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

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1   ABSTRACT

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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

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1. Introduction

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

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

because they modify the availability of resources for other organisms through physical and chemical changes in their surrounding soil environment (Jones et al., 2010, 1994; Rillig et al., 2016). As a consequence, they fulfil numerous soil-based ecosystem services (Blouin et al., 2013). While anecic earthworms, and to a lower extent endogeic and epigeic earthworms, are of particular importance for cropping systems (Bertrand et al., 2015; van Groenigen et al., 2014), epigeic earthworms play a key role in organic matter decomposition in deciduous forests because of the ingestion of poorly decomposed litter (Manna et al., 2003) and the interactions they established with decomposer microorganisms (Gómez-Brandón et al., 2012; Monroy et al., 2008), which explains their use in vermicomposting (e.g. Suthar et al., 2008).

For these reasons, it is essential to identify the environmental factors that may influence earthworm prevalence and abundance in ecosystems (Curry, 1998; Palm et al., 2013), especially in the context of global changes. Indeed, anthropogenic activities, including urbanisation and agriculture, are responsible for considerable modifications of the natural environment through e.g. light, noise and chemical pollutions, temperature modifications and habitat fragmentation. These changes may have considerable impact at the individual level and in terms of population dynamics and functioning (e.g. Dupont et al., 2015; Johnston et al., 2015; Orwin et al., 2015). To cope with these natural (e.g. soil heterogeneity, daily and seasonal cycles, etc.) or human-induced environmental constraints, high sensory capacities associated with acclimatization or dispersal abilities may have been naturally selected in earthworm species (e.g. Fisker et al., 2011; Spurgeon and Hopkin, 2000). Amongst other things, we expect species exposed to frequent environmental changes to benefit from a large tolerance range, meaning from high flexibilities (e.g. earthworms exposed to changing concentrations of pollutants should benefit from high flexibility in the synthesis of detoxification proteins; Lukkari et al., 2004) or from the capacity to escape from these 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**

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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 ± se: 2 ± 7%, 0 ± 6% and 0 ± 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 ± se: 31 ± 5%, 27 ± 5%

204   and 4 ± 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

2.5 Statistical analyses

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

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

3.2 Comparison of diffusion and dispersal behaviour between functional groups

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

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

3.2.3 Population density - There was no significant effect of population density ($\chi^2_{df=1}$=1.83, 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) on dispersal rate (Fig. 5). The results were quite similar when considering the number of earthworms found at the end of the experiment as the explanatory variable: there was a significant interaction between the final density and species on the dispersal rate ($\chi^2_{ddl=2}$=15.66, P<0.001) but final density tended to influence dispersal rate in anecic 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 epigeic, anecic and endogeic earthworms).

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

4. Discussion

4.1 Diffusion and dispersal behaviour in epigeic earthworms

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

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

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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

446 **5. Acknowledgments**

19

454   **6. References**

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599

	E. fetida	*E. andrei*	*L. rubellus*
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)

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Table 1 Comparison of diffusion behaviour (mean ± se) among epigeic earthworms. Significant differences between species are indicated by different letters (a, b).

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	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
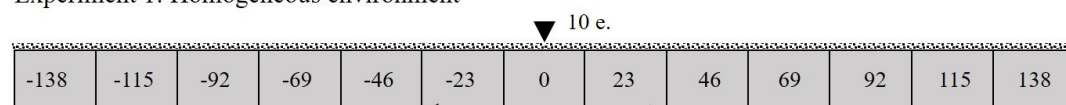
General design for experiments 2 and 3
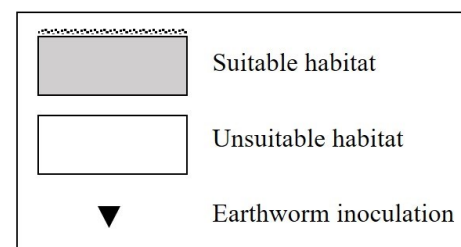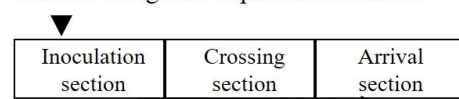
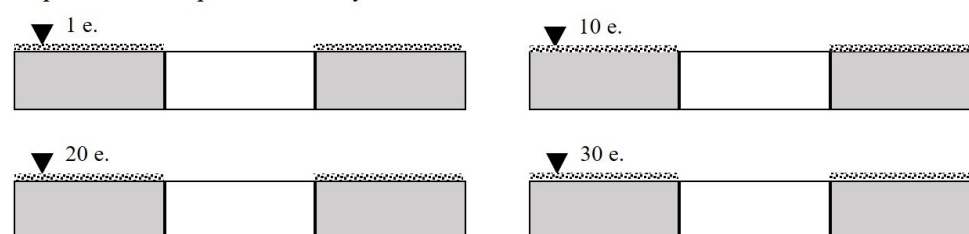Experiment 2: Habitat quality

