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1 Role of different size classes of organisms in cropped soils: what do litterbag experiments tell us? A
2 meta-analysis.

3

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10

11 Abstract

12 Soil organisms are essential for the functioning of agrosystems, especially in the process of litter
13 decomposition. Litterbags constitute one common way to assess litter decomposition and to
14 investigate the role of the different groups of soil organisms in the decay activity. However, there is
15 currently no standardized litterbag protocol to measure the effects of soil organisms on litter
16 decomposition. Furthermore, litterbag studies remain scarce in agrosystems and little information is
17 available about the influence of different groups of soil organisms depending on agricultural
18 practices. The development of cropping systems that rely on high soil biodiversity and fertility
19 however requires a detailed understanding of these processes. In order to address this need and to
20 have an overview of the existing protocols, we conducted a review on litterbag experiments in
21 annually cropped soils. We collected information on the experimental design (e.g. duration, number
22 of replicates), litterbags (e.g. size, mesh), climate, soil type, standing crop, enclosed litter (e.g. litter
23 type, quality) and methods used to characterize organic matter decomposition and soil organisms.
24 The effects of soil organisms of different size classes (meso- and macrofauna) was assessed with a
25 meta-analysis performed on studies using litterbags of different mesh sizes. The general effect size of
26 soil macrofauna, mesofauna (in addition to soil microorganisms) and of their combination was

27 assessed with a three-level random-effect model accounting for the random effect at the study level.
28 This effect was compared for subgroups based on climate, soil, standing crop, agricultural system and
29 litter type as categorical factors, and for depth of bags, duration of the experiment and size of litter
30 pieces as continuous factors. Macrofauna, mesofauna and the combination of both were found to
31 significantly increase litter decomposition. Surprisingly, meso- and macrofauna contributed equally
32 to litter decomposition and their effects were not additive (when comparing the role of meso- and
33 macrofauna independently and simultaneously). These effects tend to be influenced by various
34 factors: climate, soil, standing crop and agricultural system for macrofauna; standing crop and litter
35 type for mesofauna; and soil, standing crop and litter type for their combined effects. Multi-mesh
36 litterbag experiments showed that even in soils with high disturbances, soil organisms of several size
37 classes have a significant impact on organic matter decomposition. While this study showed that
38 both soil macrofauna and mesofauna increased litter decomposition in annual cropping systems,
39 there are still numerous gaps in our knowledge of the impacts of the agronomic (e.g. cropping
40 system, practices, crop type) and environmental contexts (e.g. climates, soils). Forecasting future
41 studies, we provide guidelines to develop a standard litterbag protocol adapted to the specificities of
42 annually cropped soils.

43

44 Keywords: litterbag, litter decomposition, soil macrofauna, soil mesofauna, agrosystems, organic
45 matter

46

47 1. Introduction

48

49 Organic matter plays a key role in soil functioning and in particular on soil fertility through the
50 release of nutrients during decomposition (Tiessen et al., 1994; Carter, 2002). In cropping systems,
51 organic matter comes from the restitution of crop residues to the soil, inputs of organic waste
52 products (e.g. livestock manure or compost) or burial of cover crops. Its distribution in soil depends

53 on agricultural practices. In particular, soil tillage leads to a more or less homogenous soil-organic
54 matter mixture over variable depths (Salinas-Garcia et al., 1997; Kay and VandenBygaart, 2002).

55 Soil organisms are essential drivers of the decomposition of organic matter. According to their size,
56 microorganisms (< 0.1 mm), mesofauna (0.1 - 2 mm) and macrofauna (> 2 mm) (Swift et al., 1979)
57 can act at different spatial and temporal scales. However, the contribution and context specific
58 effects of different groups of soil organisms during decomposition is still not well known. In addition,
59 the density and diversity of soil organisms are generally lower in agrosystems than in any other
60 ecosystem (Tsiafouli et al., 2015; Joimel et al., 2017). Intensive management of cropping systems
61 affects soil quality in the short and long term by modifying physical, chemical and biological soil
62 characteristics, with the intensity of changes depending on pedoclimatic conditions and farming
63 practices (Hati et al., 2007; Mazzoncini et al., 2010). These changes can strongly affect
64 decomposition, thus threatening core ecosystem functions such as nutrient cycling (Bradford et al.,
65 2002; Chen et al., 2020). A detailed understanding of the role of soil organisms during organic matter
66 decomposition is fundamental to develop agroecology and to implement systems that will rely on
67 soil biodiversity and fertility.

68 To address the gaps on the role of soil organisms on decomposition, numerous studies were
69 conducted under laboratory conditions (Huhta, 2007). However, these experiments showed
70 limitations as they can present lower diversity than in field conditions (Kardol et al., 2016).
71 Consequently, the simulated biodiversity and modification of soil properties are not representative
72 of the reality, which could be addressed by studies *in situ*.

73 Litterbags and teabags constitute one common way to assess decomposition *in situ* and over a long
74 period of time (Didion et al., 2016). The litterbag technique was developed in the middle of the 19th
75 century (Crossley and Hoglund, 1962; Edwards and Heath, 1963), while the teabag method was
76 introduced recently (Keuskamp et al., 2013). The advantage of litterbags is that they contain organic
77 matter that can be adapted to the context of the experiment. In addition, litterbags can be used to
78 study the contribution of different groups of soil organisms to litter decomposition by selectively

79 excluding some fauna size classes. This selection can occur either by using different mesh sizes in
80 order to physically exclude some organisms, or by a chemical treatment inhibiting part or all of the
81 organisms. The exclusion of organisms by mesh size has sometimes been criticized due to a potential
82 effect of different mesh sizes on decomposition (Anderson, 1973; Bradford et al., 2002), but this
83 technique was approved as a reliable method to quantify the role of soil organisms in litter mass loss
84 (Seastedt, 1984; Bokhorst and Wardle, 2013). However, contrary to the teabag method, no
85 standardized method is currently available for one who wants to start a litterbag experiment. Yet
86 litterbags mimic surface or buried crop residues in cropping systems and therefore allow looking at
87 the main factors affecting their decomposition. Forecasting future studies on soil biodiversity in
88 agricultural context, a standard protocol adapted to the specificities of annually cropped soils could
89 be beneficial.

90 The litterbag method has been subjected to several reviews and meta-analyses, focusing on the
91 history of the method (Huhta, 2007) and on the impacts of several factors on litter decomposition,
92 namely soil fauna (Seastedt, 1984; Kampichler and Bruckner, 2009; Frouz et al., 2015; Zhang et al.,
93 2015; González and Lodge, 2017; Frouz, 2018), climate and litter quality (García-Palacios et al., 2013;
94 Zhang et al., 2015; Krishna and Mohan, 2017), nitrogen addition (Knorr et al., 2005) and pesticides
95 (Knacker et al., 2003). In a first review, Seastedt (1984) estimated microarthropods to increase litter
96 decomposition by 23%. The meta-analysis of Kampichler and Bruckner (2009) confirmed the positive
97 effect of microarthropods over several land-use types, notably in agricultural soils. In a later meta-
98 analysis, Frouz et al. (2015) found macrofauna to significantly increase litter removal but not litter
99 mineralization. García-Palacios et al. (2013) and Zhang et al. (2015) estimated that exclusion of all
100 fauna from litterbags, by physical or chemical methods, decreased litter decomposition by 27% and
101 35% respectively. Recently, Huang et al. (2020) found that high diversity of earthworm functional
102 groups increased litter and soil organic carbon decay in tree plantation and forests. In forest
103 ecosystems, soil detritivores were reported to strongly increase leaf litter and wood debris
104 decomposition, with macrofauna or mesofauna having a larger impact depending on the forest type

105 and climatic conditions (González and Lodge, 2017; Krishna and Mohan, 2017). Previous reviews
106 were mostly focused on forest ecosystems or grasslands (González and Lodge, 2017; Krishna and
107 Mohan, 2017), while studies on cropped soils remain scarce (Knacker et al., 2003; Kampichler and
108 Bruckner, 2009). Furthermore, none of these reviews or meta-analyses investigated the comparative
109 effect of different size classes of organisms. In this context, we provide here the first study to assess
110 litter decomposition for several size classes of soil organisms in annually cropped soils.

111 The objectives of this study were (1) to assess the effects of different size classes of soil organisms on
112 litter decomposition in annually cropped soils through the litterbag method and (2) to provide an
113 overview of the existing protocols of the litterbag method in cropping systems. To this end, we
114 conducted a meta-analysis of litterbag experiments in annually cropped soils. In particular, we aimed
115 to quantify the effects of soil organisms of different size classes (meso- and macrofauna) in studies
116 using bags of different mesh sizes.

