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1 **Seasonal variations in macrofauna distribution according to the distance from a**
2 **herbaceous strip in a Mediterranean alley cropping plot**

3

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26 **Abstract**

27 In alley cropping systems, herbaceous strips planted with trees are added into cropped fields.
28 These systems could provide a favorable habitat for many organisms, producing shade in
29 summer and litter in autumn, but their impacts on soil macrofauna are poorly studied, with
30 most samplings limited to one date and therefore one season only. This study investigated the
31 seasonal variations in the spatial distribution of soil macrofauna in a Mediterranean alley
32 cropping plot. We sampled three different shading treatments: a strong shading treatment with
33 lightly-pruned trees, a light shading treatment with pollarded trees, and a no-shade treatment
34 without trees in the herbaceous strips. We measured the density of macrofauna individuals
35 classified into different taxonomic and functional groups by the extraction of 25*25*25 cm
36 soil cores in the herbaceous strip (with or without trees), and in the crop alley at 1 m and 2.5
37 m from the herbaceous strip. We found a similar response of macrofauna density to the
38 distance from the herbaceous strip for all shading treatments. However, this response was
39 strongly dependent on the season. In spring, just after soil tillage, most soil macrofauna
40 presented higher densities in the herbaceous strip than in the crop alley, except for plant
41 feeders. In early summer, this trend was mostly visible for earthworms, Diplopoda and adult
42 Coleoptera. In autumn, higher densities in the herbaceous strip than in the crop alley were
43 only significant for anecic and endogeic earthworms, while other macrofauna categories
44 presented similar densities at all distances from the herbaceous strip, due to an increase in
45 macrofauna density in the crop alley. These large seasonal variations in spatial distribution of
46 soil macrofauna highlight the importance of temporal repetitions when studying community
47 responses to agroforestry system design and management. The mechanisms by which
48 population densities increased in the crop alley a few months after soil perturbation require
49 further investigation.

50

51

52 **Keywords**

53 herbaceous strip; soil macrofauna; alley cropping; earthworm; agroforestry; market gardening

54

55

56 **Abbreviations**

57 HS refers to herbaceous strip

58

59 **1. Introduction**

60

61 We are facing a global decrease in biodiversity, partly associated with landscape
62 simplification and with current dominant agricultural practices (Habel et al., 2019;
63 McLaughlin and Mineau, 1995). Agroforestry, or the association of trees and agriculture, can
64 promote an increase in animal biodiversity in cropped fields, because of the addition of new
65 and more diverse habitats (Jose, 2009). For example, agroforestry has been shown to impact
66 positively the presence of birds and of pollinator insects compared to simplified agricultural
67 areas (Udawatta et al., 2019). Its impacts on soil dwelling fauna have been far less studied,
68 especially in the Mediterranean zone, and so far work has focused mainly on earthworms or
69 organisms of the soil surface such as adult carabids (Marsden et al., 2020).

70 In addition to its purely conservational value, soil-dwelling fauna performs essential roles in
71 ecosystem functions, and increases in its diversity and density could improve the
72 multifunctionality of agricultural land (Bender et al., 2016). Among them, litter-feeders
73 (mainly earthworms, woodlice and millipedes) contribute to the decomposition of organic
74 matter and to associated nutrient turnover through litter comminution and modification of
75 microbial activity in their guts and fresh feces (Barrios, 2007; David, 2014; Frouz, 2018), and

76 to carbon storage in old feces (Frouz, 2018; Wolters, 2000). Some earthworms incorporate
77 fresh organic matter into the mineral soil, where it can be protected from degradation and
78 contribute to carbon storage (Bossuyt et al., 2005), which has also been shown for millipedes
79 (Filser et al., 2016). Conversely, earthworms feeding on stabilized particulate organic matter
80 contribute to mineralize it (Lavelle et al., 2006). Earthworm activity can also improve soil
81 structure by the creation of burrows, soil decompaction and the creation of an organo-mineral
82 horizon (Lavelle et al., 1998). In addition, the regulation of the invertebrate community by
83 animal feeders is increasingly studied for pest control (Holland et al., 2017), and is performed
84 by organisms living in the soil (Chilopoda, most larvae of Coleoptera, etc) or dependent on
85 the soil for their larval stage or overwintering (insect predators at their adult stage) (Geiger et
86 al., 2009). The soil can also host larvae of future crop pollinators. Practices promoting soil
87 fauna abundance and diversity should thus be favored in a context of reduction of chemical
88 inputs.

89 In alley cropping agroforestry, trees are organized in rows in order to facilitate crop
90 management practices along alleys. A strip of around 2 m wide is uncultivated below the
91 trees, and an associated understory vegetation is initially sown or appears spontaneously,
92 mostly herbaceous. The lack of disturbance, permanent soil cover and source of additional
93 food resources from this non-exported vegetation creates a specific habitat in these
94 herbaceous strips. They are an overwintering site for most surface-dwelling invertebrates
95 living in alley cropping systems (Boinot et al., 2019), present higher earthworm densities than
96 crop fields and crop alleys (Cardinael et al., 2019), and host high densities of woodlice
97 (D'Hervilly et al., 2020; Pardon et al., 2019, 2020) and millipedes (Pardon et al., 2019). This
98 herbaceous strip could particularly be a reservoir of macrofauna, i.e. soil fauna larger than 2
99 mm, then able to disperse towards the crop alley over wider distances than mites or
100 springtails, for example. However, proof is still lacking that the herbaceous strip really

101 benefits the establishment of diverse and abundant communities in the crop alley, as studies
102 of spatial heterogeneity in alley cropping systems are scarce and show contrasting results. For
103 example, no variation in earthworm density was found in crop alleys with the distance from
104 the herbaceous strip by Cardinael et al. (2019), while earthworm density was negatively
105 impacted by herbaceous strip proximity in some sites (D’Hervilly et al., 2020; Rivest et al.,
106 2020). In addition, the effect of the distance from the herbaceous strip is also probably
107 influenced by tree properties, as they determine the quantity and quality of litter added in the
108 crop alley and the strength and range of the microclimate effect. For example, woodlice and
109 millipede activity were positively affected by old but not young tree row proximity in one
110 study (Pardon et al., 2019), and a gradient in earthworm density from the tree to the center of
111 the crop alley was found in a Canadian system for some tree species only (Price and Gordon,
112 1999). Finally, most studies rely on one single sampling season, while conceptually, dynamic
113 exchanges between herbaceous strips and crop alleys can be expected to depend on the period
114 of the year, driven by adverse or favorable properties of the crop alley or by soil organism life
115 cycles affected by climatic conditions.

116 This study aims to determine the seasonal variations of soil macrofauna distribution according
117 to the distance from a herbaceous strip (HS) for different shade treatments in an alley
118 cropping plot. We made the hypotheses that (i) HS can be a specific shelter for macrofauna,
119 leading to higher faunal densities in HS than in crop alleys; (ii) this bimodal density
120 distribution is particularly visible during certain seasons when conditions are not favorable for
121 soil fauna in the crop alley, and replaced by a gradient-type distribution during other seasons
122 due to soil macrofauna dispersal from the HS towards the crop alley; and (iii) this HS shelter
123 effect is less visible in the presence of strongly-shading trees than in the presence of lightly-
124 shading trees or without trees, as tree-induced changes in microclimate and in litter and soil
125 organic matter presence may render crop alley conditions more favorable for soil macrofauna.

126

127 **2. Methods**

128

129 **2.1. Site description**

130 The study took place in an experimental alley cropping plot of 2,250 m² located near
131 Vézénobres in the South of France (44.058 N, 4.111 E), included in a wider alley cropping
132 site. The climate is Mediterranean (temperature of 15.2 °C and 760 mm of precipitation per
133 year on average, French Institute of Meteorology Météo France). The soil is on recent alluvial
134 deposits, loamy in the first 25 cm depth with a pH of around 8, 16 % of CaCO₃ and a CEC of
135 9.5 cmol⁺ kg⁻¹ on average (basic soil properties are detailed in Table 1 and Table S1 in the
136 Supplementary resources). These soil properties were determined at the beginning of the
137 sampling in 2018. Texture was analyzed on decarbonated soil sieved at 2 mm. Bulk density
138 was determined with the cylinder method (dry weight of soil sampled in 100 cm³ cylinders).
139 Soil organic carbon content was measured with an elemental analyser (Thermo Fisher
140 Scientific Flash 2000) on soil sieved at 2 mm and ground at 250 µm.

