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How good are epigeic earthworms at dispersing? An investigation to compare epigeic to endogeic and anecic groups

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1 **ABSTRACT**

2

3 Dispersal capacities can strongly determine an individual's ability to respond to changing
4 environmental conditions, which would consequently influence the structure of natural
5 communities. Nonetheless, we know little about the dispersal behaviour of soil organisms,
6 despite some of these organisms, such as earthworms, have key roles in ecosystem
7 functioning (e.g. organic matter decomposition). We expect that species exposed to frequent
8 environmental changes would benefit from the capacity to escape from adverse environmental
9 conditions and to disperse to settle in a more suitable habitat. In earthworms, we expect the
10 epigeic group, which lives at or close to the soil surface, to have evolved higher dispersal
11 capacities than the two other functional groups – anecic and endogeic, which live deeper in
12 the soil. In this study, we investigated dispersal and diffusion behaviour of three species of
13 epigeic earthworms (i.e. *Eisenia fetida*, *Eisenia andrei* and *Lumbricus rubellus*) and compared
14 these behaviours with those of anecic and endogeic earthworms, whose behaviour has been
15 previously measured through similar experiments. In accordance with our hypothesis, our
16 study shows that dispersal behaviour of epigeic earthworms depends on habitat quality and
17 population density, but that those responses vary among species and that it differs only to a
18 limited extent from behaviour of anecic and endogeic earthworms.

19

20 Key words: density-dependent dispersal, departure, diffusion behaviour, ecosystem engineers,
21 functional groups, habitat quality

22

23 **1. Introduction**

24

25 Dispersal is a central ecological process that allows colonization of new habitats and
26 exploitation of spatially and temporally variable resources (Ronce, 2007). Active dispersal of
27 animals (as opposed to passive dispersal, where individuals are transported by an external
28 agent, and has not necessarily a cost for the disperser) is the result of three successive
29 behavioural stages (following the definition given by Clobert et al., 2009, 2001). It involves
30 the departure from a breeding site, crossing to a new place, and settlement (Clobert et al.,
31 2009). It is thought to depend on the balance between the costs and benefits of dispersal
32 (Bonte et al., 2012; Bowler and Benton, 2005), which are strongly determined by both
33 environmental conditions (e.g. habitat quality, habitat fragmentation, patch size, density,
34 predation; Bonte et al., 2006; Schtickzelle et al., 2006) and individual life traits (e.g. age,
35 hormonal levels, movement abilities). Therefore, dispersal capacities are expected to strongly
36 determine an individual's ability to respond to changing environmental conditions, which
37 would consequently influence the dynamics and persistence of populations, the distribution
38 and abundance of species, the structure of natural communities but also the functioning of
39 ecosystems (Cuddington and Hastings, 2004). Nonetheless, we know little about the dispersal
40 behaviour of soil organisms, even if some of these organisms, such as earthworms, play key
41 roles in ecosystem functioning (Blouin et al., 2013).

42

43 Earthworms species are often classified into three functional groups based on their
44 morphology, and their foraging behaviour (Bouché, 1977, 1972): endogeic earthworms live
45 and feed in the soil, epigeic earthworms mainly live and feed on the leaf litter at the soil
46 surface, anecic earthworms make vertical burrows in soil and feed on leaf litter which they
47 drag into their burrows. Earthworms are of primary importance for ecosystem functioning

48 because they modify the availability of resources for other organisms through physical and
49 chemical changes in their surrounding soil environment (Jones et al., 2010, 1994; Rillig et al.,
50 2016). As a consequence, they fulfil numerous soil-based ecosystem services (Blouin et al.,
51 2013). While anecic earthworms, and to a lower extent endogeic and epigeic earthworms, are
52 of particular importance for cropping systems (Bertrand et al., 2015; van Groenigen et al.,
53 2014), epigeic earthworms play a key role in organic matter decomposition in deciduous
54 forests because of the ingestion of poorly decomposed litter (Manna et al., 2003) and the
55 interactions they established with decomposer microorganisms (Gómez-Brandón et al., 2012;
56 Monroy et al., 2008), which explains their use in vermicomposting (e.g. Suthar et al., 2008).
57 For these reasons, it is essential to identify the environmental factors that may influence
58 earthworm prevalence and abundance in ecosystems (Curry, 1998; Palm et al., 2013),
59 especially in the context of global changes. Indeed, anthropogenic activities, including
60 urbanisation and agriculture, are responsible for considerable modifications of the natural
61 environment through e.g. light, noise and chemical pollutions, temperature modifications and
62 habitat fragmentation. These changes may have considerable impact at the individual level
63 and in terms of population dynamics and functioning (e.g. Dupont et al., 2015; Johnston et al.,
64 2015; Orwin et al., 2015). To cope with these natural (e.g. soil heterogeneity, daily and
65 seasonal cycles, etc.) or human-induced environmental constraints, high sensory capacities
66 associated with acclimatization or dispersal abilities may have been naturally selected in
67 earthworm species (e.g. Fisker et al., 2011; Spurgeon and Hopkin, 2000). Amongst other
68 things, we expect species exposed to frequent environmental changes to benefit from a large
69 tolerance range, meaning from high flexibilities (e.g. earthworms exposed to changing
70 concentrations of pollutants should benefit from high flexibility in the synthesis of
71 detoxification proteins; Lukkari et al., 2004) or from the capacity to escape from these
72 detrimental environmental conditions and to disperse to settle in a more suitable habitat.

73 The three functional groups of earthworms inhabit three different niches whose exposure to
74 aboveground conditions increases from the endogeic group to the epigeic group. The
75 aboveground environment is characterized by a high temporal and spatial heterogeneity.
76 Therefore, epigeic earthworms have to face highly fluctuating environments (e.g. temperature
77 and humidity changes) and are more directly exposed to soil inputs (e.g. pesticides,
78 hydrocarbons, fertilizer, etc.), soil surface state (e.g. subsidence exerted by vehicles,
79 ploughing or bioturbations) and predators. Consequently, we may expect epigeic earthworms
80 to have evolved higher sensibility to surface conditions (i.e. quicker responses) and higher
81 dispersal abilities (i.e. lower dispersal costs, associated with physiological and anatomical
82 adaptations for low latency and high speed movements) than endogeic and anecic groups.

83

84 Habitat (i.e. soil and litter) structure (e.g. particle size distribution), composition (e.g. amount
85 of organic carbon) and pH, both linked to bioavailability of chemicals in soils and
86 earthworms' ability to move in the habitat, are expected to influence earthworm habitat
87 preference (Lanno et al., 2004) and as a consequence dispersal behaviour. Moreover, the
88 amount of food in the environment is often limited; therefore, food availability per individual
89 is negatively correlated with population density (Curry, 1998). Alternatively, population
90 density may affect soil physical and chemical properties (Jones et al., 2010, 1994; Rillig et al.,
91 2016), which may lead to facilitating mechanisms (Caro et al., 2012; Mathieu et al., 2010).
92 Nonetheless, to our knowledge, few studies have investigated the environmental factors that
93 influence dispersal behaviour in earthworms. Caro et al. (2013, 2012) and Mathieu et al.
94 (2010) showed that low soil quality increased dispersal rate of *Aporrectodea icterica*,
95 *Allolobophora chlorotica*, *Aporrectodea caliginosa* (endogeic species) and of *Aporrectodea*
96 *longa*, *Lumbricus terrestris* and *Aporrectodea giardi* (anecic species) (Caro et al., 2013;
97 Mathieu et al., 2010). Moreover, the absence of litter increased dispersal rate in *Dendrobaena*

98 *venata*, an epigeic species (Mathieu et al., 2010). High intraspecific density also increased
99 dispersal rate in the three anecic species and in *A. icterica* but not in *A. chlorotica* and *A.*
100 *caliginosa*. Finally, while dispersal speed was increased by conspecifics through the use of
101 existing galleries in *Aporrectodea giardi* (Caro et al., 2012), dispersal rate was reduced by the
102 pre-use of soil in *A. icterica* (Mathieu et al., 2010). Previous studies on earthworm dispersal
103 were mostly carried out on endogeic and on anecic groups (Caro et al., 2013, 2012) or on a
104 single epigeic species (Mathieu et al., 2010). Therefore, we still know little about the dispersal
105 behaviour of the epigeic group and whether it is different from the two other groups.