117

118 2. Materials and methods

119

120 2.1 Data collection

121

122 Literature was surveyed in November 2019 for studies assessing the effect of soil organisms on litter
123 decomposition with the litterbag method. We searched in all the Web of Science databases, with no
124 restriction on the publication year, for papers containing the keywords “litter”, “decomposition,
125 degradation, decay or breakdown”, “*fauna, *organism*, animal*, *flora, *arthropod*,
126 *invertebrate*, collembola*, springtail*, earthworm*, lombric*, fungi, bacter* or nematod*”,
127 “*bag*” and “soil*”. In addition, we deliberately excluded papers containing the words “bagasse*”,
128 “stream*”, “marine” and “aquatic”. The search returned 1040 results. Further studies were added by
129 checking articles included in previous reviews (Knacker et al., 2003; Kampichler and Bruckner, 2009;
130 García-Palacios et al., 2013; Frouz et al., 2015; Zhang et al., 2015). In total, 1106 articles were

131 collected through the different search paths. Studies had to meet the following criteria to be
132 selected:

- 133 - they should discuss the decomposition of organic matter or nutrient loss using the litterbag
134 method and provide sufficient information about the protocol (e.g. mesh size) ;
- 135 - they should focus on agricultural soils, more precisely on annually cropped soils, but not on
136 agroforestry, orchards, vineyards, grasslands, fallows, bare soils and field margins ;
- 137 - they should present data on organic matter decomposition (e.g. mass loss, decomposition
138 rate), and not focus on a specific component only (e.g. lignin) ;
- 139 - they should use only physical methods based on different mesh sizes to exclude soil
140 organisms from litterbags, and not chemicals (e.g. naphthalene) ;
- 141 - at least two different mesh sizes had to be used for the litterbag experiment ;
- 142 - the experiments should be conducted *in situ* ;
- 143 - the experiments should not assess the effect of plant protection products on litter
144 decomposition ;
- 145 - the publication had to be written in English, French or German (which excluded mostly
146 Chinese and Portuguese papers).

147 Finally, 22 studies fit all of the previous criteria. These 22 studies were used to conduct our review
148 and the data extracted from 17 of the 22 studies were used for the meta-analysis (see the list in
149 supplementary material). In the case of studies that took interest in several land-uses, the following
150 analyses on study parameters and results focus only on the data related to cropland.

151

152 2.2 Data extraction

153

154 For the 22 selected studies, we recorded the parameters related to geographical location (country),
155 climate, soil type, standing crop and cropping system. In order to facilitate comparisons, climate
156 types were denominated according to the five groups defined by the Köppen climate classification:

157 tropical, dry, temperate, continental and polar; and soil types according to the FAO soil classes
158 (World Reference Base for Soil Resources, 2014). When not given in the study, climate was deduced
159 from the location of the study and by using regional climate maps, and soil types were collected in
160 papers reporting experiments on the same sites.

161 We investigated the general design of the experiments: duration, number of sites and plots, number
162 of replicate bags, number of sampling dates, sampling days, placement and depth of litterbags in soil.
163 Information was also collected about the litterbags characteristics (bag size, mesh size, material,
164 closure technique) and on the type of litter used in bags (litter quality, amount per bag, size of litter
165 residues).

166 We collected data on litter decomposition. Twenty studies reported the decomposition as the
167 percentage of remaining mass or initial mass loss in litterbags. Nine studies provided the
168 decomposition rate, corresponding most of the time to the coefficient of the exponential model
169 fitted on the data of remaining mass through time. If available, original data were extracted,
170 otherwise they were obtained from graphics using the WebPlotDigitizer tool (Ankit Rohatgi,
171 <https://automeris.io/WebPlotDigitizer>). If standard deviation, standard error or confidence interval
172 were missing, we attributed the mean value of all standard deviations reported in studies selected
173 for the same analysis. In addition, we summarized data on collected groups of soil organisms,
174 sampling techniques and available measurements.

175 In order to gather decomposition data related to soil organisms of different size classes, we grouped
176 mesh sizes used in the studies into three categories corresponding to the size classes of organisms
177 that could enter bags. The fine mesh bags corresponded to bags with a mesh size lower than 0.1 mm,
178 allowing access to litter to both microfauna (e.g. nematodes) and microflora (e.g. bacteria, fungi).
179 The medium mesh bags had a mesh size comprised between 0.1 and 2 mm, allowing additional
180 access to mesofauna which main representatives are microarthropods such as Collembola and Acari.
181 Finally, the coarse mesh bags had a mesh size larger than 2 mm, thus enabling access to macrofauna
182 organisms such as earthworms, carabids and other insects.

183 The role of the meso- and macrofauna in the decomposition of organic matter was determined from
184 "paired observations" corresponding to the comparison between values of litterbag mass lost from
185 two different mesh sizes (fine and medium, medium and coarse, or fine and coarse), studied under
186 the same conditions. Each time point and each modality given in the studies provided individual
187 paired observations with duration corresponding to the sampling time. Thus, several paired
188 observations were reported for each study. Hereafter, we will distinguish "study" (i.e. publication)
189 and "paired observation" (i.e. result obtained in a study) with n the number of paired observations
190 included in the analysis.

191

192 2.3 Data analyses

193

194 The mass loss rate (MLR) was calculated for each mesh group as $MLR = \%ML/t$, where $\%ML$ is the
195 percent mass loss in litterbags at the time t (days). In addition, the fauna effect (FE) on litter mass
196 loss was assessed by comparing the mass loss obtained in different bags such as $FE = \%ML_1 -$
197 $\%ML_2$ where $\%ML_1$ and $\%ML_2$ are the percentage of mass loss in larger (coarse or medium) and
198 smaller (medium or fine) mesh bags respectively (adapted from Seastedt, 1984). Statistical tests were
199 conducted to assess if differences in mass loss rate were significantly affected by factors such as
200 climate, soil, crop, agricultural systems and litter types, and to assess if overall macrofauna and
201 mesofauna effects on decomposition were significantly different. For this purpose, the normality and
202 homogeneity of variances were tested with a Shapiro-Wilk test ($\alpha > 0.05$) and a Bartlett test ($\alpha >$
203 0.05) using R package *stats*. As normality was not met, a Generalized Linear Mixed-effect Model
204 (GLMM) with a gamma distribution, a fixed effect for the studied factor and a random effect for
205 study level was applied, followed by Tukey HSD post-hoc tests. In order to obtain only positive
206 values, data on the fauna effect were transformed by adding to each value the maximum fauna
207 effect. Then, ANOVA with a χ^2 -test was performed to compare models with and without the studied
208 factor. The mass loss or fauna effect were influenced by the studied factor if the Akaike Information

209 Criterion (AIC) was significantly lower for the model with the factor than for the model without ($P <$
210 0.1).

211 The role of the meso- and macrofauna in litter decomposition was assessed by comparing mass loss
212 in bags of different mesh size groups. The first set of analyses investigated the effect of macrofauna
213 comparing coarse and medium mesh bags (based on the results of 12 studies containing 201 paired
214 observations), the second set was on the effect of mesofauna comparing medium and fine mesh bags
215 (10 studies, 126 paired observations), and the last set on the effect of combined macro- and
216 mesofauna comparing coarse and fine mesh bags (7 studies, 75 paired observations). Paired
217 observations with a duration lower than 14 days were not included in the statistical analyses, but
218 were represented on the graphical representation of litter mass loss and fauna effect. Litterbags
219 including several groups of organisms were considered as “treatment” and bags excluding one or
220 several groups included in the treatment as “control” (coarse vs medium, medium vs fine and coarse
221 vs fine respectively). The effect size (ES), or standardized mean difference between treatment and
222 control, and the 95% confidence interval (CI) were computed for individual paired observations and
223 overall results using the Hedges’g calculation (Hedges and Olkin, 1985). A three-level random-effect
224 model was applied, with random effects at the paired observation and at the study level. This allows
225 to account for the lack of independence of paired observations from the same study, considering
226 similar modalities but differing in sampling time. In addition, the heterogeneity between studies was
227 calculated with the I^2 (Higgins and Thompson, 2002). Heterogeneity above zero reveals that the
228 variability in the observed effect size is larger than one expected based on sampling variability. This
229 may be explained by differences between studies according to one or several factors (e.g. climate,
230 soil type), meaning that different subgroups of studies will have a significantly different mean effect
231 size.

232 The role of different soil organisms in the decomposition of litter was compared for different
233 categorical factors (climate, soil, crop, agricultural systems and litter type) and for continuous factors
234 (depth of bags, duration of the experiment and size of litter pieces) considered as moderators to

235 conduct a subgroup analysis. The effect of moderators was assessed with the Cochran Q-statistic and
236 a χ^2 -test was performed to test its significance. A significant Q-statistic indicated that the moderator
237 influenced the effect size ($P < 0.05$) and thus that part of the total heterogeneity could be explained
238 by this difference. Except for climate, we only presented results for subgroups with more than 10
239 paired observations.

240 These analyses were performed using R software version 3.6.3 (R Development Core Team 2020) and
241 the *lme4* (Bates et al., 2015), *multcomp* (Hothorn et al., 2008), *metafor* (Viechtbauer, 2010) and
242 *dmetar* packages (Harrer et al., 2019).