141 Hybrid walnut trees (*Juglans nigra* L. x *Juglans regia* L.) spaced 10 m apart were planted in
142 1995. Cereal and legume crops were grown with conventional practices between the tree rows
143 until 2010 (mostly wheat and rapeseed, with some fallow periods). Since then, the plot has
144 been converted to organic farming.

145 The experiment was set up in 2015, after a year of sunflower cultivation with reduced tillage
146 and no fertilizer, followed by a cover crop. The experimental plot was divided into three
147 shade treatments of 750 m² each (Fig. 1a). In the strong shade treatment (shade ++), trees
148 were only lightly pruned as usually done in agroforestry systems (mean diameter at breast
149 height of 0.37 ± 0.07 m in 2017). In the light shade treatment (shade +), trees were strongly
150 pruned to obtain pollarded trees (mean diameter at breast height of 0.33 ± 0.08 m in 2017).

151 Pruning took place in February 2015 and again in February 2018. In the last treatment, no tree
152 was present (no shade), as trees initially present had been removed in 2011. Each treatment
153 consists of three 8 m-wide and 25 m-long crop alleys and their adjacent herbaceous strips
154 (HS), planted with trees in treatments shade ++ and shade + (Fig. 1a). HS are 2 m wide,
155 covered with spontaneous vegetation and mowed about twice a year in each treatment
156 (characteristics of the vegetation are detailed in Table 1 and Table S1 in the Supplementary
157 materials). Each crop alley is made up of 5 mulched raised beds (with rameal chipped wood
158 on 2 to 3 cm width or hay on 7 cm width alternating each year), about 90 cm wide and 20 cm
159 high, parallel to the HS (Fig. 1b). In each shade treatment, the three crop alleys are managed
160 as a rotation of 3 vegetable crops (carrots, tomatoes and lettuces), meaning that in a given
161 year only one crop alley in each shade treatment is planted with tomatoes. The order of
162 rotation of the different vegetables between the different crop alleys is the same for all shade
163 treatments. Soil was rotary tilled and beds formed at the beginning of the experiment in 2015,
164 and then soil was always rotary tilled after carrot production. After tomatoes or lettuces, beds
165 were only consolidated with a hoe. Fertilization was similar for all productions, with the
166 addition of ricinus oil cakes in 2015 (250 kg ha⁻¹), and 2016 (400 kg ha⁻¹), and of poultry
167 manure in 2017 and 2018 (560 kg ha⁻¹ each year). No pesticides were used except in 2018
168 when slug pellets were applied (Ferramol at 0.08 kg ha⁻¹). Crops are drip irrigated during
169 summer.

170

171 **2.2. Sampling design and plot management during sampling**

172 Macrofauna samplings took place in April (16th to 23rd) i.e. spring, June (18th to 22nd) i.e.
173 early summer and November (14th to 21st) i.e. late autumn of 2018 to take into account
174 seasonal variability. Rainfall during the year of the experiment was of 166 mm (January), 59
175 mm (February), 72 mm (March), 90 mm (April, first sampling), 101 mm (May), 4 mm (June,

176 second sampling), 20 mm (July), 56 mm (August), 19 mm (September), 257 mm (October)
177 and 226 mm (November, last sampling, Bellegarde weather station, monitoring data from the
178 INRAE CLIMATIK platform managed by the AgroClim laboratory of Avignon, France data).
179 No sampling was carried out during late summer because the rainfall was very low, thus
180 limiting the chance of finding soil macrofauna. Only the crop alleys planted with tomatoes
181 were sampled in order to ensure homogeneous management practices. In these crop alleys,
182 raised beds were rotary tilled in March and covered with a 2 to 3 cm-thick layer of ramial
183 chipped wood obtained from walnut prunings. Different varieties of tomato plants previously
184 grown in the nursery were planted a week after the first sampling (1.6 plants per m²). Each
185 crop alley received two top dressings of poultry manure in March and in April after tomato
186 plantation, for a total of 560 kg ha⁻¹. Tomato plants were drip-irrigated from June (before our
187 sampling date) to mid-September. The previous crops in these crop alleys were lettuces
188 (2015), tomatoes (2016) and carrots (2017). HS were mowed after the June sampling date and
189 at the end of summer. In tomato beds, manual weeding was regularly performed until the end
190 of September, when tomato harvesting stopped.

191 Sampling was designed in order to investigate the effect of the distance from the HS in
192 different shading conditions. Macroinvertebrates were sampled along transects perpendicular
193 to the HS with three distances from the HS (0 m i.e. in the middle of the HS, 1 m from the HS
194 border i.e. in the closest tomato bed to the HS, and 2.5 m from the HS border i.e. in the next
195 tomato bed) (Fig. 1b). For each shade treatment (shade++, shade + and no shade) and at each
196 sampling season, each of the three distances from the HS was sampled eight times (eight
197 transects were made), meaning 24 samples were taken for each shade treatment for a given
198 season (72 samples per season all treatments combined, thus 216 samples in total). All
199 samples were taken in the same crop alley for a given shade treatment as only one crop alley
200 was planted with tomatoes in each shade treatment, and as no replication of the shade

201 treatments was available on this experimental plot. In the treatments with trees (shade ++ and
202 shade +), four of these transects started at an HS sampling position located 1m from the
203 nearest tree, and four others started at an HS sampling position located 5m from the nearest
204 tree (Fig. 1b).

205

206 **2.3. Macroinvertebrate sampling**

207 At each sampling point, macroinvertebrates were hand sorted from soil blocks of 25*25*25
208 cm (adapted from Anderson and Ingram, 1993). Earthworms were kept alive in water, and
209 then counted and determined at species level under laboratory conditions, and classified into
210 the three main ecological categories anecic, endogeic and epigeic following Bouché (1977).
211 Other macroinvertebrates were kept in ethanol, and then counted and determined under
212 laboratory conditions. Chilopoda were determined at order level, while insects and Diplopoda
213 were determined at family level when possible. Count values obtained were expressed as
214 densities (individuals per m²). As ants presented a wide variation in their densities (due to
215 their properties as social insects), ant density was separated in three density classes (no
216 individuals found, between one and 240 individuals per m², and more than 240 individuals per
217 m²). This classification was chosen to make a distinction between no ants present, few ants
218 presents (240 individuals per m² refers to 15 individuals found in a soil block, abundance after
219 which ant counts always reached high numbers of individuals which could not be counted
220 precisely), and probable ant hill. A feeding group was attributed to each category of
221 macrofauna when possible. Diplopoda, Isopoda and larvae of Diptera were classified as litter-
222 feeders. Araneae, Chilopoda, Staphylinidae and larvae of Carabidae, Staphylinidae and
223 Cantharidae were classified as animal-feeders. Elateridae, Curculionidae and larvae of
224 Lepidoptera, Elateridae, Curculionidae and Melolonthinae were classified as plant-feeders,
225 although they consume different parts of the plants. Anecic earthworms were classified at 50

226 % as soil-feeders, and at 50 % as litter-feeders based on anecic earthworm gut analyses by
227 Bernier (1998), while endogeic earthworms were all classified as soil-feeders and epigeic
228 earthworms were all classified as litter-feeders.

229

230 **2.4. Statistical analyses**

231 To investigate the effect of the distance from the HS within the different seasons and shade
232 treatments, macroinvertebrate density (grouped in taxonomic and feeding groups, as well as
233 ecological categories anecic, endogeic and epigeic for earthworms) was analyzed using
234 generalized linear models fitted by quasi Poisson law (with a log link function). These
235 analyses were not run for each earthworm species individually, as most species did not
236 account for enough individuals. Distance from the HS (0, 1 or 2.5 m), shade treatment (shade
237 ++, shade + or no shade) and season (April, June or November) and their interactions were
238 used as fixed factors. Significant effects were determined by type II F tests and followed by
239 pairwise comparisons (Tukey). Significance level was set to 5 %. As no significant difference
240 was found for macrofauna density between transects distant 1 m and 5 m from the tree in the
241 shade treatments with trees (shade ++ and shade +), all transects were treated as simple
242 replicates, whatever their distance from the tree (data not shown). Analyses were run using R
243 statistical software (version 3.6.2) (R Core Team, 2019) with packages *lme4* (Bates et al.,
244 2015), *car* (Fox and Weisberg, 2019) and *emmeans* (Lenth, 2019). Ant density classes were
245 analyzed with a cumulative link model, using the *ordinal* R package (Christensen, 2019).
246 Species richness (i.e. number of different species) and the Shannon diversity index were
247 calculated for earthworms at species level (*vegan* package in R, Oksanen et al., 2019), and
248 analyzed using generalized linear models (species richness) or analyses of variance (Shannon
249 index) with the same fixed factors season, distance from the HS and shade treatment.