Experiment 3: Population density

Fig. 2. Dispersal rate (mean ± 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).
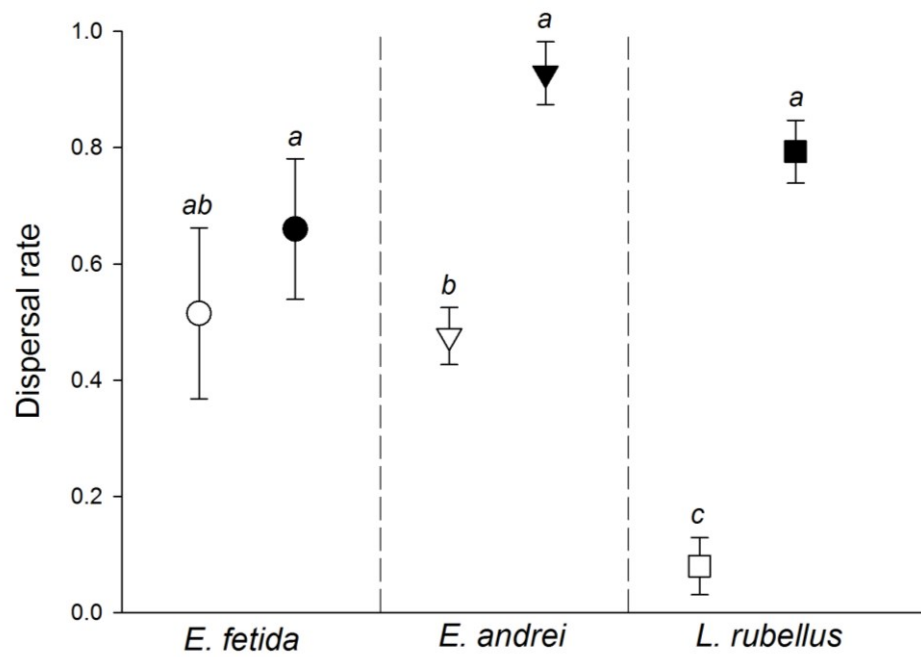
Fig. 3 Relationship between dispersal rate and population density (i.e. 1, 10, 20 or 30 earthworms) in three epigeic earthworm species. The points are slightly shifted around the correct densities to be clearly distinguishable one from another.
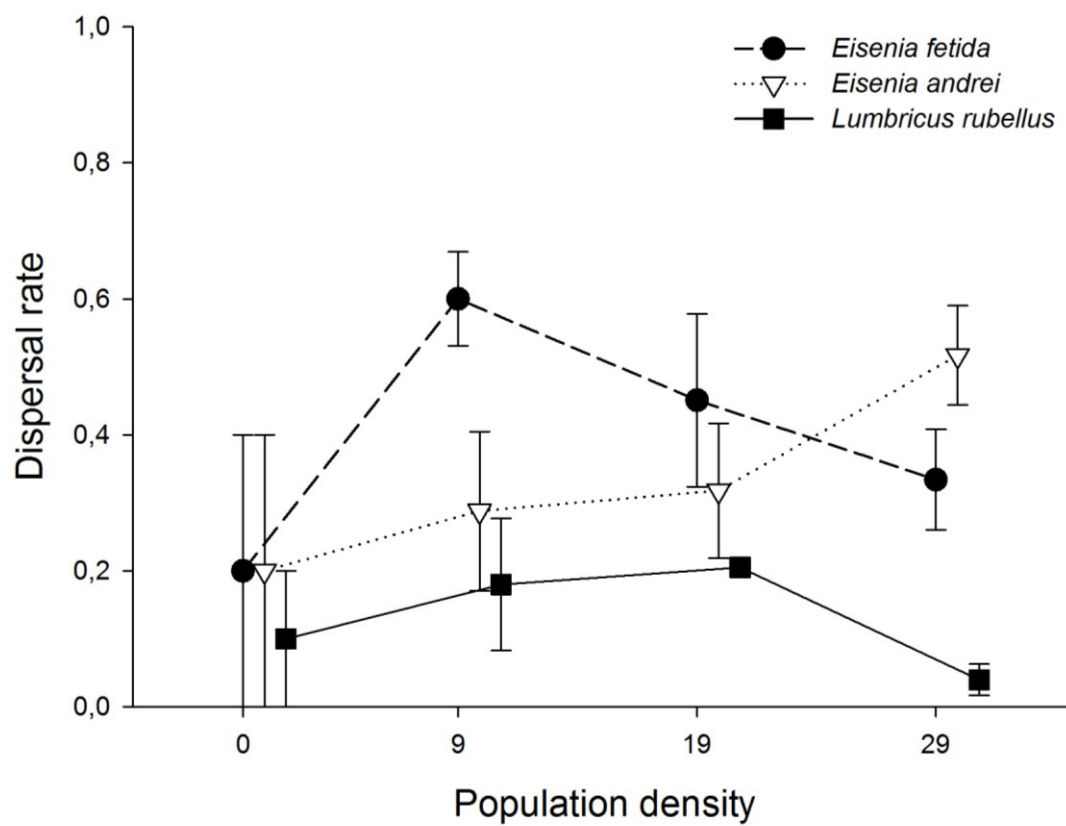