243

244 3. Results

245

246 3.1 General characteristics of studies

247

248 The 22 selected studies were located all around the world, mostly across Europe (36%) but also in
249 Asia (18%), South America (18%), North America (14%) and Africa (14%) (Table 1). In relation with
250 their location, 54% of the studies occurred under temperate climate, and few studies under tropical
251 (18%), continental (18%) and dry (9%) climates (Table 1). The soil type was highly variable. Several
252 studies were conducted on Luvisol (24%) and Cambisol (14%) which are favorable to agriculture. The
253 others occurred in nine different soil types (e.g. Ferralsol, Fluvisol, Lixisol, Kastanozem) (Table 1).

254 Most of the studies were conducted on annual crops under conventional agriculture (54%) and no-
255 tillage agriculture (32%) (Fig. 1a; Table 1). Only two studies were conducted under organic
256 agriculture, one on minimum tillage and one on relay cropping. The most common crops at the time
257 of the study were maize (32%), barley (23%), soybean (18%) and wheat (14%) (Fig. 1b).

258 Collected studies had different objectives with some investigating the effect of climate (e.g. Peña-
259 Peña and Irmler, 2018; Yin et al., 2019), land-use (e.g. Tian et al., 1998; Yang et al., 2018) or litter
260 type (e.g. Ouédraogo et al., 2004; Carlesso et al., 2019). They also focused on various agricultural

261 practices, mainly tillage (e.g. House and Stinner, 1987; Domínguez et al., 2010), but also fertilization
262 (Weil and Kroontje, 1979), conventional vs organic management (Domínguez et al., 2014; Yin et al.,
263 2019) and genetically modified vs non-modified crops (Zwahlen et al., 2007). Finally, some authors
264 also used litterbags to assess the decomposition activity of specific organisms (e.g. Jensen, 1985;
265 Vreeken-Buijs and Brussaard, 1996).

266

267 3.2 General design of litterbags experiments

268

269 Studies were mostly conducted on a single agricultural site (82%), while studies on several sites were
270 scarce (18%, e.g. Domínguez et al., 2010; Peña-Peña and Irmeler, 2016) (Table 1). The number of plots
271 ranged from one to 60 and plot size varied from 0.5 x 0.5 m to 120 x 30 m. However, studies with
272 only one plot comprised 3 to 100 subplots within this plot, which we considered as plots.

273 Duration of experiments ranged from 27 to 392 days, being on average 206 days (Table 1). The
274 number of sampling dates ranged from one to 10 (Fig. 1c). Litterbags were mainly sampled between
275 5 and 120 days after their addition into soil, but in some studies they were sampled after more than
276 300 days (Fig. 1d). Seven studies considered annual or seasonal dynamics and in this case,
277 experiments lasted up to three years. Three types of sampling schemes were identified namely short
278 studies with few sampling dates, long studies with few or many sampling dates.

279 The number of replicate bags per modality ranged from 3 to 30 (Table 1). Bags were placed on the
280 surface (32%) or buried in soil between 3 and 35 cm (50%); however information on depth was
281 missing in several studies (18%) (Table 1). Sometimes bags were placed on the surface and then
282 buried at the time of tillage (e.g. Jensen, 1985; Domínguez et al., 2014).

283

284 3.3 Litterbag characteristics

285

286 Within the selected studies, 59% used litterbags with two mesh sizes (27% medium + coarse; 18%
287 fine + medium; 14% fine + coarse), 32% with three (23% fine + medium + coarse; 4% fine + two
288 medium; 4% coarse + two medium) and 9% with four mesh sizes (fine + coarse + two medium). The
289 mesh size ranged from 0.003 to 10 mm (Fig. 1e). Fine mesh ranged from 0.003 to 0.08 mm, medium
290 mesh from 0.1 to 2 mm, and coarse mesh from 4 to 10 mm. The most common mesh sizes for each
291 category were 0.02 mm (54%), 1 mm (29%) and 5 mm (31%).

292 The main material to construct litterbags was nylon or another synthetic polyester. Some studies
293 however used stainless steel or brass in order to prevent bags from being decomposed by termites
294 (tropical climate). The size of bags was mainly comprised between 10 x 10 cm and 20 x 20 cm (Table
295 1). The closure of bags was only discussed in seven publications. Bags were either sewn or glued.

296 Some authors improved the technique to limit litter losses in soil, after sampling and during
297 transportation. For instance, Yang et al. (2018) sewed 0.01 mm mesh patches to the bottom of their
298 litterbags. Jensen (1985) and Carlesso et al. (2019) used transportation bags or boxes, but they
299 showed that mass loss during transportation was not significant in regards of the total mass loss. Tian
300 et al. (1992, 1998) placed pieces of wood inside litterbags to avoid litter compression. Finally, to
301 rewet the litter and standardize the initial microflora in all litterbags, Vreeken-Buijs and Brussaard
302 (1996) soaked all the litterbags in diluted filtered soil extract one night prior their incorporation into
303 soil.

304

305 3.4 Litter characteristics

306

307 Litter consisted of straw or leaves (Table 1). The most commonly used materials were C3 cereals
308 (50%) such as wheat (27%) or rice (9%), C4 cereals (32%) such as maize (23%) or sorghum (9%),
309 Fabaceae (27%) including crops (clover, vetch, alfalfa) and shrubs leaves (*Gliricidia sepium* (Jacq.)
310 Steud., *Leucaena leucocephala* (Lam.) de Wit, *Senna siamea* (Lam.) H.S.Irwin & Barneby), and grasses

311 (14%) (Fig. 1f). Tree leaves (poplar, *Acioa barteri* (Hook.fil. ex Oliv.) Engl.), Brassicaceae (rapeseed,
312 mustard) and manure were also used.

313 The C:N ratio of the litter, specified in six studies, ranged between 8 and 153. The C:N ratio was often
314 the highest for C4 cereals (13 to 72), and remains high for C3 cereals (12 to 77). Comparatively,
315 Fabaceae presented lower C:N ratios (9 to 57). However, C:N ratio was highly variable between
316 studies for the same litter.

317 The amount of litter per bag ranged from 0.5 to 100 g, depending on the size of bags and the litter
318 used. In some works, the size of residues was standardized by cutting litter into pieces of 1 to 10 cm
319 length. Prior to introduction in bags, litter was often air or oven-dried between 20 °C (Valckx et al.,
320 2011) and 105 °C (Carlesso et al., 2019).

321

322 3.5 Litter decomposition

323

324 The litterbags, once collected, were either brushed or rinsed under water to remove soil particles,
325 roots, plant debris other than litter, and sometimes fauna. The bags were then dried between 20 and
326 105 °C, and weighed. In some cases, the litter was removed from the bags before being weighed. In
327 nine studies, litter was burnt between 500 and 800 °C in order to measure ash free dry weight. Some
328 studies performed additional analyses (e.g. C, N contents) to characterize the litter after
329 biodegradation.

330 Enclosed litter lost more than half of its initial mass after a year or less in 57%, 46% and 23% of the
331 coarse (n = 199 observations), medium (n = 254) and fine (n = 128) litterbags respectively (Fig. 2).

332 Mass loss rate was significantly influenced by climate in medium mesh bags only, and by soil and
333 crop type in all mesh bags (Table S1). Agricultural systems did not significantly influence mass loss
334 rate (Table S1). In medium mesh bags, mass loss was faster under tropical and continental climates
335 than under dry ($P < 0.001$) and temperate climates ($P < 0.05$), and faster under temperate than under
336 dry climate ($P < 0.001$) (Fig. 2a-c). In addition, mass loss was faster in Acrisol than in Luvisol for all

337 mesh bags (coarse and fine : $P < 0.001$, medium: $P < 0.05$), in Cambisol than in Luvisol in coarse ($P <$
338 0.001) and fine mesh bags ($P < 0.001$), and in Lixisol than in Luvisol in coarse ($P < 0.001$) and medium
339 mesh bags ($P < 0.01$). Furthermore, mass loss was faster in fields cropped with C4 cereals than with
340 C3 cereals for medium ($P < 0.05$) and fine mesh bags ($P < 0.001$).

341 Litter decomposition was also significantly dependent on litter type, regardless of the mesh size (Fig.
342 2d-e, Table S1). The degradation of C3 cereals was significantly slower than that of C4 cereals in
343 medium ($P < 0.05$) and fine bags ($P < 0.001$), and slower than that of Fabaceae in all bags (coarse and
344 medium: $P < 0.05$, fine: $P < 0.001$). More precisely, wheat decomposed significantly faster than maize
345 in all bags (coarse, medium, fine: $P < 0.01$). It is noteworthy that C3 cereals, except for rice, were
346 always used under temperate climate. In contrast, C4 cereals, especially maize, were used under all
347 climate types.