106
107 To investigate diffusion and dispersal behaviour of epigeic earthworms, we performed three
108 different experiments on three epigeic species (i.e. *Eisenia fetida*, *Eisenia andrei* and
109 *Lumbricus rubellus*), following the same experimental protocol as a previous experiment
110 (Caro et al. 2013). We investigated diffusion behaviour in a homogeneous environment
111 (experiment 1), to measure earthworm propensity to explore, their distance of exploration and
112 their tendency to follow their conspecifics. We measured dispersal rate in response to habitat
113 quality (experiment 2) or in response to population density (experiment 3). Then, we
114 compared diffusion and dispersal behaviours of epigeic earthworms with that of the two other
115 functional groups: anecics and endogeics, whose behaviours have been previously measured
116 through similar experiments (Caro et al., 2013). We expected high specificity in epigeic
117 dispersal behaviours because of their specific relative selective pressures.

118

119 **2. Methods**

120

121 **2.1 Subjects and housing**

122 Free-living adult earthworms from three epigeic species – *Eisenia fetida*, *Eisenia andrei* and
123 *Lumbricus rubellus* - were collected in November 2015 from several rural locations in Ile-de
124 France, near Paris, France (between 48°69'N, 2°60'E and 48°74'N, 2°68'E). Earthworms
125 were kept in acclimatizing mesocosms (12 cm x 10 cm x 8 cm) filled with suitable soil (see
126 2.2 Diffusion and dispersal mesocosms set-up) with a density of 10 earthworms per
127 mesocosm, at a constant 17°C. Before the start of the trials (section 2.3) earthworms were
128 acclimatized for a period of at least 3 weeks, depending on their capture date and the trial
129 dates, to remove potential stress effects of capture. Acclimatizing mesocosms were
130 humidified and enriched with homogenized horse dropping twice a month. All individuals
131 were kept for at least three weeks before onset of experiments. The species names used herein
132 conformed to the Fauna Europaea web site.

133

134 **2.2 Diffusion and dispersal mesocosms set-up**

135 First, we investigated diffusion in a homogeneous environment (experiment 1). Then, two
136 different environmental factors were tested on epigeic earthworm dispersal: population
137 density (experiment 2) and habitat quality (experiment 3). The experiments' setting followed
138 the protocol used by Caro et al. (2013). Diffusion behaviour in a homogeneous environment
139 was tested in mesocosms (300 cm x 20 cm x 20 cm) that consisted of a suitable habitat. The
140 suitable habitat consisted of grassland soil collected from a brunisol at the IRD research
141 centre (48°54'N, 2°29'E), which hosts large earthworm populations. Because epigeic
142 earthworms mainly inhabit litter, lime leaves (*Tilia vulgaris*) were added on the surface of the
143 suitable soil. This litter is generally well consumed by earthworms (Hendriksen, 1990). This
144 first experiment tested the natural spread of individuals while removing the effect of
145 heterogeneity. The mesocosms were divided in 13 regular sections (each 23 cm long) which
146 were named according to their distance from the central section (see Fig. 1).

147 The influence of population density and habitat quality were investigated in dispersal
148 mesocosms (100 cm x 20 cm x 20 cm; Mathieu et al., 2010), which were divided into three
149 equal sections (see Fig. 1): the “inoculation” section (1) was a suitable habitat in population
150 density trials and either a suitable or an unsuitable habitat in habitat quality trials; the
151 “crossing” section (2) was always an unsuitable habitat; finally, the “arrival” section (3) was
152 always a suitable habitat. The suitable habitat was similar to the one previously described (i.e.
153 grassland soil + leaf litter). The unsuitable habitat consisted of a sandy soil collected from a
154 luvisol in an area deprived of earthworms and litter in the forest of Fontainebleau (48°24’N,
155 2°44’E). Because of their niche, epigeic earthworms were expected to be strongly affected by
156 litter quality. Therefore, the unsuitable soil was not topped with litter. We checked in a
157 preliminary experience that the three species did prefer the suitable soil to the unsuitable one.
158 Both soils were air dried, sieved to 2 mm and rewetted manually at 25% of humidity. Lime
159 leaves were washed, air dried and soaked in tap water for 15 minutes. Soil (suitable or
160 unsuitable) was filled to 5 cm high and 2 cm high of lime leaves were spread on the top of
161 appropriate sections. This setup allowed the reproduction of the three stages of dispersal:
162 departure, crossing and settlement in a suitable site (Clobert et al., 2009). The unsuitable
163 habitat in the crossing section represented a physical barrier generating dispersal costs. It
164 allowed us distinguishing between mechanisms of diffusion (random movements with
165 potentially returns in the starting point) from active dispersal (Clobert et al., 2009). As
166 expected, diffusion rate in a homogeneous high quality habitat was higher than dispersal rate
167 from a high-quality habitat (see Table 1 and Fig. 2), verifying that our dispersal mesocosm
168 set-up successfully induced a dispersal cost, and suggesting that dispersal rate rather than
169 diffusion rate was measured in dispersal experiments.

170

171 **2.3 Diffusion and dispersal trials**

172 When investigating diffusion behaviour in a homogeneous environment (experiment 1), we
173 simultaneously inoculated 10 earthworms of the same species in the central section of a three-
174 meter long mesocosm (i.e. section 0). To avoid earthworms from escaping during inoculation,
175 earthworms were placed in the centre of a rectangular plastic gate (12 cm x 10 cm x 6 cm)
176 previously buried at 1.5 cm deep in the centre of the inoculation section, which was ever in
177 the middle of the mesocosm (experiment 1) or at the left (experiments 2 and 3). We checked
178 that all earthworms entered the soil or remained motionless before removing the gate and
179 closure of the mesocosms. Each trial of the first experiment (experiment 1) lasted 24h; this
180 time was short enough to prevent individuals from reaching the end of the mesocosms and
181 going back towards the inoculation section. At the end of each trial, the 13 sections were
182 separated and the number of earthworms per section was counted. We calculated diffusion
183 rate as the proportion of individuals that left the central section. Despite the mesocosms being
184 carefully closed, some earthworms escaped; the escape rate was low during the diffusion trials
185 (mean \pm se: $2 \pm 7\%$, $0 \pm 6\%$ and $0 \pm 0\%$ in *E. fetida*, *E. andrei* and *L. rubellus*, respectively).
186 In order to take into account these escapes, diffusion rates were calculated as the number of
187 individuals that left the central section (i.e. section 0) compared to the number of individuals
188 that were found in the inoculation section at the end of a trial. We also investigated the mean
189 of the absolute distance crossed and the tendency to follow conspecifics as the absolute value
190 of the difference in the diffusion rates to the right and to the left of a starting section; thus the
191 tendency to follow their conspecifics varies from 0 (individuals equally distributed in each
192 side) to 1 (all individuals in only one side).

193 When investigating the effect of habitat quality on dispersal rate (experiment 2), we
194 simultaneously inoculated 10 earthworms of the same species in a one meter long mesocosm.
195 When testing the effect of population density on dispersal rate (experiment 3), we inoculated
196 earthworms in the mesocosm, at one of these four densities: 1, 10, 20 or 30 individuals of the

197 same species. Each trial of experiments 2 and 3 lasted 7 days. At the end of each trial, the 3
198 sections were separated in order to prevent earthworms from switching between sections. Soil
199 and lime leaves were carefully searched and earthworms were removed. Earthworms were
200 then replaced in their resting mesocosms. The number of earthworms per section was
201 counted; earthworms found in the arrival section were considered as disperser, while
202 earthworms found in the inoculation and crossing section were considered as non-dispersers.
203 Some of the earthworms also escaped these dispersal devices (mean \pm se: $31 \pm 5\%$, $27 \pm 5\%$
204 and $4 \pm 5\%$ in *E. fetida*, *E. andrei* and *L. rubellus*, respectively). The escape rate did not
205 depend on the initial density ($\chi^2_{ddl=1}=0.01$, $P=0.909$). Nonetheless, dispersal rates were
206 calculated as the number of individuals in the arrival section compared to the number of
207 individuals found in the two other sections at the end of the trials, which allowed measuring
208 dispersal behaviour rather than departure behaviour. Each experimental design (i.e.
209 homogeneous environment, high quality, low quality, density 1, density 10, density 20 and
210 density 30) was replicated 5 times per species under the same conditions of light (a daily
211 photoperiod of 10h) with temperature fluctuating between 15°C and 17°C.