250 Variations in macrofauna community composition between distances from the HS and shade
251 treatments were evaluated with a principal component analysis using densities in taxonomic
252 groups at order or family level when possible (packages *FactoMineR* and *ggplot2* in R) (Lê et
253 al., 2008; Wickham, 2016) for each season. Groups with too few individuals (median equal to
254 0) were excluded from the analysis. Earthworms were separated into the ecological groups
255 anecic, epigeic and endogeic to account for their different behaviors. In order to account for
256 large differences in density between taxonomic groups, data were standardized to the
257 maximal density measured for each taxonomic group (maximal margin method of function
258 *decostand*, *vegan* package in R, Oksanen et al., 2019).

259

260 **3. Results**

261

262 **3.1. Macrofauna community composition**

263 Identified macrofauna were mostly earthworms (17 ± 12 % standard deviation, 32 ± 17 % and
264 29 ± 15 % of macrofauna individuals in the no shade, shade + and shade ++ treatments
265 respectively), Chilopoda (9 ± 9 %, 10 ± 10 % and 20 ± 16 % respectively), Diplopoda ($21 \pm$
266 12 %, 13 ± 10 % and 4 ± 6 % respectively) and Coleoptera (26 ± 13 %, 17 ± 16 % and $21 \pm$
267 18 % respectively). Formicidae represented up to an estimated 82 % of all individuals in some
268 samples (while their mean contribution was estimated to 12 ± 19 %, 10 ± 16 % and 7 ± 14 %
269 in the no shade, shade + and shade ++ treatments respectively) (Table S2 in the
270 Supplementary materials).

271 The principal component analysis based on macrofauna density in the different taxonomic
272 groups shows variable patterns with the season. In April and June, the principal component
273 analysis mostly isolates sampling points of the HS from those of the tomato beds along the
274 first axis (representing 23 % of the variance in April and 25 % of the variance in June) (Fig.

275 2a and Fig. 2b). In April, it is explained by more epigeic and anecic earthworms, Julidae and
276 Isopoda in the HS than in the tomato beds. In June, it is explained by more epigeic
277 earthworms, Julidae and Staphylinidae in the HS than in the tomato beds. The separation of
278 sampling points from the different shade treatments is much less clear, and takes place along
279 axis 2, which explains a lower part of the variance (16% in April, 15 % in June) (Fig. 2a and
280 Fig. 2b). In the opposite, the separation between the HS and the tomato beds is not clear in
281 November, where it is driven by component 2 (16 % of the variance, Fig. 2c), while the first
282 component (22 % of the variance) clearly isolates the shade treatments from one another,
283 especially the no shade treatment from shade ++. There were particularly more Polydesmidae
284 and Elateridae larvae in the no shade treatment compared to other treatments, while the shade
285 ++ treatment is additionally characterized by lower densities of endogeic earthworms and of
286 Julidae compared to other treatments. The tomato beds at 1 m or 2.5 m from the HS could not
287 be separated at any season.

288

289 **3.2. Macrofauna density in taxonomic groups**

290 The response of macroinvertebrate density to the distance from the HS was similar in all
291 shade treatments (Table S3 in the Supplementary materials, significant interaction between
292 distance from the HS and shade treatment for Diplopoda only, and probably due to large
293 differences in densities between shade treatments, see Fig. S1 in the Supplementary
294 materials). However, macrofauna density was different between shade treatments, with
295 especially lower densities in shade ++ compared to other treatments for most taxonomic
296 groups (except Chilopoda, cf Table S2 in the Supplementary materials).

297 The effect of the distance from the HS on macroinvertebrate density varies with the
298 taxonomic group and the season, as shown in Table 2 and Table S3 in the Supplementary
299 materials (significant effect of the interaction between the distance from the HS and the

300 season for Lumbricidae, Diplopoda, Isopoda, Chilopoda and adult Coleoptera). At all seasons,
301 earthworms presented significantly higher densities in the HS compared to the tomato beds (1
302 and 2.5 m from the HS), and ants presented higher densities in the HS compared to 2.5 m
303 from the HS (Table 2). Diplopoda presented higher densities in the HS than 2.5 m from the
304 HS in April, and higher densities in the HS compared to all tomato beds (1 and 2.5 m from the
305 HS) in June, but not in November. Isopoda presented higher densities in the HS than in the
306 tomato beds (1 and 2.5 m from the HS) in April only. Adult Coleoptera presented higher
307 densities in the HS compared to 1 m from the HS in April, and compared to both 1 and 2.5 m
308 from the HS in June, while no difference was found in November. In the opposite, Chilopoda
309 presented higher densities at 1 m from the HS than in the HS in November, while no
310 difference was found at other seasons. Dermaptera and Coleoptera larvae did not vary
311 significantly with the distance from the HS at any season (no significant effect of the
312 interaction between distance from the HS and season or of the distance from the HS alone,
313 Table S3 in the Supplementary materials). No significant difference between 1 and 2.5 m
314 from the HS was found for any season or taxonomic group. The attenuation of differences in
315 macrofauna density between the HS and the tomato beds in November is due to a significant
316 increase in macroinvertebrate density at this season compared to April and June in the tomato
317 beds but not in the HS for earthworms, Diplopoda, Isopoda and Chilopoda (Table 2).

318

319 **3.3. Earthworm diversity**

320 Seven species of earthworms were found in all shade treatments (Table 3). Earthworm
321 diversity varied with the distance from the HS (Table 3). Species richness was higher in the
322 HS than both 1 and 2.5 m from the HS in April and June, and than 2.5 m from the HS in
323 November. The Shannon index presented a significant decreasing gradient from the HS to 2.5
324 m from the HS for all seasons.

325 The response of earthworm density to the distance from the HS varies with their ecological
326 category (Fig. 3). Anecic earthworms presented higher densities in the HS compared to 1 and
327 2.5 m from the HS at all seasons, especially due to *Aporrectodea nocturna* (Table 3).
328 Endogeic earthworms presented higher densities in the HS compared to 1 and 2.5 m from the
329 HS in April and June, but only compared to 2.5 m from the HS in November, especially due
330 to *Allolobophora chlorotica* and to *Aporrectodea rosea*. Epigeic earthworms (all of
331 *Lumbricus castaneus* species) presented higher densities in the HS compared to 2.5 m from
332 the HS in April, and compared to both 1 and 2.5 m from the HS in June, but no significant
333 difference was found anymore in November for epigeic density between distances from the
334 HS, because of a large increase in epigeic density in the tomato beds between June and
335 November.

336

337 **3.4. Feeding groups**

338 The distribution of macrofauna in the plot varies according to the feeding group considered
339 (Fig. 4). Litter-feeders presented higher densities in the HS compared to tomato beds in April
340 and June, but not in November (Fig. 4a). This result was mostly driven by litter-feeding
341 earthworms and Diplopoda. Soil-feeding earthworms presented higher densities in the HS
342 than in the tomato beds at all seasons (Fig. 4b). Animal-feeders presented higher densities in
343 the HS than in the tomato beds in April only (Fig. 4d). Animal-feeders were mostly
344 Chilopoda, especially in June and November. Plant-feeders presented a different pattern from
345 other groups, with a significantly lower density in the HS compared to the tomato beds in
346 April (Fig. 4c). Plant-feeders were mostly Coleoptera larvae, of which a huge proportion
347 consisted of Elateridae ($85 \% \pm 27 \%$).

348

349 **4. Discussion**

350

351 **4.1. Constant patterns of macrofauna distribution throughout seasons**

352 Throughout all seasons, HS macrofauna communities were characterized by higher densities
353 of litter-feeders but similar Dermaptera and Chilopoda densities, compared to communities
354 found in the tomato beds.