348

349 3.6 Effect of soil organisms on litter decomposition

350

351 In parallel to monitoring litter decomposition, the fauna was in some cases extracted from the soil
352 (27%), from the litterbags (27%) or both (9%), using MacFayden or Berlese extractors for mesofauna
353 (50%) and hand sorting for macrofauna (45%). Microorganisms were studied in 18% of the studies.
354 Seven studies considered two size classes and only one the three size classes (Miura et al., 2008). The
355 most studied groups of soil fauna were Collembola (45%), Acari (36%), Lumbricidae (32%), Araneae
356 (18%), Enchytraeidae (14%) and Nematoda (14%) (Table 1). However, some studies also took interest
357 at Coleoptera, Isoptera, Myriapoda (Chilopoda, Diplopoda, Symphyla, Pauropoda), Crustacea
358 (Isopoda), Annelida, Dermaptera, Diptera, Hymenoptera (Fomicidae), Lepidoptera, Orthoptera,
359 Psocoptera, and larvae (Coleoptera, Diptera) (Table 1). Most of the studies assessed organism's
360 density or biomass, while diversity (richness, diversity indexes) was only discussed in five studies.
361 Microbial activity was characterized *via* respiration (CO_2 measurements) or substrate-induced
362 respiration. Only one study focused on functional groups, gathering together microarthropods

363 according to their feeding habits (Vreeken-Buijs and Brussaard, 1996). Finally, six studies assessed
364 the “fauna effect” as the difference of mass loss between bags including and excluding soil fauna.

365

366 3.6.1 Role of macrofauna

367

368 Soil macrofauna had a significant positive effect on the decomposition of organic matter in litterbags
369 with a mean fauna effect of 9.4% (Fig. 3a, d; range = [-20.3%, 83.5%]) and a mean effect size of 0.66
370 (Figs. 4a and S1; 95% CI = [0.37; 0.96], $P < 0.0001$, $n = 201$ paired observations). A moderate
371 heterogeneity between studies was observed ($I^2 = 72.3\%$). A negative mean fauna effect occurred in
372 22.2% of the paired observations (Fig. 3a, d).

373 The effect of macrofauna on litter decomposition was dependent on the climate ($P < 0.0001$), soil (P
374 < 0.0001), crop types ($P < 0.0001$) and agricultural systems ($P = 0.0003$) (Fig. 4b, Table S2).

375 Macrofauna effect on decomposition was the highest under dry (ES = 3.12; $n = 36$ paired
376 observations) and continental (1.40; $n = 8$ from only 1 study) climates (Fig. 4b), being especially high
377 during the early stages of decomposition and then decreasing with time (Fig. 3a). In comparison, it
378 was lower under tropical (0.28; $n = 40$ from 1 study) and temperate (0.23; $n = 117$) climates (Fig. 4b),
379 for which it remained quite steady over time (Fig. 3a). Furthermore, the macrofauna played a
380 particularly important role for the litter degradation in Cambisols (4.19; $n = 26$), and had a lower but
381 significant effect in Nitisols (0.70; $n = 12$ from 1 study), Luvisols (0.53; $n = 25$), Gleysols (0.43; $n = 30$
382 from 1 study) and Lixisols (0.31; $n = 58$) (Fig. 4b). It was not significant in Kastanozem soils (0.14; $n =$
383 22) (Fig. 4b). Conversely, the effect size was significantly negative in Acrisols (-0.26; $n = 24$ from 1
384 study). The effect of macrofauna also varied with the standing crop, with a maximum effect size
385 observed in sorghum fields (3.12; $n = 36$) followed by wheat (0.82; $n = 10$), barley (0.49; $n = 53$) and
386 soybean fields (0.49; $n = 10$). It was not significant under maize fields (0.10; $n = 82$) (Fig. 4b).
387 However, it was difficult to discriminate the effects of dry climate and sorghum cultivation as they
388 co-occurred in the same studies (Reddy et al., 1994; Ouédraogo et al., 2004). Finally, macrofauna

389 demonstrated a significant positive effect on decomposition under conventional systems (0.53; n =
390 77), and a rather low and not significant effect under no-tillage systems (-0.04; n = 50) (Fig. 4b).
391 The type of litter did not significantly influenced the effect of macrofauna (P = 0.11) (Fig. 4b, Table
392 S2). However, the macrofauna was observed to play a very important role in the degradation of C4
393 residues such as maize (1.41; n = 34) (Fig. 4b), especially in the early stages of degradation (Fig. 3d).
394 Its role was less important and later for C3 residues such as wheat (0.42; n = 50) and rice (0.42; n =
395 26) (Fig. 4b). It was not significant for local residues (0.16; n = 11) (Fig. 4b). The macrofauna effect
396 fluctuated for Fabaceae and tree leaves for which it was sometimes positive or negative (Fig. 3d).
397 The depth of bags had a positive significant influence on the effect of macrofauna (P < 0.0001), but
398 not the duration of the incubation in field (P = 0.14) or the size of the litter pieces (P = 0.87) (Table
399 S3).

400

401 3.6.2 Role of mesofauna

402

403 Soil mesofauna had a significant positive influence on the decomposition of organic matter in
404 litterbags with a mean fauna effect of 6.6% (Fig. 3b, e; range = [-7.5%, 48.7%]) and a mean effect size
405 of 0.31 (Figs. 5a and S2; 95% CI = [0.11; 0.52], P = 0.003, n = 126 paired observations). The
406 heterogeneity was low ($I^2 = 40.2\%$). A negative mean fauna effect appeared in 29.5% of the paired
407 observations (Fig. 3b, e).

408 The effect of mesofauna was significantly influenced by the crop types (P = 0.003), while no
409 significant difference was found between different climates (P = 0.99), soils (P = 0.57) or agricultural
410 systems (P = 0.06) (Fig. 5b, Table S2). Mesofauna effect on decomposition was significantly positive
411 under temperate climate only (ES = 0.31, n = 110 paired observations), but not under continental
412 (0.49, n = 8) and tropical climates (0.36, n = 8) for which it increased with time (Fig. 3b). The lack of
413 difference for the climate subgroup could be explained as almost all the experiments were
414 conducted under temperate climate (n = 110). Moreover, mesofauna had a non-significant positive

415 effect on decomposition in Fluvisol (0.67; n = 14), Cambisols (0.59; n = 20), Luvisols (0.42; n = 48) and
416 Nitisol (0.33, n = 12), and a non-significant negative effect in Acrisols (-0.01; n = 24 from 1 study) (Fig.
417 5b). In addition, mesofauna played an important role on the litter decomposition in wheat fields
418 (1.35; n = 14) compared to rapeseed (0.64; n = 12 from 1 study), maize (0.18; n = 45), barley (0.09; n
419 = 33) and sugar beet fields (0.05; n = 10 from 1 study) for which its effect was not significant (Fig. 5b).
420 Finally, a significantly positive mesofauna effect on decomposition was observed under conventional
421 systems only (0.14; n = 49).

422 Mesofauna effect on decomposition was also dependent on the litter type ($P = 0.03$) (Fig. 5b, Table
423 S2). The mesofauna particularly increased the decomposition of C4 cereals such as maize (0.65; n =
424 34) (Fig. 5b), especially at the early stage of decomposition (Fig. 3e). Comparatively, it did not
425 significantly increase the degradation of C3 cereals such as wheat (0.09; n = 43) (Fig. 5b), with low or
426 negative effect, only increasing at the later stage of the decomposition (Fig. 3e). Finally, the
427 mesofauna effect tended to increase with time for tree leaves (Fig. 3e) and fluctuated for Fabaceae
428 (Fig. 5b).

429 The duration of the experiment significantly influenced the effect of mesofauna on decomposition (P
430 = 0.002), but not the depth of litterbags ($P = 0.98$) or the size of litter pieces ($P = 0.71$) (Table S3).

431

432 3.6.3 Combined impact of both macro- and mesofauna

433

434 Soil macro- and mesofauna together contributed positively and significantly to the decomposition of
435 litter compared to microorganisms only. The mean fauna effect of combined macro- and mesofauna
436 on litter decomposition was 10.8% (Fig. 3c, f; range = [-15.3%, 85.9%]) and the mean effect size was
437 0.75 (Figs. 6a and S3; 95% CI = [0.34; 1.17], $P = 0.0004$, n = 75 paired observations) (Fig. 6a). A
438 moderate heterogeneity was observed ($I^2 = 73.75\%$). The mean fauna effect was negative in 18.5% of
439 the paired observations (Fig. 3c, f). The cumulative effect was lower than the effect obtained by the
440 addition of the macrofauna and the mesofauna effects that reached 16.0%. In addition, it should be

441 noted that the individual fauna effects of macrofauna and mesofauna were not significantly different
442 ($P = 0.36$).