212

213 **2.4 Comparison of diffusion and dispersal behaviour between functional groups**

214 We compiled the data obtained in these experiments with those obtained in a previous similar
215 study on anecic and endogeic earthworms (Caro et al., 2013) in order to compare dispersal
216 behaviour between functional groups. Note that in order to take into account for the specific
217 ecology of epigeics, the suitable and unsuitable habitats slightly differed in our study from the
218 ones in Caro et al. (2013): we added a layer of leaf litter on top of the suitable soil, and soil
219 depth was reduced to 5 cm high instead of 15 cm in the previous study. Both studies aimed at
220 mimicking a suitable and an unsuitable habitat, which necessarily implied some minor habitat
221 differences to adjust to the focus group.

222

223 **2.5 Statistical analyses**

224 **2.5.1 Diffusion and dispersal behaviour in epigeic earthworms** - To investigate whether
225 the diffusion rate, the mean distance crossed and the tendency to follow conspecifics in a
226 homogeneous environment varied between species (experiment 1), we performed a
227 Generalized Linear Model (GLM) with a binomial distribution (model 1) and Linear Models
228 (model 2 and 3), respectively: diffusion rate, diffusion direction or the mean distance crossed
229 was the dependent variable and species identity was the explanatory variable. In order to test
230 the effects of habitat quality (model 4) and population density (model 5) on dispersal rate, we
231 used GLM with binomial distributions: dispersal rate was the dependent variable and habitat
232 quality (i.e. high vs. low), species identity (i.e. *Eisenia fetida*, *Eisenia andrei*, *Lumbricus*
233 *rubellus*) and their interactive effects (model 4) or population density (i.e. 1, 10, 20, 30),
234 species identity and their interactive effect (model 5) were the explanatory variables. Because
235 some of the earthworms escaped during the experiment and we have no means to know when
236 it happened, we also tested the effect of final density on dispersal rate (model 5) by
237 considering the number of earthworms that have been found at the end of the experiment as
238 the explanatory variable instead of the number of earthworms inoculated.

239 **2.5.2 Comparison of diffusion and dispersal behaviour between functional group** – We
240 compared the results from our three experiments on epigeic species to the ones obtained in a
241 previous study with a similar experimental setup carried on three species of anecic (*A. longa*,
242 *L. terrestris* and *A. giardi*) and three species of endogeic earthworms (*A. chlorotica*, *A.*
243 *icterica* and *A. caliginosa*; Caro et al., 2013). We re-run our five previous models aggregating
244 our results with the results from the previous study. In model 1 (Generalized Linear Mixed
245 Models), 2 and 3 (Mixed-Effects Models), functional group was the explanatory variable and
246 species was added as a random factor. In models 4 and 5 (Generalized Linear Mixed Models),

247 the interactive effect between habitat quality or population density and functional group (i.e.
248 epigeic, anecic, endogeic) was the explanatory variable and species identity was added as a
249 random factor. Finally, we performed a Partial Least Squares – Discriminant Analysis (PLS-
250 DA; mixOmics and RVAideMemoire packages in R) to compare dispersal behaviour between
251 functional groups as a combination of the diffusion rate in homogeneous environment, the
252 mean distance crossed in homogeneous environment, the tendency to follow conspecifics, the
253 mean sensitivity to habitat quality (calculated as the difference between the mean dispersal
254 rate from low quality habitat and from high quality habitat within a species), the sensitivity to
255 population density (calculated as the slope of the regression between dispersal rate and
256 population density), averaged for each species. PLS-DA is a supervised multivariate analysis
257 that classifies groups of observations (i.e. functional groups) based on multivariate predictors
258 (results from the different experiments; i.e. diffusion rate, mean distance crossed, tendency to
259 follow conspecifics, sensitivity to habitat quality and sensitivity to population density), and
260 which helps to identify which variables best discriminate the groups.

261 Statistical analyses were performed using R software (version 3.1.2). Full models included all
262 factors and covariates and all their interactions. We retained final models based on their AIC.

263

264 **3. Results**

265

266 **3.1 Diffusion and dispersal behaviour in epigeic earthworms**

267 **3.1.1 Homogeneous environment (experiment 1)** – Diffusion behaviour in an homogenous
268 environment was significantly different between species ($\chi^2_{df=2}=14.97$, $P=0.001$): diffusion
269 rate was lower in *L. rubellus* than in *E. fetida* ($F_{1,8}=6.57$, $P=0.010$) and *E. andrei* ($F_{1,8}=14.18$,
270 $P<0.001$; Table 1). The mean distance crossed was also significantly different between
271 species ($F_{2,12}=5.61$, $P=0.019$): the mean distance crossed was shorter in *L. rubellus* than in *E.*

272 *andrei* ($F_{1,8}=8.20$, $P=0.022$, Table 1). The tendency to follow conspecifics was not
273 significantly different between species ($F_{2,12}=1.22$, $P=0.329$; Table 1).

274

275 **3.1.2 Habitat quality (experiment 2)** –There was a significant interaction between habitat
276 quality and species identity on the dispersal rate ($\chi^2_{df=2}=10.49$, $P=0.005$; Fig. 2): in all three
277 species, dispersal rate was higher when earthworms were inoculated into a low quality habitat
278 than into a high quality habitat ($\chi^2_{df=1}=5.15$, $P=0.023$; $\chi^2_{df=1}=17.40$, $P<0.001$ and $\chi^2_{df=1}=45.09$,
279 $P<0.001$ for *E. fetida*, *E. andrei* and *L. rubellus*, respectively). However, dispersal rate from
280 high quality habitat significantly differed between species ($\chi^2_{df=2}=24.89$, $P<0.001$): *L. rubellus*
281 dispersed less from high habitat quality than the two other species ($\chi^2_{df=1}=16.58$, $P<0.001$ and
282 $\chi^2_{df=1}=21.48$, $P<0.001$ for *E. fetida* and *E. andrei*, respectively); dispersal rate from low
283 quality habitat did not differ between species ($\chi^2_{df=2}=5.24$, $P=0.073$).

284

285 **3.1.3 Population density (experiment 3)** – There was a significant interaction between
286 population density (i.e. 1, 10, 20, 30) and species identity on the dispersal rate ($\chi^2_{df=6}=27.38$,
287 $P<0.001$; Fig. 3): dispersal rate increased with increasing population density in *E. andrei*
288 ($\chi^2_{df=1}=7.85$, $P=0.005$), while it decreased with increasing population density in *L. rubellus*
289 ($\chi^2_{df=1}=15.81$, $P=0.001$); the correlation between dispersal rate and population density was not
290 significant in *E. fetida* ($\chi^2_{df=1}=3.00$, $P=0.083$). The results were quite similar when considering
291 the number of earthworms found at the end of the experiment as the explanatory variable;
292 there was a significant interaction between the final density and species identity on the
293 dispersal rate ($\chi^2_{df=2}=24.44$, $P<0.001$): dispersal rate increased with increasing the final
294 density in *E. andrei* ($\chi^2_{df=1}=12.95$, $P<0.001$) while it decreased with increasing population
295 density in *L. rubellus* ($\chi^2_{df=1}=5.36$, $P=0.021$) and *E. fetida* ($\chi^2_{df=1}=5.19$, $P=0.023$).

296

297 **3.2 Comparison of diffusion and dispersal behaviour between functional groups**

298 **3.2.1 Homogeneous environment** - There was no significant effect of functional group on
299 diffusion rate in an homogenous soil ($\chi^2_{df=2}=1.90$, $P=0.387$; Table 2), on the mean distance
300 crossed ($\chi^2_{df=2}=0.91$, $P=0.634$; Table 2) and on the tendency to follow conspecifics
301 ($\chi^2_{df=2}=0.23$, $P=0.890$; Table 2).

302

303 **3.2.2 Habitat quality** - There was a significant interaction between habitat quality and
304 functional group on the dispersal rate ($\chi^2_{ddl=2}=16.59$, $P<0.001$; Fig. 4): in all three functional
305 groups, dispersal rate was higher when earthworms had been inoculated into a low quality
306 habitat than into a high quality habitat ($\chi^2_{ddl=1}=46.62$, $P<0.001$; $\chi^2_{ddl=1}=112.51$, $P<0.001$ and
307 $\chi^2_{ddl=1}=67.05$, $P<0.001$ for epigeic, anecic and endogeic earthworms respectively). However,
308 dispersal rate from low quality habitat significantly differed between functional groups
309 ($\chi^2_{ddl=2}=7.34$, $P<0.026$): it was lower in endogeic earthworms than in the two other functional
310 groups ($\chi^2_{ddl=1}=5.29$, $P=0.021$ and $\chi^2_{ddl=1}=4.43$, $P=0.035$ when compared to anecic and epigeic
311 earthworms, respectively); on the contrary, dispersal rate from high quality habitat did not
312 significantly differed between functional groups ($\chi^2_{ddl=2}=3.06$, $P=0.216$).