355 Earthworms presented higher densities in the HS compared to both tomato beds at all seasons,
356 especially due to anecic earthworms. Higher earthworm densities in HS than crop alleys were
357 also found by Cardinael et al. (2019) in France and Rinvest et al. (2020) in Québec for different
358 alley cropping plots mostly cultivated with cereals and legume crops, and by Crittenden et al.
359 (2015) in the Netherlands for herbaceous margins of fields cultivated with cereals and tuber
360 crops. Anecic earthworms live in permanent burrows in the soil. HS were probably a
361 favorable habitat to them as they were not subject to soil perturbation, while anecic
362 earthworms were probably negatively impacted by the repeated destruction of their burrows
363 and the lack of adequate food resources and protection against predators at the soil surface in
364 the tomato beds (Chan, 2001). *Aporrectodea nocturna*, the main anecic earthworm species
365 found in this study, is in particular known to reuse its burrows intensively (Capowiez, 2000).
366 In addition, endogeic earthworms always presented higher densities in the HS than 2.5 m
367 from the HS. Endogeic earthworms were probably strongly impacted by the recent rotary
368 tillage as they live and feed inside the soil. Similarly, ants also presented higher densities in
369 the HS than 2.5 m from the HS at all seasons. Anthills were probably repeatedly destroyed by
370 intensive tillage in the tomato beds. In agreement with us, Boinot et al. (2019) found more
371 activity density of ants in the tree row than in the crop alley in mature alley cropping systems
372 cultivated with cereals in the south of France. In spatially structured systems like the one
373 studied here, spatial differences in soil properties (e.g. higher soil organic carbon
374 concentrations and stocks under tree rows such as often found in agroforestry systems

375 (Cardinael et al., 2017)) could contribute to explaining locally higher densities of earthworms.
376 However in our case, basic soil characteristics, including organic matter content, did not vary
377 according to sampled positions (Table 1), therefore differences in macrofauna communities
378 are more likely related to other changes in habitat characteristics caused by vegetation
379 structure and management practices.

380 Dermaptera and Chilopoda density did not vary between HS and crop alleys at any season.
381 Similarly, Smith et al. (2008b) did not find significant differences in Chilopoda abundance
382 between grass margins and the adjacent wheat crop in England. These organisms are able to
383 move quite fast and could have recolonized tomato beds more rapidly than other soil-dwelling
384 organisms such as earthworms and larva after tillage. While adult Coleoptera have a faster
385 dispersal, particularly flying Staphylinidae, they did not present the same pattern, probably
386 because they use different habitats for living and feeding.

387

388 **4.2. Seasonal variations in macrofauna distribution**

389 Despite a constant general trend, this study reveals some seasonal variations in the differences
390 between HS and tomato bed macrofauna communities, which could be due to climatic
391 variations or to crop management. In April, most soil macrofauna was probably negatively
392 impacted by the recent soil perturbations in the tomato beds. Smith et al. (2008b) indeed
393 found that soil scarification reduces macrofauna density, but that populations recovered
394 within a season after soil scarification. In the present study, these macrofauna categories seem
395 to have recovered in November, or even in June for Isopoda. The recovery in November
396 could have been amplified by the interruption of weeding and of other management, allowing
397 the colonization of tomato beds by herbaceous vegetation, probably providing food and
398 habitat usually not found in crop alleys for soil macrofauna. In addition, November 2018 was
399 a particularly rainy month, which could have favored macrofauna activity. More generally,

400 Mediterranean regions are affected by strong climate variability: spring is not always a
401 favorable season as it can sometimes be too dry, summer is generally very dry and hot, and
402 intense rainfall events can occur in autumn, with variable timing and amplitude. Endogeic
403 macrofauna is very sensitive to such variations in rainfall and temperature, with a limited
404 activity in summer, and as found in this study a potential increase in activity in autumn. The
405 herbaceous strip could act as a refuge in unfavorable seasons, by buffering climatic conditions
406 compared to the exposed crop alley. In addition, some soil macrofauna taxa require different
407 habitats at different periods of the year. In spring, macrofauna is probably found in the places
408 where it overwintered, i.e. probably buffered habitats such as the HS. In summer, macrofauna
409 concerned by aestivation (such as epigeic and anecic earthworms) is probably not present in
410 places submitted to high temperatures and fast desiccation such as the crop alley, with little
411 plant cover of the soil, low bulk density and fragile structure due to rotary tillage. The specific
412 effect of the climatic conditions versus agricultural practices, particularly soil tillage, is
413 however difficult to determine as each agricultural practice is strongly associated with the
414 season.

415 Epigeic earthworms and isopods are usually present at very low densities in tilled soils,
416 probably because of the reduction in adequate shelter and food at the soil surface (Hassall and
417 Tuck, 2007; Pelosi et al., 2009). Higher densities of isopods in tree rows compared to crop
418 alleys have already been found in spring similarly to us in both young and old sites with
419 cereals or tuber crops in Belgium and France (D'Hervilly et al., 2020; Pardon et al., 2019),
420 and isopods have been shown to hibernate in tree rows in mature alley cropping plots in the
421 south of France (Boinot et al., 2019). Epigeic earthworms have also been shown to be mostly
422 present in tree rows in spring in France (Cardinael et al., 2019; D'Hervilly et al., 2020) or in
423 field margins in July (Crittenden et al., 2015) compared to the neighboring crop. In addition,
424 higher densities of Diplopoda were also found in tree rows than in adjacent crops by Pardon et

425 al. (2019). However, our study demonstrates that Isopoda, epigeic earthworms and Diplopoda
426 can be present in the crop alley at similar densities to those of the HS in autumn, their
427 establishment being probably favored in our case by the shelter provided by ramial chipped
428 wood presence at the soil surface of the tomato beds. Tomato bed irrigation in June probably
429 further favored early colonization by isopods, limiting the usual adverse conditions of the
430 summer. Surprisingly, it did not favor epigeic earthworms whose presence was mostly
431 restricted to the HS in June, although they are known to be positively affected by increases in
432 soil humidity and litter presence at the soil surface (Bouché, 1977). Temperatures were
433 probably too high for epigeic earthworm activity in summer, and ramial chipped wood was
434 probably a more interesting resource for Isopoda than for epigeic earthworms.

435 Adult Coleoptera were mostly Staphylinid beetles and Carabids in our study. Andersen
436 (1997), and Smith et al. (2008b) found respectively more Carabid and Staphylinid beetles or
437 more Coleoptera in field margins than in the cereal crop fields (in Norway and England
438 respectively), similarly to what we found in April and June. The higher densities of adult
439 Coleoptera in the HS than in the tomato beds in April and June could be due to additional
440 prey for the animal-feeders in the HS as usually described for margin habitats (Landis et al.,
441 2000). It could also be due to their behavior, as most of them feed at night (Martin-Chave et
442 al., 2019a), and could use the HS as a shelter during the day.

443 Contrary to our hypothesis, no significant difference was found between distances 1 m and
444 2.5 m from the HS for macrofauna density at all seasons. However, we only investigated the
445 HS close vicinity, due to the limited size of our experimental plot (crop alleys were only 8 m
446 wide), which could have hidden some effects. For example, Smith et al. (2008a) found higher
447 macrofauna density up to 3 m from field margins compared to the middle of the field in
448 England. However, while the HS presented higher endogeic earthworm density than both
449 tomato beds in April and June, endogeic earthworm density was only significantly higher in

450 the HS than 2.5 m from the HS in November, suggesting a positive effect of HS vicinity on
451 endogeic earthworm density in November. A positive effect of tree row proximity on
452 earthworm density has already been suggested by Price and Gordon (1999). A possible
453 explanation is that most macrofauna dispersed from the HS to at least 2.5 m from the HS in
454 the crop alley in November, but that this dispersion was more limited for endogeic
455 earthworms, whose movements are slowed as they are restricted to the soil.

456 Plant-feeding Coleoptera larvae presented higher densities in the tomato beds than in the HS
457 in April, and no differences between distances from the HS at other seasons. These
458 Coleoptera were mostly wireworms (Elateridae), known to be detrimental to crops, which
459 could explain their preference for the crop alley. However, wireworms are usually destroyed
460 directly or indirectly by tillage (Parker and Howard, 2001), which was performed only a
461 month before the first sampling season. Wireworms could have been located deeper in the soil
462 in March during tillage, or soil cover by ramial chipped wood could have limited their
463 predation after exposure at the soil surface. In addition, the use of rotary tillage could have
464 made it easier for them to dig into the loose soil (particularly low bulk density in the crop
465 alley).