443 The fauna effect on decomposition was dependent on soil ($P = 0.002$) and crop type ($P = 0.01$), but
444 not on climate ($P = 0.10$) or agricultural system ($P = 0.32$) (Fig. 6b, Table S2). Soil fauna played a very
445 important role in the litter decomposition under continental climate ($ES = 2.04$; $n = 8$ paired
446 observations from 1 study) (Fig. 6b), especially at the early stages of decomposition (Fig. 3c). It was
447 also important under tropical climate (1.19 ; $n = 20$ from 1 study) (Fig. 6b), for which it increased with
448 time (Fig. 3c). It tends to be lower under temperate climate (0.47 ; $n = 47$) (Fig. 6b) and seemed quite
449 steady over time (Fig. 3c). In addition, soil fauna provided a significant increase in litter
450 decomposition in Ferralsols (1.19 ; $n = 20$ from 1 study), and to a lesser extent in Luvisols (0.45 ; $n =$
451 25) (Fig. 6b). Contrastingly, soil fauna effect was negative but non-significant in Acrisols (-0.29 ; $n = 12$
452 from 1 study) (Fig. 6b). Nevertheless, it was not possible to discriminate the effects of tropical
453 climate and Ferralsol soil type as they co-occurred in one study (Peña-Peña and Irmeler, 2016).
454 Furthermore, soil fauna positively influenced litter decomposition in soybean (1.88 ; $n = 10$ from 1
455 study) and barley fields (0.63 ; $n = 33$), and not significantly in maize fields (0.33 ; $n = 28$) (Fig. 6b).

456 The implication of soil fauna also depended on the litter type ($P = 0.03$) (Fig. 6b, Table S2). Following
457 the trends separately observed for macro- and mesofauna, soil fauna was highly involved in the
458 degradation of C4 cereals such as maize (1.35 ; $n = 24$) (Fig. 6b), particularly at the early stage of
459 decomposition (Fig. 3f). In addition, it demonstrated a positive but non-significant effect on Fabaceae
460 such as soybean (1.21 ; $n = 10$) (Fig. 6b), slightly increasing with time (Fig. 3f). This effect was lower
461 and not significant for C3 crops such as wheat (0.26 ; $n = 20$ from 1 study) (Fig. 6b), for which it was
462 negative at the early stage of decomposition and increased at the later stages (Fig. 3f). Finally, fauna
463 effect tended to increase with time for the decomposition of tree leaves (Fig. 3f).

464 The duration of the experiment ($P = 0.01$) had a significant positive influence on fauna effect, such as
465 the size of litter pieces ($P < 0.0001$) which indicates that large litter pieces required more

466 intervention of fauna than small litter pieces. No significant relations were found with the depth of
467 litterbags ($P = 0.64$) (Table S3).

468

469 4. Discussion

470

471 4.1 Role of soil organisms in litter decomposition

472

473 The role of the soil organisms on litter decomposition in cropping systems was confirmed as our
474 meta-analysis demonstrated a significant positive effect of macrofauna (FE = 9.4%, ES = 0.66),
475 mesofauna (FE = 6.6%, ES = 0.31) and combined macro- and mesofauna (FE = 10.8%, ES = 0.75).
476 These results are consistent with previous reviews and meta-analyses assessing the role of
477 macrofauna (Frouz et al., 2015), mesofauna (Seastedt, 1984; Kampichler and Bruckner, 2009) and
478 total soil fauna (Zhang et al., 2015) on litter decomposition.

479 Macrofauna and mesofauna effects on decomposition were not significantly different in annually
480 cropped soils. Similarly, in forest soils the overall effects of macrofauna and mesofauna were not
481 reported to differ, but to vary in different ecosystems (González and Lodge, 2017; Krishna and
482 Mohan, 2017). The balance between macrofauna and mesofauna effects could be due to the distinct
483 roles of the main macrofauna and mesofauna organisms and to the variation in taxa within both
484 groups.

485 Macrofauna organisms are highly efficient for the burrowing, breakdown and digestion of litter, thus
486 displacing a large amount of litter. After digestion most of the organic matter is returned to the soil
487 in the form of feces (Frouz, 2018). However, the assimilation efficiency varies greatly among the
488 different groups of macrofauna (Frouz, 2018). In the collected studies, earthworms were very often
489 the main macro-decomposers. Earthworms are essential for the mixing of litter in soils and for its
490 transformation through comminution (Barrios, 2007). They consume organic matter together with
491 soil, which results in the creation of microaggregates in their feces with a reduced decomposition

492 rate of organic matter compared to the initial litter (Frouz, 2018). Under dry climates, the high
493 macrofauna effect was mostly attributed to termites that are reported to be one of the main actors
494 of litter decomposition in arid areas (Martínez-Yrizar et al., 2007). Termites have a high assimilation
495 efficiency allowing them to convert a great proportion of the ingested litter into their own biomass
496 (Culliney, 2013), thus releasing less organic matter directly after the digestion of litter.

497 Mesofauna effect on decomposition is, on the other hand, mostly indirect and attributable to
498 microarthropods such as Collembola and Acari (Culliney, 2013). They take part in decomposition
499 through the digestion and the breakdown of litter, but their effect on decomposition is mostly due to
500 the regulation of microbial populations by grazing (Seastedt, 1984). Indeed, oribatid mites and
501 Collembola have mouthparts adapted to the fragmentation of organic matter that enable them to
502 feed on the adhering microorganisms (Seastedt, 1984). In addition, predatory microarthropods
503 feeding on bacterial and fungal nematodes can also protect microbial populations and stimulate litter
504 decomposition (Santos et al., 1981). The regulation of microorganisms by microarthropods was
505 suggested to ensure continuous and regulated supply of nutrients to plants and thus to prevent
506 nutrient loss (Culliney, 2013).

507 Despite the observed mean positive effect, several studies related a negative effect of soil fauna on
508 decomposition (e.g. House and Stinner, 1987; Heisler, 1994). Those studies were not sharing specific
509 characteristics. A main driver of the effects of macrofauna and mesofauna could be the balance
510 between predatory and prey organisms within these two groups. Previous studies demonstrated that
511 in sites dominated by predaceous macrofauna the litter mass loss in coarse bags decreased due to
512 the predation on mesofauna prey (Frouz et al., 2015). In addition, the positive effect of mesofauna
513 on decomposition may be counterbalanced by an over-grazing of microorganisms by
514 microarthropods (Beare et al., 1992; Heisler, 1994), which could conduct to null or negative total
515 observed effect on decomposition.

516 Furthermore, the effects of macrofauna and mesofauna were not additive as the mean fauna effect,
517 combining macrofauna and mesofauna, was lower than the addition of the two effects. The non-

518 additive aspect of the fauna effects on decomposition could be explained by the existence of
519 facilitative (e.g. resource use complementarity) and inhibitory (e.g. competition, predation)
520 interactions between soil organisms (Heemsbergen et al., 2004). These interactions are assumed to
521 explain why the combined effect of soil organisms on litter decomposition cannot be predicted with
522 the simple sum of their individual effects (Coulis et al., 2015).

523 Litter decomposition was increasingly faster in fine, medium and coarse mesh litterbags respectively,
524 which may indicate an effect of the inclusion of a larger group of soil fauna. However, the protocols
525 set up in the selected studies allow studying the role of macrofauna and mesofauna in litter
526 decomposition, but they do not allow discussing the role of microorganisms, which are present in all
527 litterbags. Still, more than aiming to estimate the individual effect of soil microorganisms, the focus
528 of future studies should be set on the interactions between soil organisms and the parameters that
529 promote microbial activity.

530

531 4.2 Factors explaining the variability of the effect of soil fauna

532

533 Litter mass loss and fauna effect on decomposition were both influenced by several factors. This
534 implies that the studied factors had direct effects on litter decomposition, but also indirect effects
535 through their impact on soil organisms. In the following section, we will discuss the influence of
536 climate, soil, agricultural systems, crop and litter type on the fauna effect on litter decomposition.
537 We aim here to illustrate the trends that are observed within the meta-analysis, even though more
538 studies would be required to conclude on the impact of these factors. In addition, one should keep in
539 mind the existence of various interactions among studied factors (e.g. climate and soil).

540

541 4.2.1 Climate

542

543 Overall, macrofauna, mesofauna and total fauna effects tend to be higher under dry and continental
544 climates, and were lower under temperate climate (Figs. 4-6). Climate and more specifically
545 temperatures and precipitations are important drivers of litter decomposition (Knacker et al., 2003;
546 Zhang et al., 2015) by influencing the decomposition activity of soil organisms (García-Palacios et al.,
547 2013; Zhang et al., 2015). Litter decomposition tends to be optimum for intermediate humidity and
548 temperature; however, the optimum will depend on the local decomposer communities and on the
549 presence of adapted species (Knacker et al., 2003; Peña-Peña and Irmler, 2016). For instance, Peña-
550 Peña and Irmler (2016) found a much higher fauna effect on decomposition in cropland during the
551 wet season than during the dry season. Contrastingly, Kampichler and Bruckner (2009) concluded to
552 a significantly higher effect of microarthropods in arid areas than in wet tropics, all land-uses
553 together. In a two-year experiment, Yin et al. (2019) also demonstrated that a slight increase in
554 temperature and change in precipitation patterns was enough to decrease the effect of soil fauna on
555 litter decomposition.