313

314 **3.2.3 Population density** - There was no significant effect of population density ($\chi^2_{df=1}=1.83$,
315 $P=0.176$), functional group ($\chi^2_{df=1}=3.64$, $P=0.162$) and their interactions ($\chi^2_{df=2}=3.03$, $P=0.220$)
316 on dispersal rate (Fig. 5). The results were quite similar when considering the number of
317 earthworms found at the end of the experiment as the explanatory variable: there was a
318 significant interaction between the final density and species on the dispersal rate
319 ($\chi^2_{ddl=2}=15.66$, $P<0.001$) but final density tended to influence dispersal rate in anecic
320 earthworms only ($\chi^2_{ddl=1}=0.30$, $P=0.584$, $\chi^2_{ddl=1}=2.81$, $P=0.094$ and $\chi^2_{ddl=1}=0.23$, $P=0.635$ in
321 epigeic, anecic and endogeic earthworms).

322

323 **3.2.4 PLS-DA components analysis** - Two components were retained in the PLS-DA: the
324 first and the second component explained 67.20% and 12.58% of the among group variation
325 respectively. The sensitivity to habitat quality, the sensitivity to population density and the
326 dispersal rate in homogeneous environment were the most important variables in the
327 projection (i.e. VIP index greater than 1). The first component was correlated with the
328 sensitivity to habitat quality ($t=-4.11$, $df=7$, $P=0.005$), while the second component was
329 correlated with the sensitivity to population density ($t=-10.87$, $df=7$, $P<0.001$), the dispersal
330 rate in homogeneous environment ($t=3.26$, $df=7$, $P=0.014$) and the mean distance crossed in
331 homogeneous environment ($t=2.77$, $df=7$, $P=0.028$).

332

333 **4. Discussion**

334

335 **4.1 Diffusion and dispersal behaviour in epigeic earthworms**

336 Our study demonstrated that dispersal behaviour of epigeic earthworms depends on habitat
337 quality and population density, and that this response varies among epigeic species.

338 Firstly, results showed a higher dispersal rate of *Eisenia fetida* and *Eisenia andrei* than of
339 *Lumbricus rubellus* from high quality habitat. This elevated basal dispersal rate may be
340 related to the narrower ecological niche of *E. fetida* and *E. andrei*, characterized by a high
341 proportion of organic matter (i.e. they inhabit compost and manure; Lee, 1985). Therefore, the
342 so-called “high quality” habitat, composed of grassland soil topped with lime leaves may
343 actually be moderately favourable for those species, consequently inducing high dispersal
344 rates. Alternatively, both species might have high basal dispersal behaviour associated with
345 high exploratory behaviour. This interpretation is supported by the results of our first
346 experiment in a homogeneous environment. Indeed, diffusion rates in homogeneous

347 environment were higher in *E. fetida* and *E. andrei* than in *L. rubellus*, and the mean distance
348 crossed was also higher in *E. andrei* than in *L. rubellus*. It might also explain the higher
349 escape rate measured in these two species than in *L. rubellus*. Moreover, our study clearly
350 demonstrated an effect of habitat quality on dispersal rate, with earthworms exhibiting a
351 higher dispersal rate in a low than in a high quality habitat. Therefore, as for anecic and
352 endogeic earthworms (Caro et al., 2013), habitat quality should be a strong driver of epigeic
353 earthworm spatial distribution in ecosystems. Future studies should identify more thoroughly
354 which habitat characteristics count for epigeic earthworms' decision to disperse. In particular,
355 we need to disentangle the role of leaf litter presence and characteristics (e.g. plant variety,
356 decomposition state) from the role of soil characteristics (e.g. composition, humidity). *E.*
357 *fetida* response to habitat quality was less pronounced comparing to *E. andrei* and *L. rubellus*
358 but also more variable between individuals, suggesting that this species would either be less
359 sensitive to habitat quality, or suffer high dispersal cost, which is doubtful regarding their
360 high dispersal rate in high quality habitat.

361

362 Secondly, our study highlighted no clear pattern of response to population density in epigeic
363 earthworms: dispersal rate increased with increasing population density in *E. andrei* but not in
364 the two other species. Insufficient information is available regarding the biotic environmental
365 factors that influence habitat choice in earthworms (but see Caro et al., 2013; Curry, 1998;
366 Mathieu et al., 2010; Palm et al., 2013). For instance, the presence of conspecifics could be
367 used as a clue of a high quality habitat (Lister, 2014). For instance, *E. fetida* lives at high
368 density, arguably because they chose patches of abundant food. In accordance, attraction
369 mechanisms were observed in this species (Zirbes et al., 2012, 2010). In contradiction,
370 dispersal rate of *E. fetida* was not negatively correlated with population density in our study.
371 Moreover, earthworms' motions and secretions (i.e. earthworm cast and mucus) induce strong

372 modifications of the physical and chemical parameters of the soil (Jones et al., 2010; Rillig et
373 al., 2016). Therefore, earthworm presence modifies the habitat in a way that may increase
374 earthworm propensity to establish (Caro et al., 2014). In accordance with this hypothesis,
375 dispersal rates of *Aporrectodea icterica* (endogeic) were lower when the soil has been pre-
376 used by conspecifics in a former experiment (Mathieu et al., 2010). On the contrary, in the
377 species *E. andrei*, population density would trigger dispersal. Positive density dependence in
378 dispersal behaviour due to resource depletion is quite widespread in animals in general
379 (Murray, 1967; Waser, 1985). Uvarov (2009) showed that more than 85% of the studies
380 found negative effects of population density on earthworm demographic parameters, whatever
381 their functional group. For instance, negative density dependence was found for growth rates
382 and maturation in *E. fetida*, *E. andrei* and *L. rubellus*. The lack of a clear relationship between
383 dispersal rate and population density in *E. fetida* and *L. rubellus* did not verify that density
384 dependent dispersal is a key mechanism regulating population dynamics in the rapidly
385 reproducing species such as *E. fetida* and most epigeic earthworms (Kammenga et al., 2003).
386 It would suggest that, in these two species, either dispersal response to population density
387 would not covary with fitness improvement, or dispersal costs were higher than its benefits
388 (Ronce, 2007). We may also hypothesize that the density tested in our experiment (i.e. 1, 10,
389 20, 30) were under the threshold needed to induce the costs associated with crowding.

390

391 **4.2 Comparison of dispersal and diffusion behaviour between functional groups**

392 The comparison of dispersal behaviour of epigeic earthworms to the ones of anecics and
393 endogeics, investigated in a previous study (Caro et al., 2013), suggests that dispersal rate of
394 endogeic earthworms from low habitat quality was lower than the one of the epigeic and
395 anecic earthworms (see Fig. 4). This would suggest that either endogeic earthworm have a
396 broader ecological niche, a reduced sensitivity to habitat quality or poorer dispersal capacities

397 (i.e. higher dispersal costs) compared to the two other functional groups. This last explanation
398 would verify our hypothesis that earthworms experiencing high interactions with the
399 aboveground environment would be more exposed to environmental stochasticity and
400 therefore likely evolved higher dispersal capacities. Future studies should disentangle these
401 hypotheses by investigating the effects of dispersal choice on fitness (i.e. survival and
402 reproductive success) or health parameters (e.g. weight variation over time).

