is only partly supported by available observations of the dynamics of earthworm species assemblages during the colonization of new habitats. For instance, Decaëns et al. (2011) described the dynamics of earthworm communities after cropping cessation in North-Western France and identified a group of 'pioneer' species that includes two anecics but also two endogeics. In the Netherlands, Eijsackers (2011) observed that recent polder soils were at first colonized by

endogeics. It is clear that our results are not directly comparable to *in situ* observations (Lee, 1985; Butt et al., 1999; Grigoropoulou and Butt, 2010), but they however suggest that earthworms have more diversified dispersal behaviours than previously assumed (Fig. 5). This highlights the importance of taking into account dispersal behaviours in studies of community assembly in new habitats or in agricultural soils where earthworms have been previously eliminated by management practices.

Despite a few similarities between species of the same functional group, we cannot deduce from our results general dispersal characteristics for each ecological category of earthworms. This is surprising because earthworm functional groups are assumed to reflect evolutionary pathways that led to the acquisition of adaptive ecological traits, and they should therefore be strongly congruent with ecological strategies evolved by species in response to e.g. predation, resource availability and/or physical constraints related to soil characteristics. Consequently, we expected species belonging to the same functional group to show similar dispersal behaviours. Alternatively, dispersal traits could be inherited from a common ancestor and in that case they should reflect the phylogenetic relationships between species. Our results do not clearly support neither the adaptive nor the phylogenetic origin of dispersal traits in earthworm species. Firstly, we found a significant degree of diversity in species dispersal behaviours within the ecological groups considered (Fig. 5). Secondly, although earthworm taxonomy is probably still not fully resolved (Decaëns et al., in press), we observed different dispersal behaviours among four species within the genus *Aporrectodea*. It therefore seems that dispersal behaviours evolved under the influence of environmental constraints that are weakly related to those that drove the evolution of functional traits, leading to the observed lack of congruence between dispersal behaviours and functional groups.

5. Conclusion

Our study highlights the diversity of dispersal behaviours among earthworm species. Considering this diversity in strategies to conserve the functional potential of earthworm communities

should be of critical importance. Indeed, pools of species with similar functional traits but responding differently to the same environmental factor should present a higher resilience when submitted to environmental disturbances. Finally, our study raises the question of the evolutionary forces (e.g. environmental disturbances, intra- and interspecific interactions) that drive the acquisition of dispersal behaviours. For instance, differences in environmental stability could lead to differences in adaptive capacity (Bonte et al., 2003; Rainio and Niemelä, 2003): a very stable environment could lead to extremely specialized species that are more likely to disperse to find optimal conditions, whereas unstable environment may lead to more generalist species.

Acknowledgement

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