556

557 4.2.2 Soil type

558

559 The soil type influenced litter mass loss in bags of all sizes as well as the macrofauna (Fig. 4) and the
560 combined macro- and mesofauna effects on decomposition (Fig. 6), but not the mesofauna effect
561 (Fig. 5). The observed positive fauna effect on decomposition in Luvisols and Cambisols may be
562 explained as they are fertile soils highly adapted to agricultural use and that do not present any
563 particular constraints for soil organisms. Furthermore, the high variability in the fauna effect in
564 Cambisols is explained as Cambisols are considered as “non-differentiated” soils that have
565 heterogeneous properties. As the most represented soil types, Luvisols and Cambisols occurred in
566 combination with different climates but it was not possible to compare their effect under similar
567 climate. Moreover, the literature on the influence of different soil types on soil organism’s
568 communities in agricultural soils is scarce (Girvan et al., 2003; Ivask et al., 2008; Khan and

569 Joergensen, 2012; Zaller et al., 2014). In addition, the few existing studies did not look at the effect of
570 soil types on the functions performed by soil organisms. Thus, further studies are required to unveil
571 the mechanisms causing soil types to influence the role of different soil organisms in decomposition.
572 Furthermore, soil characteristics, rather than soil types only, are required to understand the impact
573 of different soils on organism's decomposition activity.

574

575 4.2.3 Crop

576

577 Crops cultivated on the field at the time of litterbag experiments influenced the litter mass loss in all
578 bags and the fauna effects on decomposition (Figs. 4-6), with a significant positive effect in fields
579 with wheat and barley (except for barley with mesofauna), and lower and non-significant effect in
580 fields with maize. Few studies have been conducted on the effect of crop type on soil biodiversity.
581 They demonstrated crop type influence on soil organism community composition, abundance and
582 diversity (Eyre et al., 2012; Lüscher et al., 2014; Crotty et al., 2015; Detheridge et al., 2016; Villenave
583 et al., 2018). Crop types were notably found to influence the abundance of predators in fields such as
584 spiders (Lüscher et al., 2014) and of bacterivorous nematodes (Villenave et al., 2018). Crops present
585 specificities such as plant structure, roots distribution or root exudates that may favor different
586 organisms. In addition, crops are associated with different practices such as the frequent use of
587 irrigation for maize crops or the relatively low need for chemicals input in wheat fields. Besides, crops
588 previously cultivated on the field were found to influence soil organisms even after the
589 establishment of a new crop (Crotty et al., 2016). The numerous differences between crop type and
590 their management make difficult to explain the specific effect of crops on the activity of
591 decomposers. Further studies are required on this point.

592

593 4.2.4 Litter

594

595 The nature of organic matter added in litterbags greatly influenced the mass loss rate in litterbags of
596 all mesh sizes. It also influenced the effects of mesofauna (Fig. 5) and combined macro- and
597 mesofauna (Fig. 6). Macro- and mesofauna considerably increased the degradation of C4 cereals
598 litter, especially at the early stage of decomposition. Contrastingly, they demonstrated low or no
599 influence on the decomposition of C3 crops such as wheat. Their influence on Fabaceae and other
600 crops was more variable and fluctuated with time. The limited availability of data on litter
601 composition in the selected papers prevented us to observe if there was a relation between litter
602 characteristics (e.g. percentages of soluble and more recalcitrant C, phosphorus, C:N ratio) and
603 decomposition. In our study, we observed a higher fauna effect for maize than for wheat litter
604 regardless of the climate and the soil type. It was surprising as maize tends to have a high C:N ratio in
605 the collected studies, probably because of its high fiber and lignin content (Sereda et al., 2015).
606 Whereas in previous studies, litters with low C:N ratio in cropping systems were sometimes found to
607 decompose faster (Vazquez et al., 2003) and to present higher fauna effect than litter with high C:N
608 ratio (Zhang et al., 2015; Peña-Peña and Irmeler, 2018).

609 Another potential explanation for the higher fauna effect on maize litter could be the home-field
610 advantage effect. Indeed, there is increasing evidence that litter decomposes faster beneath the
611 plant from which it was derived, the so-called home-field advantage effect, because of the
612 adaptation of the local soil community to the standing plant species, either by adapted activities,
613 changes in community composition or a combination of several processes (Milcu and Manning,
614 2011). The home-field advantage effect increased litter decomposition rate by 7.5% for local litter
615 according to Veen et al. (2015). In addition, the home-field advantage effect was demonstrated to be
616 higher for more recalcitrant litter as specialized decomposer communities are required to degrade it
617 rapidly (Milcu and Manning, 2011). In our meta-analysis, half of the experiments using maize litter
618 were conducted under maize fields, thus with a potential home-field advantage effect, while only
619 few experiments using wheat litter were conducted under wheat fields.

620

621 4.2.5 Agricultural practices

622

623 Agricultural systems significantly influenced macrofauna effect on decomposition (Fig. 4) but not
624 litter mass loss in bags or other fauna effects in our study (Figs. 5 and 6). Macrofauna effect on
625 decomposition was significantly higher in conventional than in no-tillage systems. Conversely,
626 previous litterbag studies found no-tillage systems to exhibit higher decomposition than
627 conventionally tilled systems (Reddy et al., 1994; Miura et al., 2008; Faust et al., 2019), but the
628 contrary was also found (Domínguez et al., 2014). Agrosystems under conventional tillage and no-
629 tillage management experience vastly different disturbance regimes, which affect the soil food web
630 (Wardle, 1995). Even if the difference between systems was not significant in our study, the effect of
631 macrofauna, mesofauna and their combined effect tend to increase litter decomposition in
632 conventional systems but not in no-tillage systems. This is surprising as macrofauna and mesofauna
633 densities are reported to be higher under low tillage systems, notably for macroarthropods (Reddy et
634 al., 1994), earthworms (Parmelee et al., 1990; Miura et al., 2008) and microarthropods (Brennan et
635 al., 2006; Dubie et al., 2011). In addition, larger organisms tend to be more sensitive to tillage than
636 smaller organisms (Wardle, 1995; Kladvko, 2001). Tillage can indeed affect soil organisms by direct
637 impacts, such as physical damages or trapping in soil pores (Kladvko, 2001), or indirect impacts such
638 as changes in soil moisture and in organic matter distribution, and destruction of microhabitats for
639 decomposers (Reddy et al., 1994; Tsiafouli et al., 2015). The lack of available information prevented
640 us from conducting further statistical analyses on the effects of agricultural practices. Yet, different
641 practices unevenly affect soil organisms, conducting to changes in community composition, which
642 can in turn strongly affect litter decomposition (Bradford et al., 2002).

643

644 4.2.6 Temporal evolution

645

646 The effect of macrofauna, mesofauna and both together varied with time, but with patterns
647 depending on the context. For instance, under dry and continental climates and for C4 cereals litter
648 fauna effects were higher at the early stage of decomposition and decreased with time. In contrast,
649 they increased slowly with time under temperate and tropical climates and for C3 cereals litter.
650 The variation in the effect of soil fauna may be related to the succession of organisms in litterbags.
651 Soil organisms successively colonize litter according to their growth and migration rate (Georgieva et
652 al., 2005). Several studies found bacteria or fungi to successively dominate the process of crop
653 residues decomposition, with the presence of associated predators controlling their activity
654 (Vreeken-Buijs and Brussaard, 1996; Georgieva et al., 2005; Jacobs et al., 2011). In addition, the
655 highest mesofauna effect on crop residues was demonstrated at the early (Beare et al., 1992) and
656 intermediate (Lekha et al., 1989) stages of litter decomposition. The intervention of macrofauna
657 organisms could occur depending on their feeding habitats, respectively in early stage of
658 decomposition if they feed directly on litter and later for predators that feed on decomposer
659 organisms.

660

661 4.3 General remarks on the meta-analysis

662

663 Our analysis sometimes faced confounding effects between the different factors. For instance,
664 studied crops were different under different climates, with a predominance of C3 crops under
665 temperate climate and C4 crops under dry climate. In addition, some factors occurred only once and
666 in the same study, such as climate and soil type for instance, due to the lack of studies under various
667 climates (e.g. continental, tropical, dry) and soil types (e.g. Ferralsol). Furthermore, the effect of
668 agricultural systems on decomposition was not clear in our analysis. However, previous case studies
669 found alternatively management practices and soil types to have more influence on soil
670 microarthropods and microorganisms (Fromm et al., 1993; Reeleder et al., 2006). Resolving the share
671 of the influence of agricultural practices and soil type in decomposition could lead to reinterpret the

672 effect of soils on decomposition and to attribute the observed effects to agricultural management
673 rather than to soil type only. Future litterbags studies may help to characterize soil fauna and litter
674 decomposition for several agricultural practices under a diversity of pedoclimatic contexts.

675 In addition, the results of our meta-analysis show a high publication bias (Fig. S4; Rothstein et al.,
676 2006), with a prevalence of broad studies with significant results over small and non-significant ones.
677 This bias could lead to over- or underestimate the comparative effect of organism's size classes.
678 Thus, we would like to encourage authors and reviewers to allow for the publications of litterbag
679 studies in agricultural areas, even if the results do not show significant differences.