403 On the contrary, none of the three functional groups showed a clear response to population
404 density (see Fig. 6) and the three groups exhibited similar behaviour in dispersal rate, in mean
405 distance crossed and in the tendency to follow conspecifics in an homogeneous environment
406 (see Table 2). Our study showed that there was significant variability in the dispersal
407 behaviour of epigeic earthworm. Such variability had also been measured in anecic and
408 endogeic groups (Caro et al., 2013). The high variability of dispersal behaviour among
409 species of the same functional group may explain the lack of clear dispersal difference
410 between earthworms' functional group. It suggests that functional group would not be the
411 main factor explaining dispersal behaviour variability between species. It would be interesting
412 to perform similar experiments on a greater number of species per functional group to lower
413 the intragroup (i.e. within functional group) variation but also to extend the time and spatial
414 scale of the diffusion experiment which may help measuring variations in diffusion behaviour
415 dynamics along time in the longer term. Alternatively, functional groups may have to be
416 redefined in view of species diffusion and dispersal behaviours; although these behaviours
417 directly influence burrowing activities, which has known impact on soil processes, soil
418 invertebrate species are mainly categorised according to their foraging behaviour and as a
419 consequence to their position in foodwebs (Lavelle, 1996; Mariani et al., 2001). Indeed,
420 several species, although belonging to a same functional group, inhabit different habitat. For
421 instance, *E. fetida* and *E. andrei* habitat (i.e. mainly composts and manures) are very different

422 from *L. rubellus* one (i.e. mainly leaf litter but also soil), despite they are all classified as
423 epigeics. This may explain the low difference of dispersal behaviour between functional
424 groups. Note also that the two comparative studies had slightly different experimental designs
425 (i.e. presence of leaves and amount of soil). Because epigeic earthworms mainly live on the
426 leaf litter at the soil surface, we assume that their dispersal behaviour only slightly depends on
427 the amount of soil. However, the presence of leaf litter, by influencing food and shelter
428 availability, likely affect dispersal behaviour of anecics, and to a lower extent of endogeic
429 earthworms. Moreover, a deeper soil (> 15 cm depth) may have been more relevant in the
430 previous study to mimic a high quality habitat for anecic earthworm. Consequently, we may
431 think that in previous experiments, dispersal rate in high quality habitat might have been
432 lower in these groups if the soil had been topped with leaf litter or had been thicker. However,
433 dispersal rate of anecic and endogeic earthworms was already very low in high quality habitat
434 (lower than 20%), suggesting that the amount of food and soil was sufficient for the
435 experimental time and would not have significantly modulated dispersal behaviour.

436

437 In addition to identifying important factors influencing earthworms' dispersal choice, our
438 study underlines the high variability in the responses to these factors among species and
439 functional groups of earthworms. These complex patterns in dispersal behaviours contribute
440 to earthworm community composition and as a consequence to ecosystem functioning. Efforts
441 in maintaining ecosystem functioning and high ecosystem services, that often relies on
442 species and functional diversity (Balvanera et al., 2006; Mace et al., 2012), should be
443 optimized by taking into account such diversity in environmental factors sensitivity and
444 consequently in dispersal behaviours.

445

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447

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452 procedure. We testify that this study does not raise any conflict of interest.

453

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	<i>E. fetida</i>	<i>E. andrei</i>	<i>L. rubellus</i>
Diffusion rate	69 ± 11% (a)	81 ± 9% (a)	44 ± 14% (b)
Mean distance crossed (cm)	31 ± 6 (ab)	63 ± 1 (a)	18 ± 3 (b)
Tendency to follow conspecifics	0.18 ± 0.08 (a)	0.44 ± 0.19 (a)	0.37 ± 0.06 (a)

604

605 **Table 1** Comparison of diffusion behaviour (mean ± se) among epigeic earthworms.

606 Significant differences between species are indicated by different letters (a, b).

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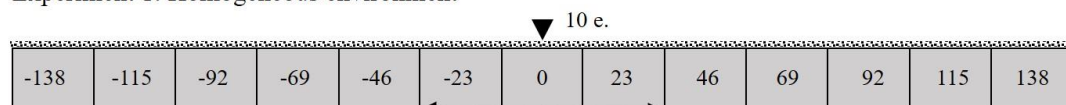
623

	Epigeic	Anecic	Endogeic
Diffusion rate	64 ± 6 %	83 ± 3 %	60 ± 10 %
Mean distance crossed (cm)	37 ± 7	60 ± 5	42 ± 13
Tendency to follow conspecifics	0.33 ± 0.07	0.43 ± 0.11	0.37 ± 0.13

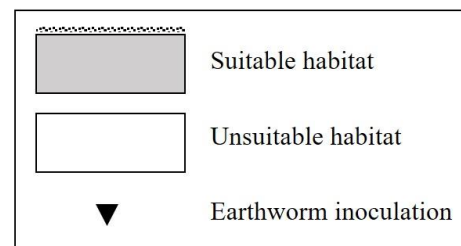
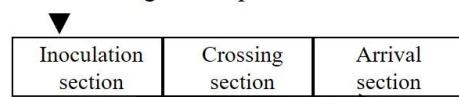
Table 2 Comparison of diffusion behaviour (mean ± se) between epigeic, anecic and endogeic earthworms. The three functional groups did not exhibit significantly different behaviour in dispersal rate, in mean distance crossed and in the tendency to follow conspecifics.

Fig. 1 Schematic representation of the experimental designs. The soil disposition in the mesocosms is symbolized by rectangles whose colour represent the nature of the habitat (suitable vs. unsuitable). The arrows indicate the section where earthworms (e.) were inoculated at the beginning of each trial.

Experiment 1: Homogeneous environment



General design for experiments 2 and 3



Experiment 2: Habitat quality



Experiment 3: Population density

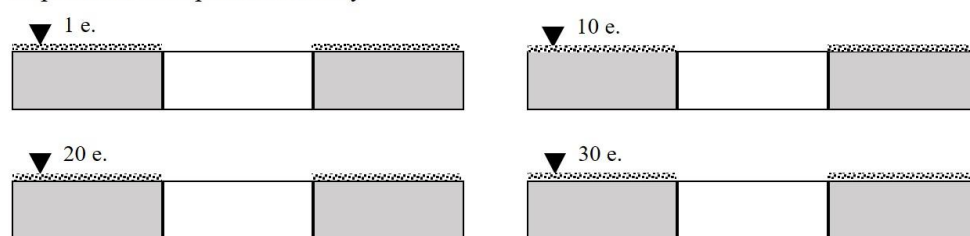


Fig. 2. Dispersal rate (mean \pm se) of three epigeic earthworm species inoculated in low quality habitat (black symbols) or in high quality habitat (white symbols). Significant differences between and among species are indicated by different letters (a, b, c).

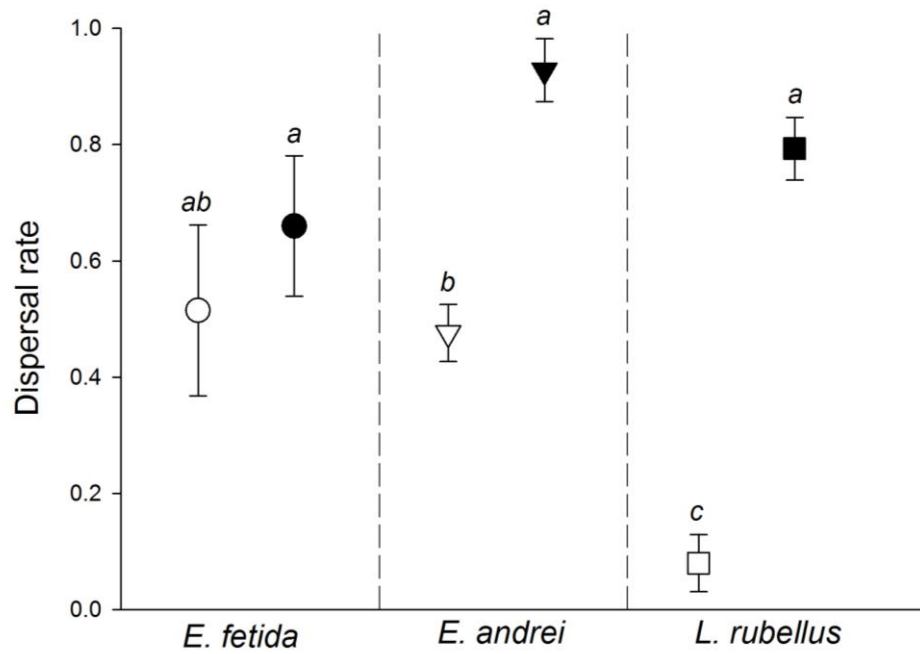


Fig. 3 Relationship between dispersal rate and population density (i.e. 1, 10, 20 or 30 earthworms) in three epigeic earthworm species. The points are slightly shifted around the correct densities to be clearly distinguishable one from another.