Fig. 4 Dispersal rate (mean ± se) of epigeic (circles), anecic (triangles) and endogeic (squares) earthworms when inoculated in low quality habitat (black symbols) or in high quality habitat (white symbols). Significant differences are indicated by different letters (a, b, c).
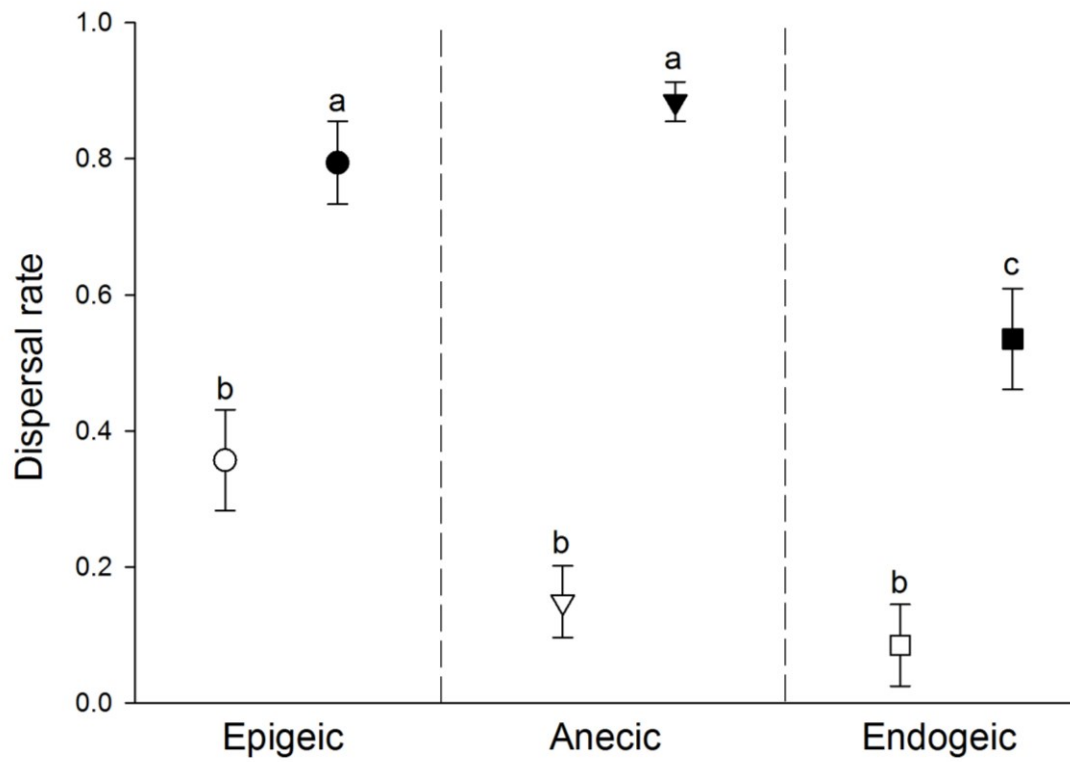
Fig. 5 Relationship between dispersal rate (calculated as the number of earthworms counted in the arrival section over the total number of earthworms) and population density (i.e. 1, 10, 20 or 30 earthworms) according to the functional group (i.e. epigeic, anecic, endogeic). The