680

681 4.4 Advantages and limitations of the litterbag method in cropped soils

682

683 Allowing for studies *in situ*, litterbags may provide a better estimate of the decomposition rate and
684 fauna effect than microcosm experiments. This is especially true in cropping systems as they are
685 submitted to various disturbances that are difficult to mimic in laboratory. In a previous review,
686 Knacker et al. (2003) concluded that the litterbag method has more advantages than other
687 approaches (i.e. minicontainer, cotton strip, detection of isotopes, bait-lamina) as it allows to apply
688 numerous measurement endpoints to assess litter decomposition under field conditions (e.g.
689 number of invertebrates, enzyme activity, chemical composition, mass loss of litter). In addition,
690 litterbags constitute a relatively easy and cost-effective method to assess litter decomposition and
691 soil organism activity in cropped soils. They require little space and no specific equipment, and allow
692 for short and long-term experiments, depending on the agricultural practices in place, with
693 numerous replicates and treatments. Furthermore, enclosed litter gives a relatively good estimate of
694 the decomposition of crop residues buried or at the surface of agricultural soils (Ouédraogo et al.,
695 2004).

696 More generally, several authors suggested that the enclosure of litter create artificial conditions that
697 can prevent accessing the real decomposition rate (Anderson, 1973; Bradford et al., 2002; Prescott,

698 2005). They notably suggested that a “mesh size effect” could explain part of the differences
699 observed between bags of different mesh sizes. Fine mesh litterbags were reported i) to be subjected
700 to microclimate with an increased moisture responsible for an over-estimation of the results (Irmler,
701 2000; Bradford et al., 2002), ii) to constitute a physical barrier that slow colonization of litter by
702 microorganisms (Wise and Schaefer, 1994), and iii) to be colonized by a small fraction of soil
703 mesofauna through egg deposition (House and Stinner, 1987; Vreeken-Buijs and Brussaard, 1996). In
704 contrast, bags with a larger mesh size were found i) to allow organisms to pull litter from the bags
705 even without degrading it (Bradford et al., 2002), ii) to increase the risk of litter loss during the
706 handling of bags or leaching due to rainfall (Kampichler and Bruckner, 2009), and iii) to ease the
707 admission of soil particles and roots within bags that washing or brushing after recollection do not
708 completely removed, which increase the final weight of litter but also increase the surface of soil-
709 litter contact and therefore the microbial decomposition activity within bags (Broadbent and Tomlin,
710 1978; House and Stinner, 1987; Heisler, 1994). Nevertheless, the scientific community considers
711 litterbags as a useful method for comparative studies and it is admitted that potential bias will be
712 similar between experiments, allowing the comparison of data collected with bags of similar mesh
713 size (Domínguez et al., 2014; Peña-Peña and Irmler, 2016).

714

715 4.5 Adapting the litterbag protocol to agricultural areas

716

717 Existing studies on litterbag experiments occurring in cropping systems enabled to provide
718 interesting results on the role of soil organisms in litter decomposition. However, forecasting future
719 studies on soil biodiversity in an agricultural context, we recommend the development of a standard
720 protocol adapted to the specificities of cropped soils. The standardization of the litterbag protocol is
721 necessary in order to increase the number of studies in cropped soils and to ease the comparison of
722 results. Previous authors already advocated for the need of a standard protocol for litterbag
723 experiments and a methodology to assess litter decomposition (Knacker et al., 2003; Kampichler and

724 Bruckner, 2009; Krishna and Mohan, 2017). However, to this day, we are not aware of the
725 publication of a standardized protocol to assess the effect of soil organisms on litter decomposition
726 in agricultural soils. There is no standard design and the litterbags used for current experiments are
727 handmade with the available means. Guidelines do exist for the use of litterbags for the risk
728 assessment of plant protection products in soils (Knacker et al., 2003; OECD, 2006), but the
729 suggested protocol is designed specifically to test the safety of chemicals and not to consider soil
730 organisms of different sizes. In the recent years, the growing interest for the use of the teabag
731 method (Keuskamp et al., 2013) was also driven by the need for a standard method to measure
732 decomposition. However, teabags do not address the standardization needs concerning soil
733 organism's effect on decomposition as they prevent to take into account the effect of large
734 organisms. Here, we provide some clues to develop a standard protocol for the use of multi-mesh
735 litterbags in cropping systems, including bag design and litter characteristics (Table 2).

736 In an agricultural context, the standardized litterbag protocol should take into account the various
737 agricultural practices and the duration of the experiments. Attention should be paid to the cropping
738 calendar and the management practices that can influence the rate of litter decomposition (e.g.
739 phytosanitary treatments, mineral and organic matter inputs) or affect the positioning of litterbags
740 (e.g. tillage, seedling, harvest, mechanical weeding).

741 Depending on the management practices in place, litterbags may be buried or placed at the surface
742 in order to limit physical disturbances and to model the placement of crop residues. Nonetheless,
743 regardless of the management system in place, the positioning of litterbags in the field could
744 significantly affect litter decomposition. Decomposition in bags could notably be influenced by the
745 distribution and community composition of soil organisms at different depths (Beare et al., 1992;
746 Ouédraogo et al., 2004). Placed on the surface, litterbags allow to better estimate the role of
747 mesofauna, which is for a large part located in the first centimeters of the soil, but could lead to
748 exclude some macrofauna organisms such as endogeic and anecic earthworms. On the other hand,

749 buried litterbags will be better connected with soil microorganisms and less impacted by weather
750 events (e.g. rain, UV), but they could be impacted by soil compaction.

751 A vast majority of the litterbag studies occurred in experimental sites, where it is easier to set an
752 undisturbed area or to remove and replace bags at the time of main disturbances. Under real
753 conditions, it is more difficult to request from farmers to set an undisturbed area, during tillage or
754 mechanical weeding for instance, and to have a precise insight of the planning of their interventions
755 ahead of time (e.g. date of harvest, tillage). Yet, the acquisition of more realistic estimates of the
756 effect of soil biota on litter decomposition required conducting experiments under real conditions.
757 Finally, in order to assess more precisely the role of soil organism's in litter decomposition and to
758 survey soil fauna in a wide range of agricultural contexts, the counting and identification of soil
759 organisms should be achieved and reported with the decomposition results whenever possible.

760

761 5. Conclusion

762

763 This meta-analysis is the first, to the best of our knowledge, to deal with multi-mesh litterbag
764 experiments in annually cropped soils and to assess the influence of different size classes of soil
765 organisms on the litter decomposition rate. It highlights the essential role of macrofauna and
766 mesofauna during organic matter decomposition in cropped soils, whereas these soils may be
767 submitted to high physical and chemical disturbances. This fauna effect on decomposition may be
768 influenced by various factors such as climate, soil, standing crop, type of enclosed litter, and in a
769 lesser extent by agricultural systems. However, more litterbag studies would be required to conclude
770 on the quantitative impact of these factors.

771 Given the variability of litterbag design and litter decomposition measurements, we pledge for a
772 standardization of the litterbag method for the forthcoming studies, in particular in cropped soils.
773 Here, we provide some guidelines to help to implement litterbag experiments while taking into
774 account the specificities of cropped soils (i.e. high soil perturbations).

775 Future multi-mesh litterbag experiments should especially focus on alternative (e.g. organic or
776 conservation agriculture) or transitioning systems and on different combinations of practices for
777 which farmers and consumers are showing a growing interest. In addition, studies are also required
778 on the effects of individual agricultural practices on soil organisms and litter decomposition, notably
779 for crop rotation, mineral or organic inputs, tillage, shallow tillage, mechanical weeding and soil
780 cover. This is necessary to determine their specific effect on the activity of different groups of soil
781 organisms and the related impacts on the soil functioning. Finally, our understanding of the biological
782 functioning of agroecosystems requires the identification of soil organisms and especially of their
783 functional traits in relation to different agricultural practices and systems.

784

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786

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791

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Table 1. Characteristics of studies selected for the meta-analysis. Time: duration of the study (days); n bag: number of replicates per modality; Size: size of bags (cm x cm); Depth: depth of bags placement in soil (cm); Fauna: studied groups of organisms.