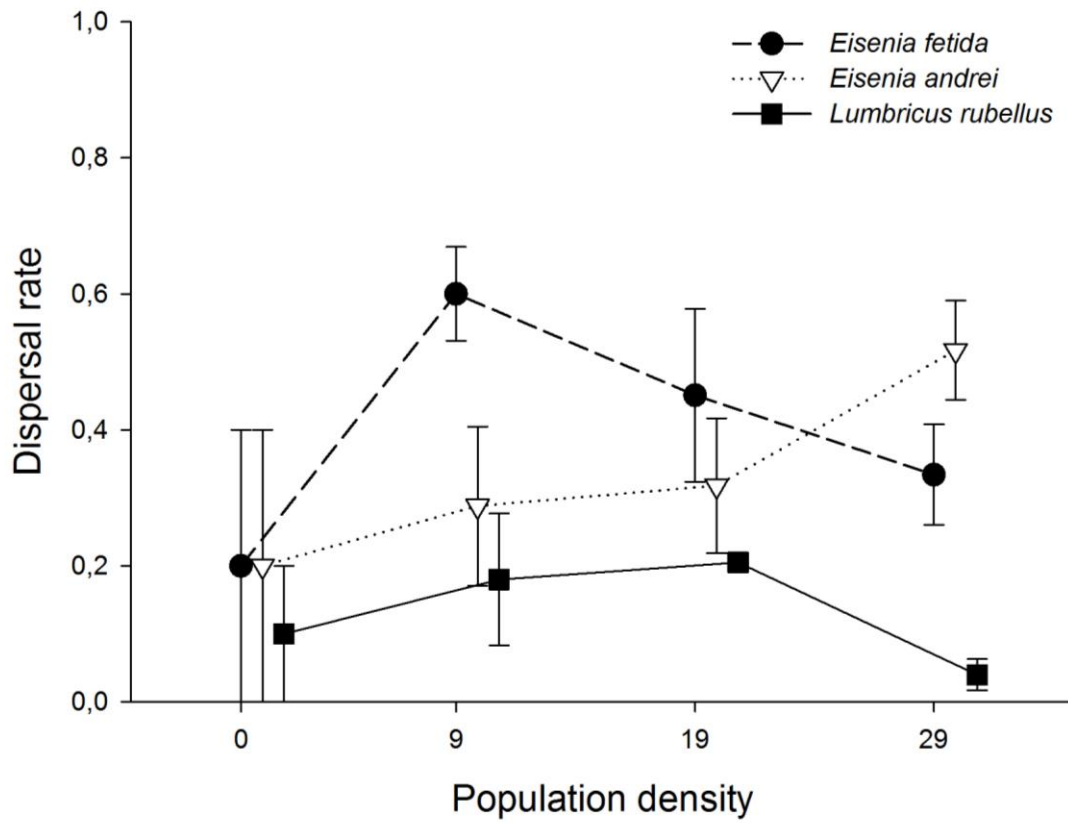


Fig. 4 Dispersal rate (mean \pm se) of epigeic (circles), anecic (triangles) and endogeic (squares) earthworms when inoculated in low quality habitat (black symbols) or in high quality habitat (white symbols). Significant differences are indicated by different letters (a, b, c).

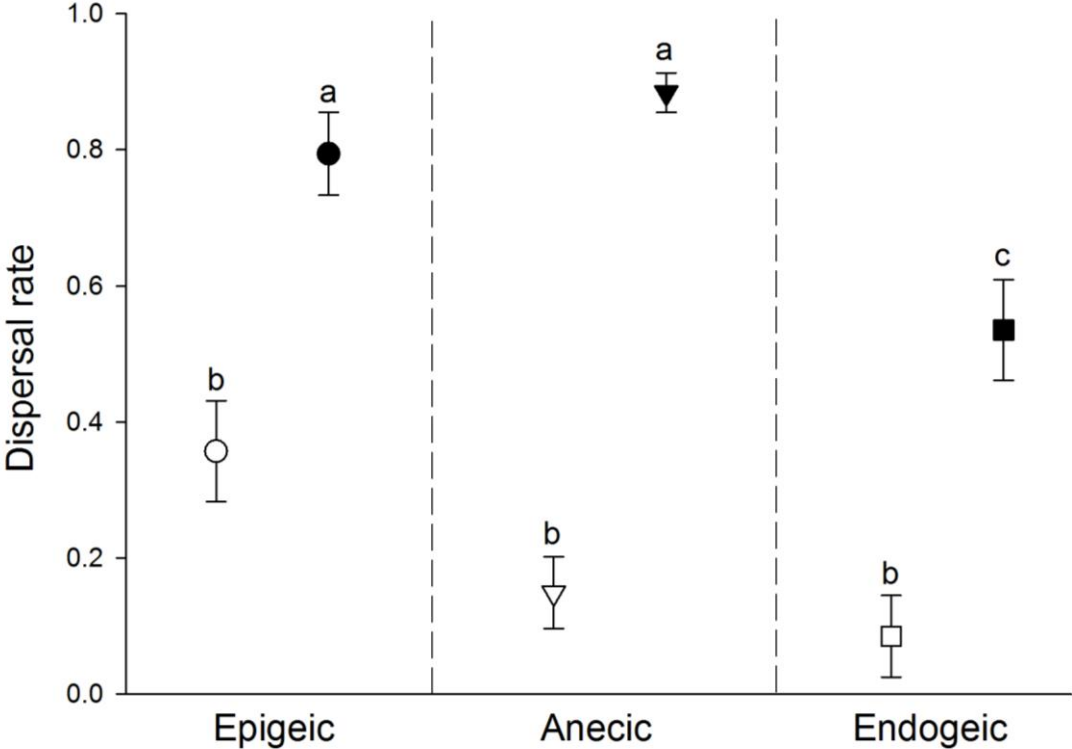


Fig. 5 Relationship between dispersal rate (calculated as the number of earthworms counted in the arrival section over the total number of earthworms) and population density (i.e. 1, 10, 20 or 30 earthworms) according to the functional group (i.e. epigeic, anecic, endogeic). The points are slightly shifted around the correct densities to be clearly distinguishable one from another.