466 Overall, the seasonal and spatial patterns observed in this study reflect taxon-specific
467 responses to a complex combination of variations in climatic conditions and management
468 practices in a spatially-structured agricultural system. The well-known impacts of soil
469 perturbation on soil fauna in agricultural systems (e.g. van Capelle et al., 2012) could be
470 partially alleviated by the inclusion of herbaceous strips, allowing the recovery of some
471 macrofauna taxa in crop alleys at certain seasons.

472

473 **4.3. Variations between shade treatments**

474 We expected to find more homogeneous macrofauna densities relative to the distance from
475 the HS in the strong-shade treatment (shade ++) than in the light shade (shade +) and no shade
476 treatments, as we expected that the more homogeneous tree shading and litter inputs would
477 attenuate the habitat differences between HS and raised beds. However, we found no effect of
478 the shade treatment on the spatial distribution of macrofauna within the plot. Shade treatments
479 most likely influenced all distances from the HS homogeneously, as soil macrofauna density
480 and community composition differed between shade treatments at a general level, especially
481 in November. Increased shade has been found to increase soil macrofauna density in tropical
482 systems (Martius et al., 2004), but has rarely been studied in temperate or Mediterranean
483 systems. Pardon et al. (2019) investigated the effect of herbaceous strips with or without trees
484 at field edges in Belgium, and found a higher woodlice density in the presence of trees and no
485 difference for millipedes, while in our study both were positively impacted in the absence of
486 trees (no shade treatment). In our study, higher shade led to a lower macrofauna density for
487 most macrofauna, Chilopoda excepted. This was particularly visible in November, possibly
488 related to a delayed and cumulative impact on populations of the shade that appeared around
489 the end of May. Similarly, Martin Chave et al. (2019b) found a lower activity density of the
490 main Carabidae in the strong shade treatment compared to lighter shade treatments in
491 September in the same experimental plot. The strong shade treatment (shade ++) was shown
492 to buffer temperature variations in this same study (Martin-Chave et al., 2019b). A strong
493 shade could have lowered temperature too much during the day in November, attenuating the
494 positive impact of autumn on macrofauna activity. The soil environment was also probably
495 strongly modulated by the soil cover by tree leaves and the limited herbaceous vegetation
496 biomass observed in November in the strong shade treatment (shade ++). This would have
497 further created buffered microclimate conditions in this treatment, and induced strong
498 differences in litter quality and quantity between shade treatments, which has been shown to

499 modulate soil macrofauna abundance and diversity (Loranger-Merciris et al., 2008; Vohland
500 and Schroth, 1999). Interestingly, earthworms and Dermaptera presented higher densities in
501 the light shade treatment (shade +) than in both strong shade (shade ++) and no shade
502 treatments, meaning the observed trends are not only the results of a variation of shade and of
503 the inputs of tree litter. While these results on the shade treatments seem interesting, it is
504 important to note that there was no replication of the shade treatments in this experiment.
505 Observations of the differences between shade treatments are thus limited to hypotheses, and
506 should be the focus of future investigations. However, the fact that the same effect of the
507 distance from the HS was observed for three different shade treatments is relevant as it
508 indicates that uncropped herbaceous strips are a possible reservoir of soil macrofauna in
509 spring and summer, independently of the presence and management of trees on these strips.

510

511 **5. Conclusions**

512

513 Herbaceous strips were shown to present higher macrofauna density and earthworm diversity
514 compared to nearby tomato beds whatever the shade treatment. This finding confirms the
515 important role of non-perturbed herbaceous strips to preserve dense and diverse macrofauna
516 communities across fields, including in alley cropping systems. However, this study reveals
517 the importance of considering seasonal variations when studying soil macrofauna in alley
518 cropping systems. The maximal seasonal activity was found to be in autumn, while most
519 samplings in crops usually take place in spring, and patterns of macrofauna distribution in the
520 plot could be quite different according to the season. The role of the season itself versus of the
521 management practices (especially soil tillage) in these differences is hard to determine as both
522 vary simultaneously, and requires further investigations with limited soil perturbation, such as
523 zero tillage experiments, or the comparison of different crop managements. A possible

524 recolonization of crop alleys by macrofauna coming from the HS via seasonal movements in
525 soil fauna after soil perturbation, as suggested by the results of this study, should be further
526 investigated.

527

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536

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698 **Figure captions**

699 **Fig. 1.** Experimental plot (a) and sampling design (b). This sampling design was repeated for
700 each shade treatment (no shade = no trees, shade + = strongly-pruned trees, shade ++ =
701 lightly-pruned trees), and for each season (April, June and November of 2018). HS stands for
702 herbaceous strip.

703

704 **Fig. 2.** Graphical representations of principal component analyses computed with
705 macroinvertebrates at order or family level (when possible), for (a) April data, (b) June data
706 and (c) November data. Earthworms were additionally separated by ecological categories.
707 Individuals are identified by their distance from the herbaceous strip in the representations on
708 the left, with red circles for 0 m, orange triangles for 1 m and yellow squares for 2.5 m.
709 Individuals are identified by their shade treatment in the representations on the right with dark
710 blue circles for the no shade treatment, light blue squares for shade + treatment, and medium
711 blue triangles for shade ++ treatment. Ellipses represent confidence intervals at 95 % around
712 barycenters. Only variables with a $\cos^2 > 0.5$ are represented.