points are slightly shifted around the correct densities to be clearly distinguishable one from another.
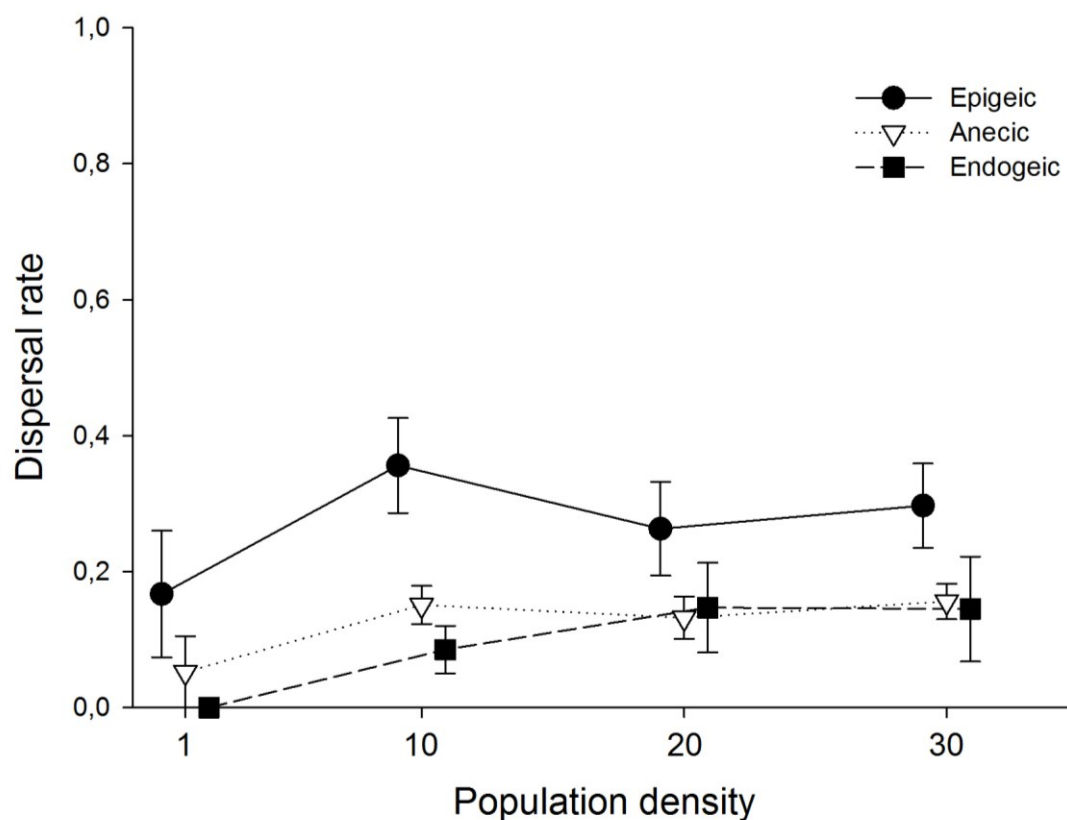
Fig. 6 Partial Least Squares - Discriminant Analysis (PLSDA function in R) on dispersal behaviour (i.e. density sensitivity, quality sensitivity, dispersal rate in homogeneous environment, mean distance crossed in homogeneous environment and tendency to follow conspecifics in homogeneous environment) between functional group (i.e. epigeic, anecic and endogeic).