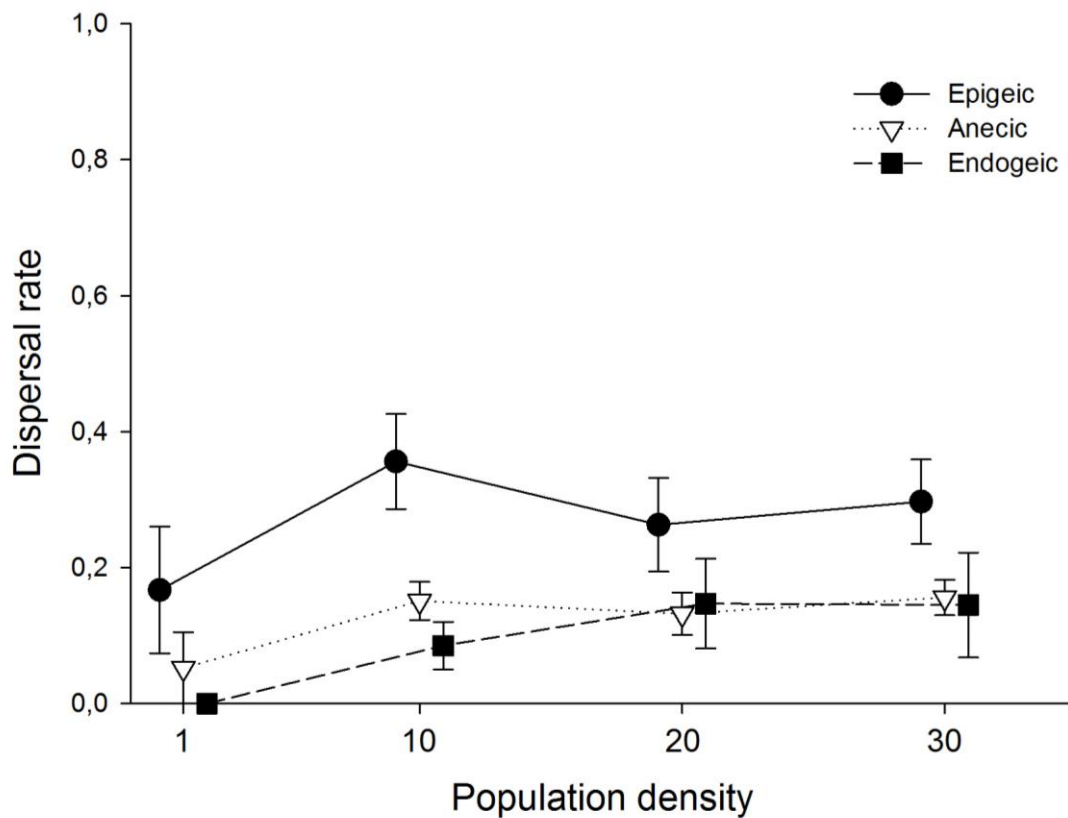
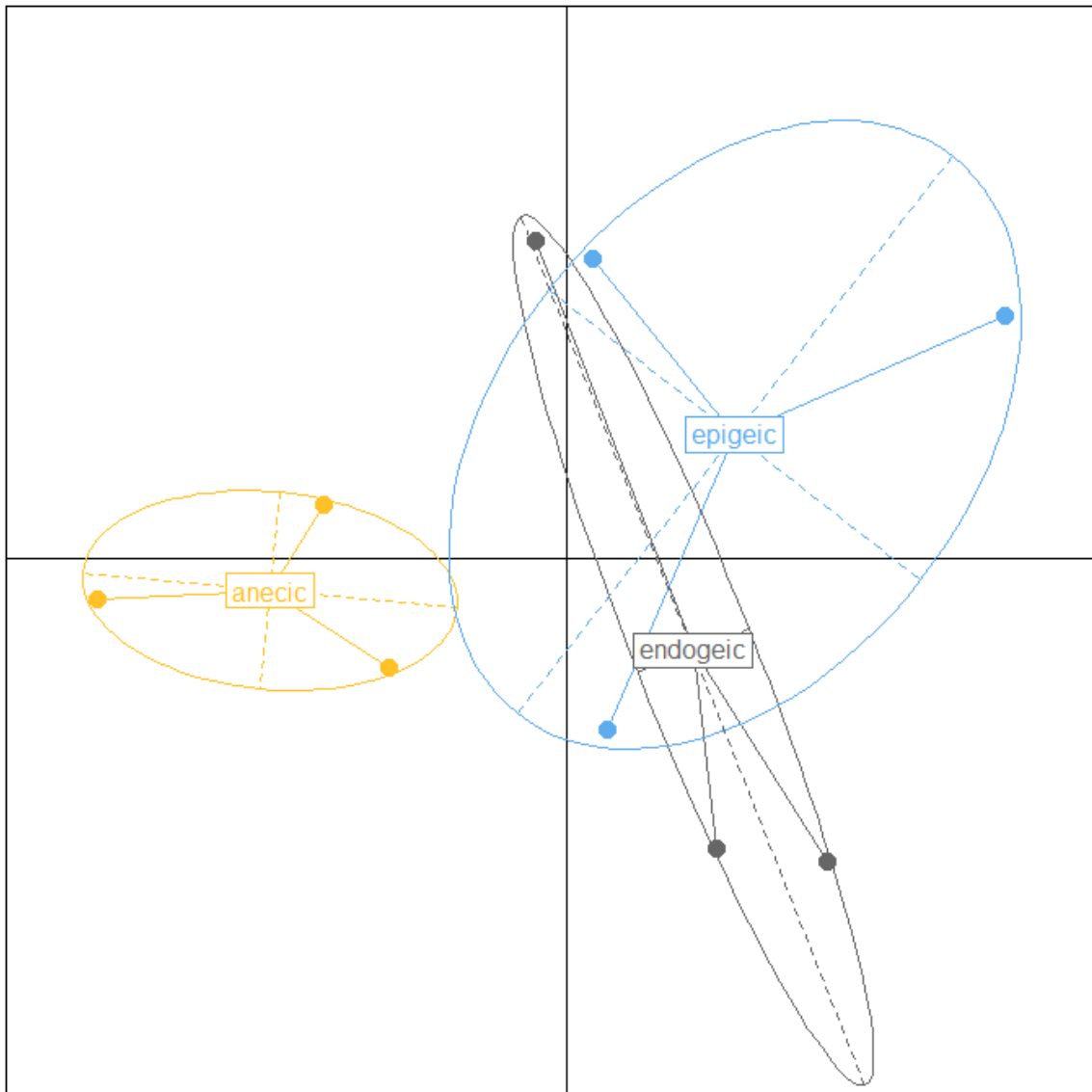
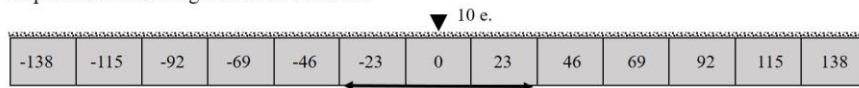


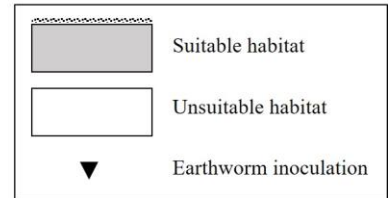
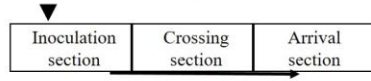
Fig. 6 Partial Least Squares - Discriminant Analysis (PLSDA function in R) on dispersal behaviour (i.e. density sensitivity, quality sensitivity, dispersal rate in homogeneous environment, mean distance crossed in homogeneous environment and tendency to follow conspecifics in homogeneous environment) between functional group (i.e. epigeic, anecic and endogeic).