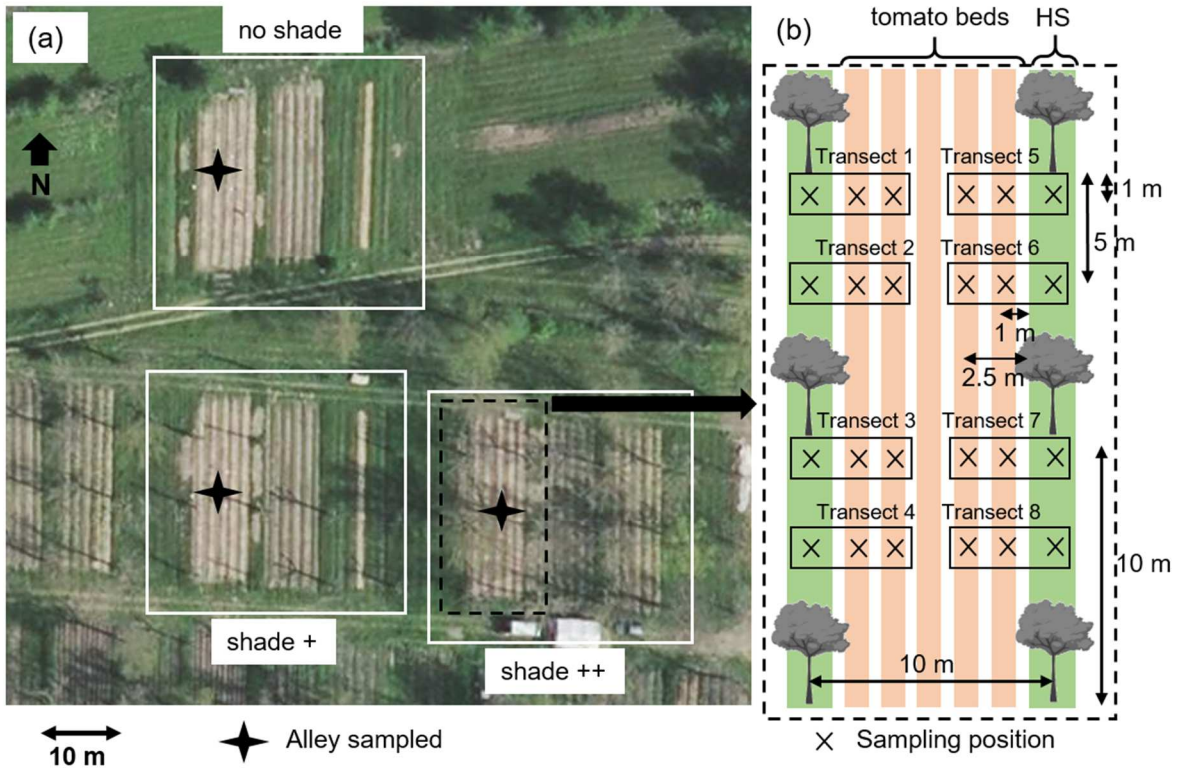
713

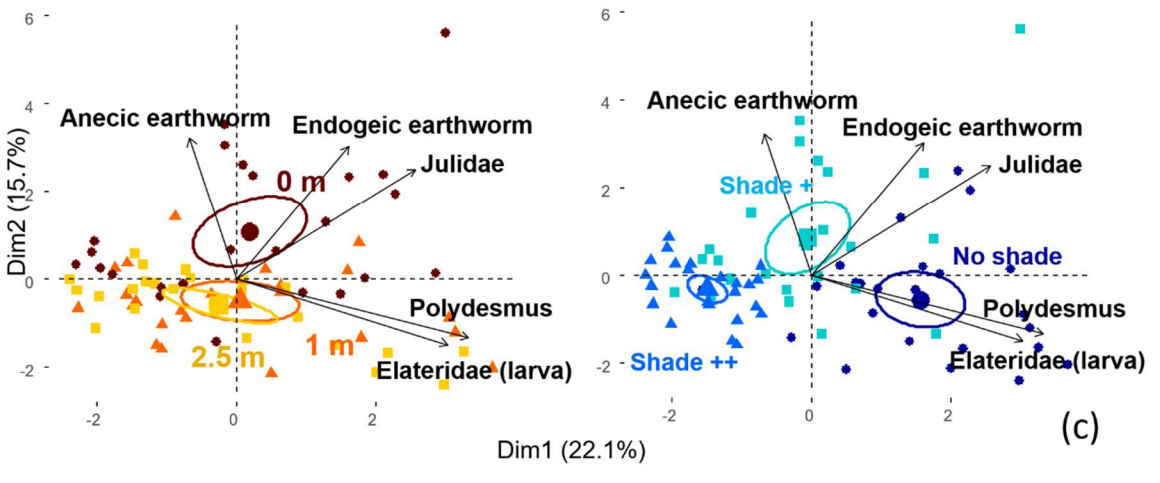
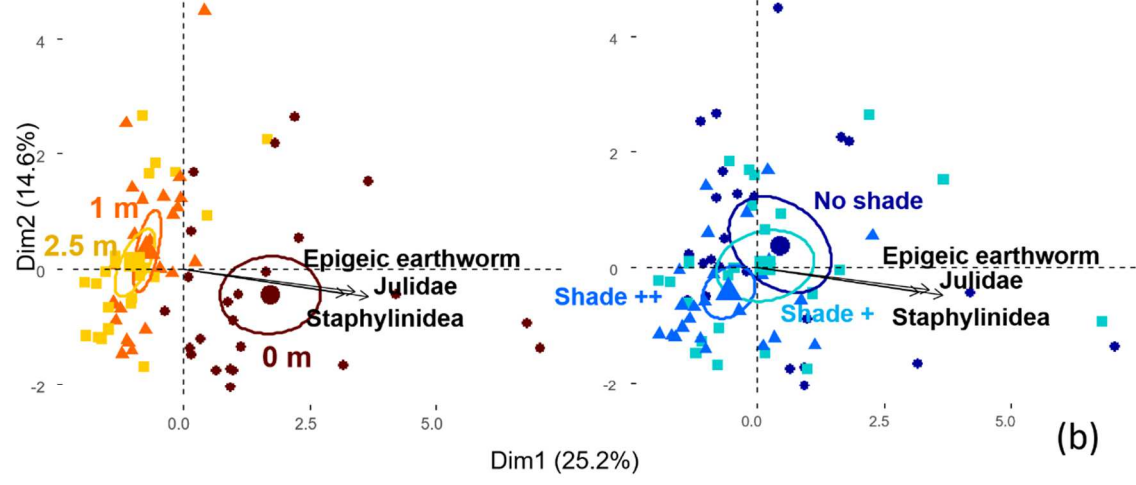
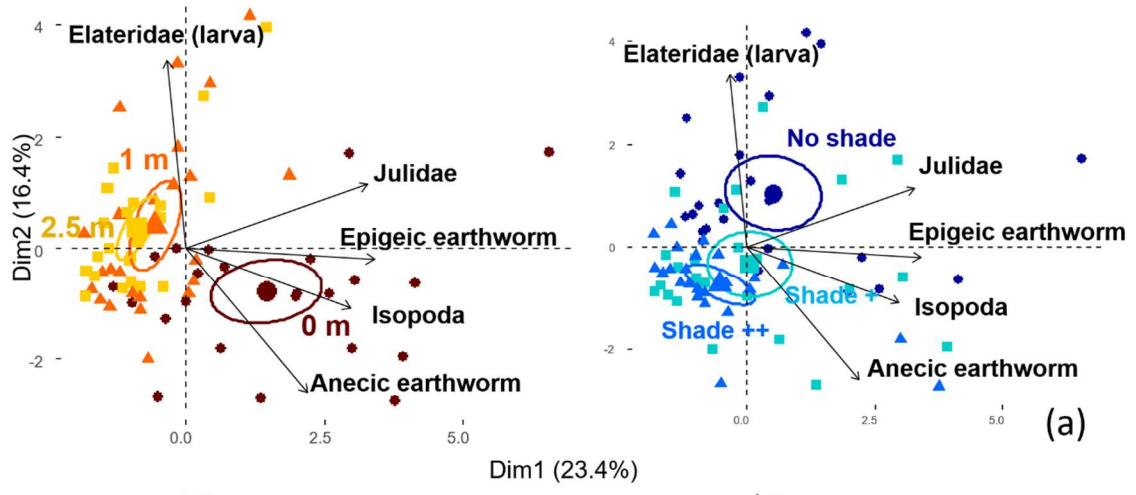
714 **Fig. 3.** Mean values of earthworm density for each earthworm ecological category at each
715 season and each distance from the herbaceous strip (HS). Different letters indicate significant
716 differences between distances from the HS for a given earthworm category and season (Tukey
717 test, p-value < 0.05) after generalized linear models fitted with a quasi-Poisson law. Error bars
718 are the standard error of the mean for each earthworm ecological category.

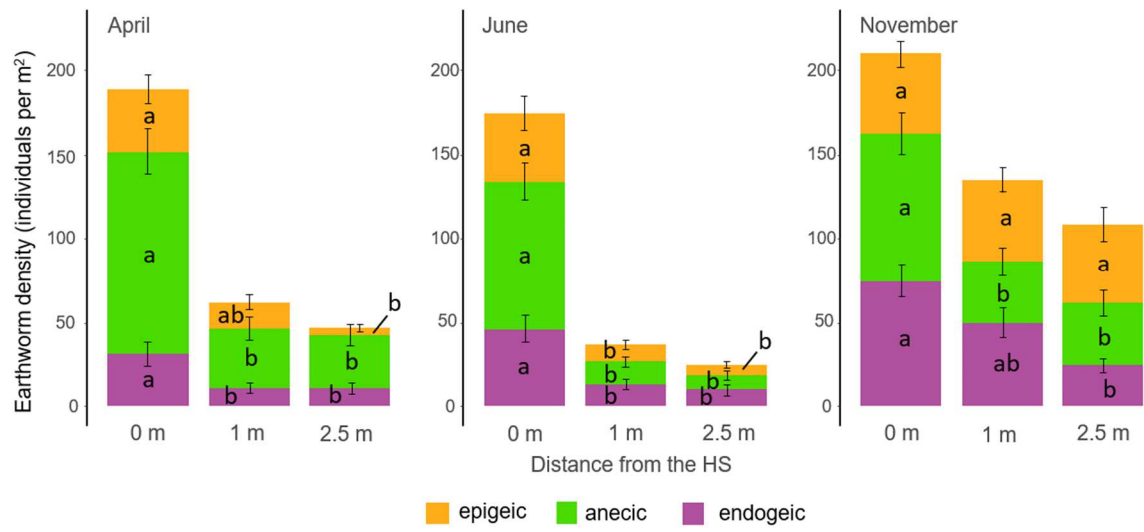
719

720 **Fig. 4.** Mean values of densities of litter-feeders (a), soil-feeders (b), plant feeders (c) and
721 animal-feeders (d) at each season and distance from the herbaceous strip (HS). Different
722 letters indicate significant differences between distances from the HS for the given season and

723 feeding group (Tukey test, p -value < 0.05) based on generalized linear models fitted with a
724 quasi-Poisson law. Error bars are the standard error of the mean for each category of
725 macrofauna included in the feeding groups.