N°	Publication	Location	Climate	Soil type	Cropping system	Time (days)	n bag	Size (cm)	Depth (cm)	Fauna	Litter
1	Broadbent & Tomlin, 1978	Canada	cont	Luvisol	C	112	8	11 x 11	5	-	maize
2	Carlesso et al., 2019	UK	temp	Cambisol	MT	180	6	5 x 6	5	-	ryegrass, wheat
3	Curry & Byrne, 1997	Ireland	temp	Gleysol	C	300	6	-	10	Lum	wheat
4	Domínguez et al., 2010	Argentina	temp	Kastanozem	NT	133	4	20 x 20	-	Ann, Ara, Colb, Ins, Lar, Lum, Myr	local, alfalfa
5	Domínguez et al., 2014	Argentina	temp	Kastanozem	C, O, NT	365	10	-	-	Colb, Lum, other	local, sorghum
6	Heisler, 1994	Germany	temp	Luvisol	C	270	4	10 x 10	10	Aca, Colb	wheat
7	House & Stinner, 1987	USA	temp	Acrisol	NT	120	9	10 x 10	0	Aca, Colb, other	clover, vetch, rye
8	Jensen, 1985	Denmark	temp	Luvisol	C	290	30	10 x 15	15	Lum, mesofauna	barley
9	Miura et al., 2008	Japan	cont	Andosol	C, NT	27	4-6	3.5 x 7	8; 18	Aca, Colb, Enc, mic, Nem, Pro	clover, wheat, sorghum
10	Ouédraogo et al., 2004	Burkina Faso	dry	Cambisol	-	90	4	15 x 18	3; 35	Ara, Colp, Der, Hym, Isop, Lum, Myr, Ort	maize, grass, dung
11	Peña-Peña & Irmeler, 2016	Brazil	trop	Ferralsol	NT	140	12	15 x 20; 20 x 20	0	-	soybean, maize
12	Peña-Peña & Irmeler, 2018	Brazil	trop	Ferralsol	C	140	12	15 x 20; 20 x 20	0	-	soybean, maize
13	Reddy et al., 1994	India	dry	Lixisol	C, NT	330	3	6 x 10	0	Aca, Colb, Isop, other	rice
14	Singh & Shekhar, 1989	India	temp	Luvisol	-	270	3	10 x 15	5; 12	-	wheat, maize
15	Tian et al., 1992	Nigeria	trop	Lixisol	-	98	4	30 x 30	0	-	tree leaves, maize, rice
16	Tian et al., 1998	Nigeria	trop	-	C, R	98	4	20 x 20	0	-	tree leaves
17	Valckx et al., 2011	Belgium	temp	Luvisol	NT	392	-	7 x 7	0	Lum	ryegrass, phacelia, mustard, rapeseed
18	Vreeken-Buijs & Brussaard, 1996	Netherlands	temp	Fluvisol	C	365	10	15 x 15	15; 25	Aca, Colb, Enc	wheat
19	Weil & Kroontje, 1979	USA	temp	Nitisol	C	70	4	10 x 15	8	Aca, Colb, mic	maize
20	Yang et al., 2018	China	temp	Fluvisol	-	365	4	15 x 20	-	Aca, Ara, Colb, Colp, Dip, Hym, Isod, Lep, Myr, Nem	tree leaves
21	Yin et al., 2019	Germany	cont	Chernozem	C, O	137	20	15 x 20	-	-	oat
22	Zwahlen et al., 2007	Switzerland	cont	Cambisol	C	240	7	10 x 10; 20 x 20	20; 10	Aca, Ara, Colb, Enc, Isod, Lar, Lum, Myr, Nem, Pso	maize

cont: continental; temp: temperate; trop: tropical; C: conventional; MT: minimum tillage; NT: no-tillage; O: organic; R: relay cropping; Aca: Acari; Ann: Annelida; Ara: Araneae; Colp: Coleoptera; Colb: Collembola; Der: Dermaptera; Dip: Diptera; Enc: Enchytraeidae; Hym: Hymenoptera; Ins: Insecta; Isod: Isopoda; Isop: Isoptera; Lar: Larvae; Lep: Lepidoptera; Lum: Lumbricidae; mic: microflora; Myr: Myriapoda; Nem: Nematoda; Ort: Orthoptera; Pro: Protozoa; Pso: Psocoptera.

Table 2. Recommendations for the standardization of litterbag experiments measuring the effect of soil organisms on litter decomposition in cropping systems.

Parameter	Goal	Standardization	Recommendations
Mesh size	Select several size groups of soil organisms	Average number and size of mesh	Select 3 mesh sizes with an opening around 0.02 mm to include microorganisms only, 1 mm to additionally include mesofauna and 5 mm to include all soil organisms.
Bag size	Enclose the quantity of litter required to conduct measurements	Single size of bag	10 x 10 cm bags limit displacement or tearing during field management and provide space for the quantity of litter required to assess decomposition over the full length of the experiment. 20 x 20 cm bags can be selected under tropical climate as litter degrade faster.
Bag material	Construct solid, biologically inert and cheap mesh bags	Single material, closure techniques	Use nylon fabric and close the edges of bags by sewing with a nylon/polyester thread or by using stainless steel staples (or monel rustproof staples for long studies). Sewing allows solid closure with limited apertures on the edges of the bags and is cheap, but may be time consuming. Staples allow gaining time, but are more expensive and may create larger apertures on the edges of the bags.
Enclosed litter	Represent crop residues typically found in the cropping systems; select standard litter to compare different sites	Standard litter management, size of litter pieces, standard litter type	Homogenize litter within all bags, select a specific part of the plant (e.g. leaves, stems) or if mixed ensure the same ratio in each bag. Cut litter in homogeneous pieces (1 to 5 cm) as the role of soil fauna differ with the size of litter. Use wheat or maize as standard litter to ease comparison between studies.
Litter amount	Fill bags with the adapted quantity of litter	Minimum litter quantity	Fill bags with a litter quantity ensuring good contact between litter and soil, and adapted to the decomposition speed. It will depend on bag size, type of litter, duration of the experiment and context (e.g. 4 - 5 g litter in 10 x 10 cm bags under temperate climate).
Positioning of bags	Allow access to organisms living in the soil; prevent field management to displace or to tear bags	Standard field placement	Place bags in the row between crop plants (Broadbent and Tomlin, 1978) and bury them vertically to limit the impact of tillage and to observe soil organisms at a greater depth (Zwahlen et al., 2007; Miura et al., 2008). In no-till systems, bags can be set at the surface.
Duration of experiment	Observe mass loss patterns during litter decomposition	Minimum duration	At least 3 months. Set length and start of the experiment according to the cropping cycle to further avoid disturbances (Ouédraogo et al., 2004; Carlesso et al., 2019).
Sampling of bags	Collect enough data on litter mass loss	Minimum number of sampling dates	Number of samplings depends on required effort (e.g. distance to field, number of bags) and on cropping calendar. More than 3 dates if the aim is to assess degradation kinetics.

Sampling of soil biota	Survey soil fauna and assess its effect on decomposition	Collection of soil organisms	Count and identify soil organisms in bags whenever possible. Extract organisms from soil sampled near area of bag deposition to get an overview of the field density and diversity.
Supplementary advice	In order to track down litterbags, use stakes and centimetric precision GPS. Stakes tend to attract megafauna (e.g. wild boars) so the ideal is to place them further away of bags, on the same crop row.		

Figure 1. Characteristics of litterbag experiments within selected studies (n = 22). (a) Cropping system. (b) Crop type. (c) Number of sampling dates. (d) Range of days within which sampling were conducted. (e) Size of mesh of litterbags. (f) Type of organic matter enclosed in litterbags.

Figure 2. Mass loss of organic matter in litterbags for different climates (a, b, c) and different litter qualities (d, e, f) in (a, d) coarse mesh (n = 204), (b, e) medium mesh (n = 266), and (c, f) fine mesh (n = 130) litterbags. Linear regressions were drawn for all data (continuous lines) and for different climates or litters (dotted lines). Coefficient of determination (r^2) are specified in brackets in the legend. Significant correlation are indicated by * ($P < 0.05$).

Figure 3. Temporal evolution of the role of soil fauna on litter decomposition in relation to climate (a, b, c) and litter types (d, e, f) with the effect of (a, d) macrofauna (n = 217), (b, e) mesofauna (n = 134), and (c, f) both macrofauna and mesofauna (n = 81). Lines indicate the limit between positive and negative fauna effect.

Figure 4. Effect size of macrofauna on litter decomposition. Represents the effect size of all the paired observations comparing coarse versus medium mesh litterbags (incl. /excl. macrofauna) with (a) the effect sizes of all paired observations (n = 201) and (b) the effect sizes for each climate, soil, crop, agricultural systems and litter subgroups. "Mean effect size" represents the overall effect size of all paired observations. Effect size of each paired observation and the associated 95% confidence interval are represented by (a) black squares and bars or (b) center and length of diamonds.

Figure 5. Effect size of mesofauna on litter decomposition. Represents the effect size of all the paired observations comparing medium versus fine mesh litterbags (incl. /excl. mesofauna) with (a) the effect sizes of all paired observations (n = 126) and (b) the effect sizes for each climate, soil, crop, agricultural systems and litter subgroups. "Mean effect size" represents the overall effect size of all paired

observations. Effect size of each paired observation and the associated 95% confidence interval are represented by (a) black squares and bars or (b) center and length of diamonds.

Figure 6. Effect size of total fauna on litter decomposition. Represents the effect size of all the paired observations comparing coarse versus fine mesh litterbags (incl. /excl. macro- and mesofauna) with (a) the effect sizes of all paired observations (n = 75) and (b) the effect sizes for each climate, soil, crop, agricultural systems and litter subgroups. "Mean effect size" represents the overall effect size of all paired observations. Effect size of each paired observation and the associated 95% confidence interval are represented by (a) black squares and bars or (b) center and length of diamonds.