Experiment 1: Homogeneous environment



General design for experiments 2 and 3



Experiment 2: Habitat quality



Experiment 3: Population density

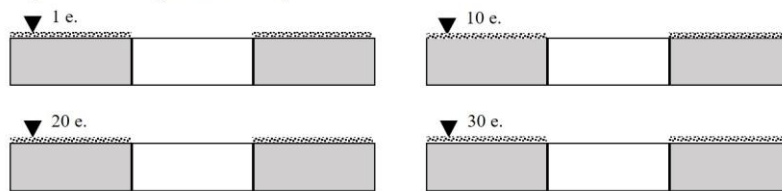


Fig. 1

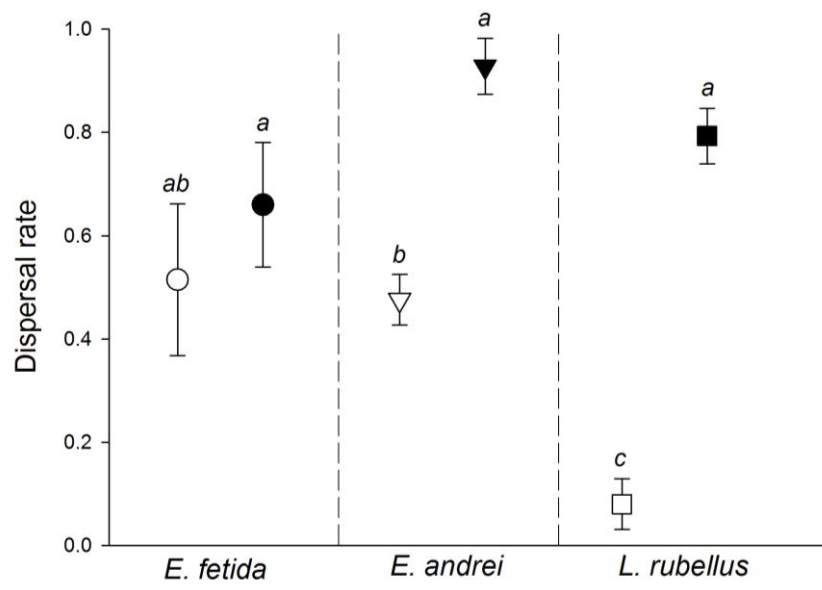


Fig. 2

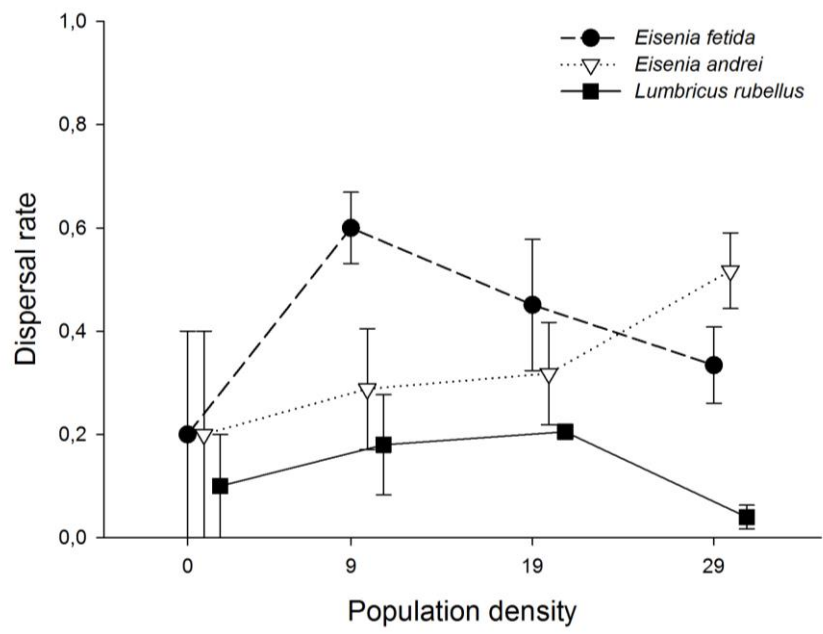


Fig. 3

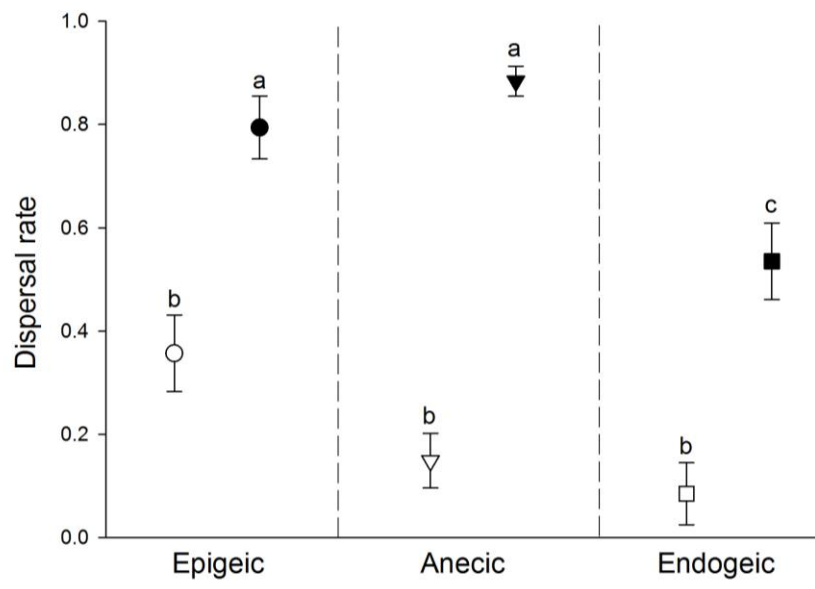


Fig. 4

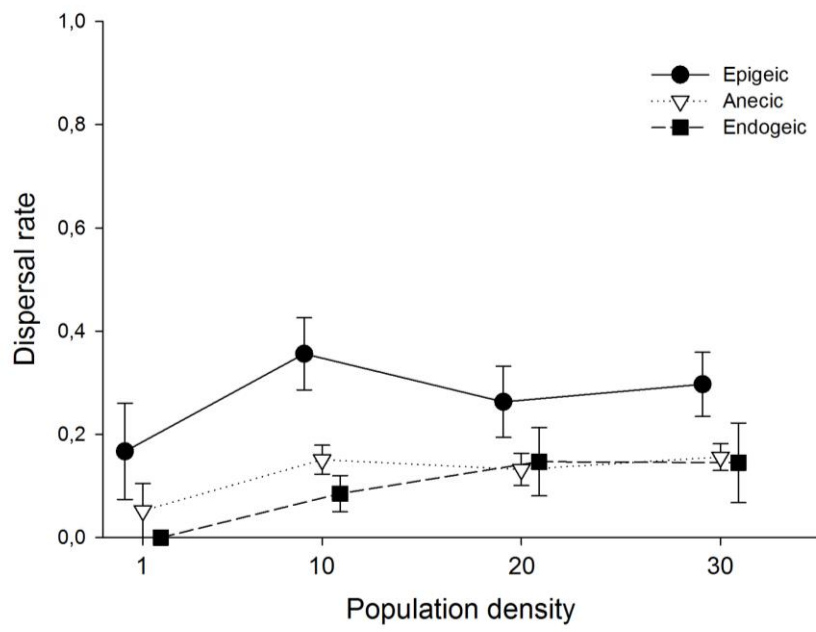


Fig. 5

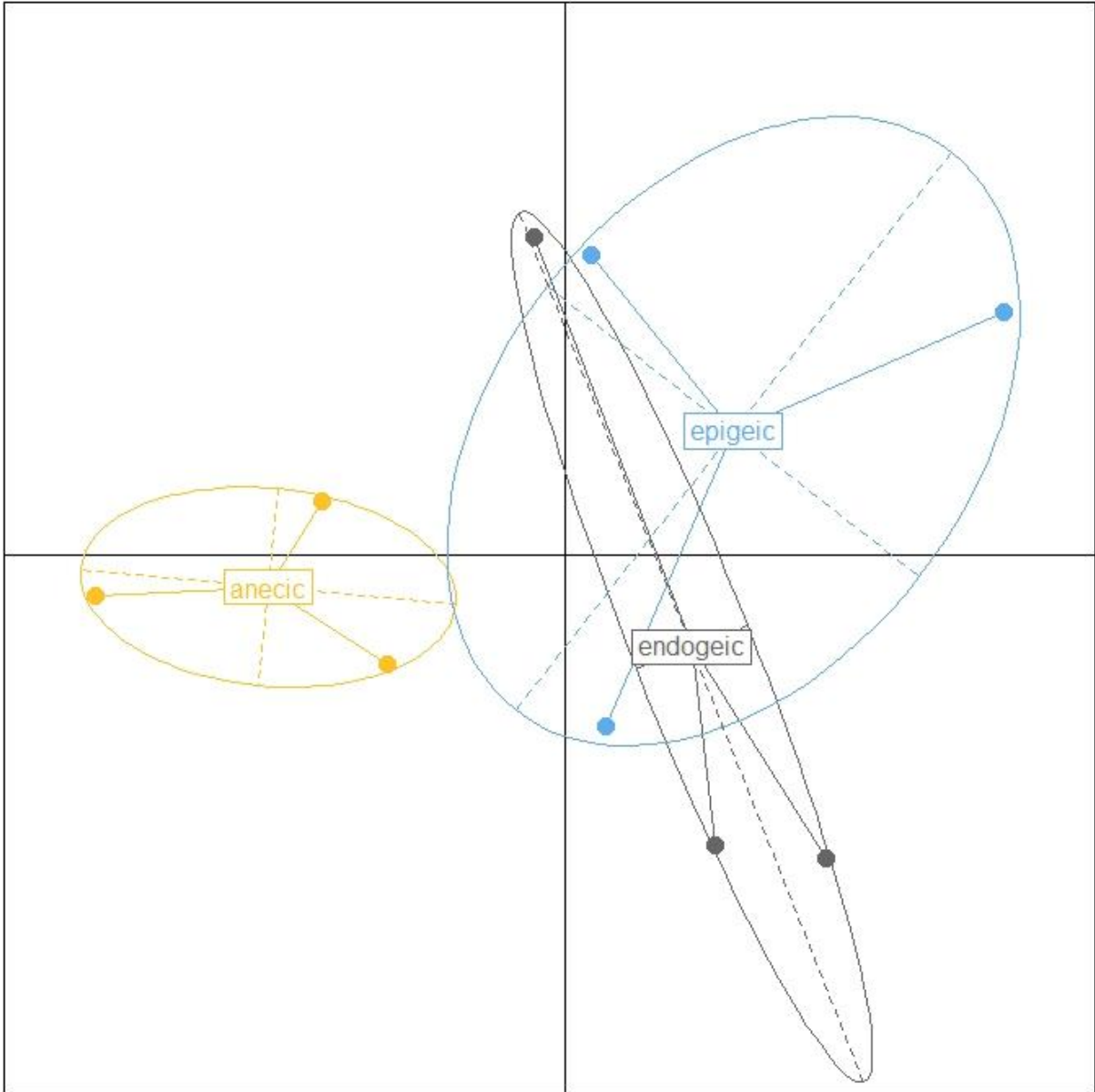


Fig. 6