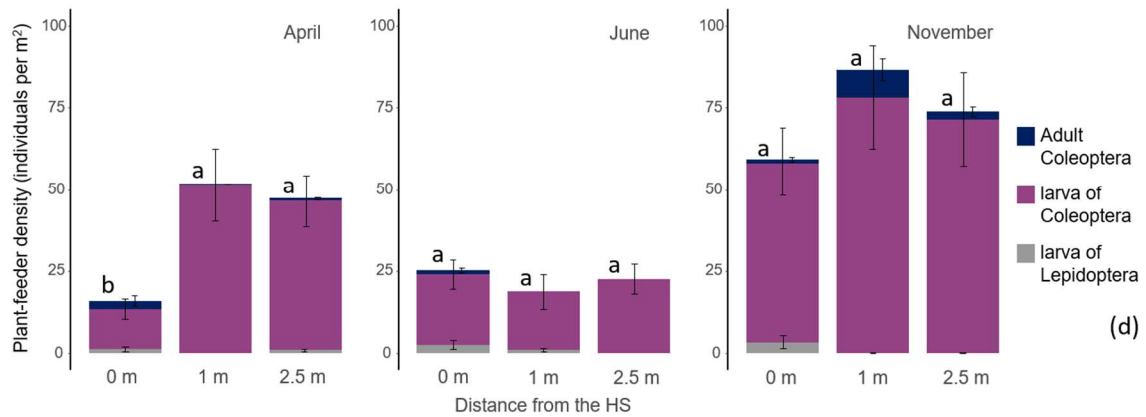
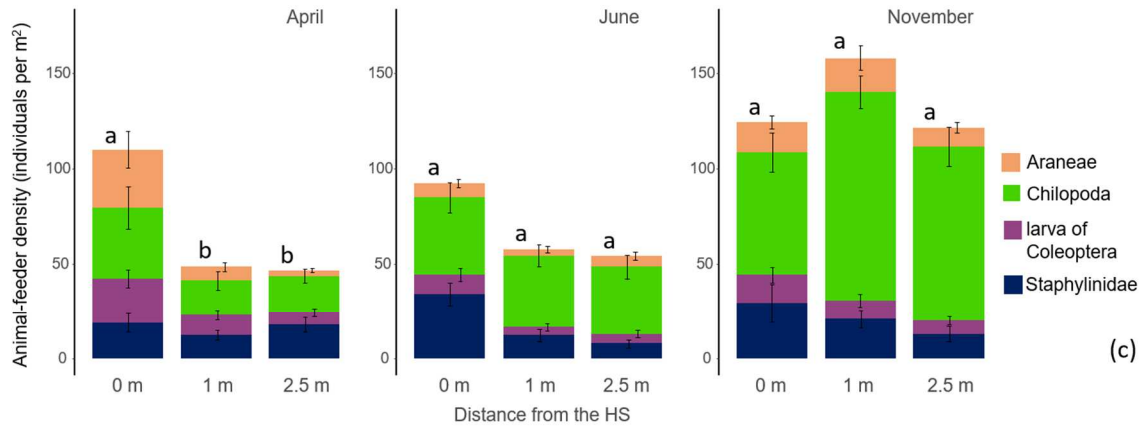
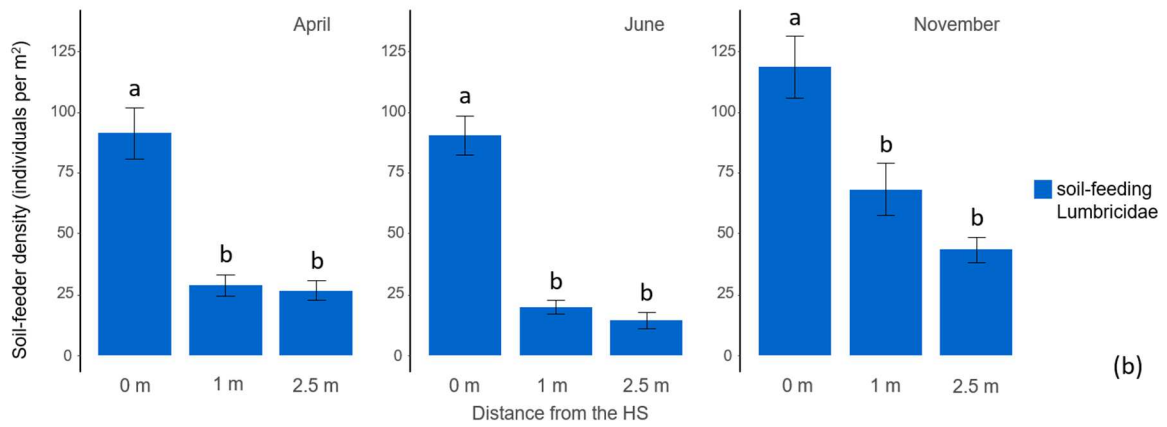
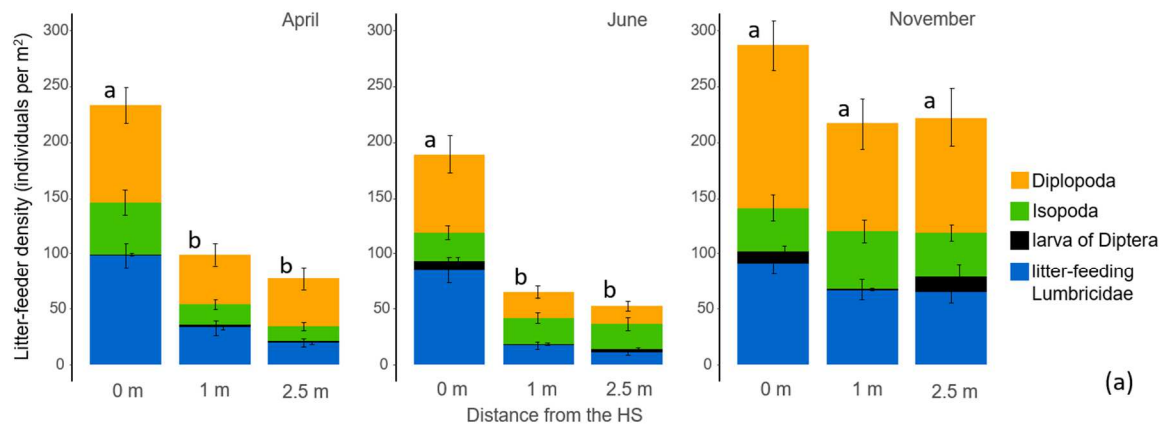


Table 1 Vegetation and soil properties (of the 0-25 cm soil layer) in each shade treatment, at different distances from the herbaceous strip (HS) (mean \pm standard deviation). Vegetation was collected in squares of 50*50 cm and oven-dried at 40 °C during a week for dry biomass determination.

Distance from the HS	No shade			Shade +			Shade ++		
	0 m	1 m	2.5 m	0 m	1 m	2.5 m	0 m	1 m	2.5 m
Texture (clay / silt / sand, g kg ⁻¹)	103 \pm 2 / 410 \pm 3 / 471 \pm 6	105 \pm 2 / 410 \pm 11 / 469 \pm 8	104 \pm 4 / 405 \pm 12 / 475 \pm 8	114 \pm 3 / 383 \pm 15 / 490 \pm 11	112 \pm 6 / 379 \pm 18 / 496 \pm 24	110 \pm 7 / 377 \pm 22 / 500 \pm 30	112 \pm 4 / 386 \pm 7 / 484 \pm 7	110 \pm 5 / 379 \pm 14 / 491 \pm 18	107 \pm 2 / 373 \pm 7 / 502 \pm 9
Bulk density (g cm ⁻³)	1.26 \pm 0.08	1.07 \pm 0.04	1.11 \pm 0.04	1.27 \pm 0.09	1.10 \pm 0.05	1.13 \pm 0.05	1.32 \pm 0.06	1.11 \pm 0.07	1.17 \pm 0.04
pH (in water)	8.2 \pm 0.0	8.2 \pm 0.0	8.2 \pm 0.1	8.1 \pm 0.1	8.2 \pm 0.0	8.2 \pm 0.0	8.1 \pm 0.1	8.3 \pm 0.1	8.2 \pm 0.0
Soil organic carbon (%)	1.5 \pm 0.2	1.7 \pm 0.3	1.6 \pm 0.2	1.9 \pm 0.1	2.0 \pm 0.2	1.7 \pm 0.1	2.0 \pm 0.2	1.9 \pm 0.1	1.8 \pm 0.2
Gravimetric water content (April/ June/ November, %)	27 \pm 3 / 24 \pm 2 / 29 \pm 2	30 \pm 3 / 32 \pm 4 / 33 \pm 3	28 \pm 1 / 30 \pm 3 / 32 \pm 2	28 \pm 1 / 23 \pm 3 / 27 \pm 1	29 \pm 1 / 29 \pm 3 / 28 \pm 1	27 \pm 0 / 26 \pm 3 / 27 \pm 1	24 \pm 4 / 25 \pm 2 / 25 \pm 1	26 \pm 1 / 26 \pm 2 / 26 \pm 1	25 \pm 2 / 24 \pm 1 / 25 \pm 1
Vegetation biomass (April / June / November, g m ⁻²)	120 \pm 94 / 629 \pm 304 / 391 \pm 243	2 \pm 6 / 77 \pm 90 / 125 \pm 150	2 \pm 4 / 62 \pm 56 / 27 \pm 30	42 \pm 37 / 426 \pm 75 / 233 \pm 135	0 \pm 0 / 191 \pm 282 / 22 \pm 27	0 \pm 0 / 79 \pm 72 / 13 \pm 16	64 \pm 62 / 404 \pm 220 / 65 \pm 31	0 \pm 0 / 14 \pm 20 / 6 \pm 9	0 \pm 0 / 24 \pm 19 / 1 \pm 3

Table 2 Mean values of macro-invertebrate densities (individuals per m²) for each distance from the herbaceous strip (HS) and each season for the three shade treatments combined. Mean values were obtained from linear generalized models fitted with a quasi-Poisson law. Values are back-transformed from the logarithmic scale used for analyses. Different lower case letters indicate significantly different values between the means for a given taxonomic group (Tukey test, p-value < 0.05). Different upper case letters indicate significantly different values between the different distance from the HS for all seasons combined when the answer was similar for all seasons (no significant effect of the interaction between season and distance from the HS in Table S3 of the Supplementary materials) (Tukey test, p-value < 0.05). Bold values and letters underline significant differences between distances from the HS for the taxonomic group and season concerned. For Formicidae, a cumulative link model was used.

	Distance from the HS	April	June	November
Lumbricidae	0 m	186.56 ab	174.03 ab	204.31 a
	1 m	59.48 d	36.04 de	129.13 bc
	2.5 m	45.45 de	25.17 e	106.55 c
Diplopoda	0 m	66.10 ab	60.32 abc	108.47 a
	1 m	29.55 bcd	18.65 d	62.87 abc
	2.5 m	25.43 cd	11.2 d	61.33 ab
Isopoda	0 m	46.30 a	23.21 ab	31.19 ab
	1 m	16.29 b	23.21 ab	47.38 a
	2.5 m	12.47 b	23.91 ab	35.74 ab
Chilopoda	0 m	31.02 cd	39.86 cd	62.76 bc
	1 m	16.66 d	39.93 cd	108.96 a
	2.5 m	17.66 d	35.74 cd	91.09 ab
Coleoptera (adults)	0 m	51.33 ab	61.74 a	35.69 abc
	1 m	19.25 c	28.38 bc	35.83 abc
	2.5 m	30.19 abc	21.85 bc	21.37 c
Coleoptera (larva)	0 m A	35.65	28.01	58.95
	1 m A	58.91	20.09	72.69
	1.5 m A	50.52	23.41	64.25
Dermaptera	0 m A	10.69	17.86	35.67
	1 m A	12.01	18.78	41.69
	2.5 m A	4.37	11.52	38.64
Formicidae ¹	0 m A	0 - 240	0 - 240	0 - 240
	1 m AB	0	0 - 240	0 - 240
	2.5 m B	0	0	0

¹ category to which the median value belongs (between 0, 0 to 240 and more than 240 individuals m⁻²)

Table 3 Mean values \pm standard deviation of the density of each earthworm species (individuals per m²), and mean values of earthworm diversity indices from generalized linear models (fitted by quasi Poisson law for species richness, and normal law for Shannon index). Different lower case letters indicate significantly different values between the means (Tukey test, p-value < 0.05). Different upper case letters indicate significantly different values between the different distance from the HS for all seasons combined when the answer was similar for all seasons (no significant effect of the interaction between season and distance from the HS in **Table S3** of the **Supplementary materials**) (Tukey test, p-value < 0.05). Bold values and letters underline significant differences between distances from the HS and seasons for index concerned.

		Distance from the HS	April	June	November
<i>Lumbricus</i>		0 m	5.33 \pm 9.03	4.00 \pm 7.08	2.67 \pm 6.09
<i>terrestris</i>	L.	1 m	2.67 \pm 7.70	0.67 \pm 3.27	2.67 \pm 6.09
(anecic)		2.5 m	0.00 \pm 0.00	0.67 \pm 3.27	1.33 \pm 4.52
<i>Lumbricus</i>		0 m	38.00 \pm 42.15	40.67 \pm 47.65	46 \pm 36.64
<i>castaneus</i>	S.	1 m	15.33 \pm 21.87	9.33 \pm 11.48	48 \pm 34.99
(epigeic)		2.5 m	4.00 \pm 11.80	6.00 \pm 9.21	46 \pm 47.49
<i>Allolobophora</i>		0 m	17.33 \pm 27.07	30.00 \pm 35.72	35.33 \pm 36.54
<i>chlorotica</i>	S.	1 m	8.00 \pm 10.55	8.00 \pm 14.92	31.33 \pm 34.18
(endogeic)		2.5 m	5.33 \pm 9.03	8.00 \pm 14.15	17.33 \pm 20.52
<i>Aporrectodea</i>		0 m	114.67 \pm 57.33	83.33 \pm 52.96	85.33 \pm 58.3
<i>nocturna</i>	E. ¹	1 m	32.00 \pm 29.08	12.67 \pm 14.14	33.33 \pm 35.60
(anecic)		2.5 m	32.00 \pm 31.65	8.00 \pm 12.48	36.00 \pm 36.32
<i>Aporrectodea</i>		0 m	14.00 \pm 16.56	12.67 \pm 14.90	28.00 \pm 26.38
<i>rosea</i>	S.	1 m	3.33 \pm 8.14	3.33 \pm 6.64	15.33 \pm 15.99
(endogeic)		2.5 m	5.33 \pm 10.19	1.33 \pm 4.52	4.67 \pm 7.43
<i>Aporrectodea</i>		0 m	0.00 \pm 0.00	4.00 \pm 4.00	8.00 \pm 8.00
<i>icterica</i>	S.	1 m	0.00 \pm 0.00	2.00 \pm 2.00	2.00 \pm 2.00
(endogeic)		2.5 m	0.00 \pm 0.00	0.00 \pm 0.00	1.33 \pm 1.33
<i>Aporrectodea</i>		0 m	0.00 \pm 0.00	0.00 \pm 0.00	3.33 \pm 3.33
<i>caliginosa</i>	S.	1 m	0.00 \pm 0.00	0.00 \pm 0.00	1.33 \pm 1.33
(endogeic)		2.5 m	0.00 \pm 0.00	0.00 \pm 0.00	1.33 \pm 1.33
Species richness		0 m	2.9 ab	3.3 ab	3.9 a
		1 m	1.9 cd	1.7 cde	3.2 ab
		2.5 m	1.4 de	1.1 e	2.3 bc
Shannon index		0 m A	2.10	2.52	3.15
		1 m B	1.72	1.52	2.57
		2.5 m C	1.36	1.20	2.01

¹ synonymy *Nicodrilus nocturnus* Bouché, 1972 (Briones et al., 2009)

