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1 **Collembola dispersion, selection, and biological interactions in urban**
2 **ecosystems: a review**

3

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12

13 **Abstract**

14 Most of the ecological predictions that are intended to be general have been made on the basis
15 of observations of aerial organisms, ignoring subterranean organisms, which are subject to
16 other - and complex - constraints compared from those present on the surface. Collembola, a
17 soil fauna group, are good biological indicators of soil quality and could be used as model
18 organisms in order to understand assembly rules of soil organisms in cities. Here we review
19 available literature on soil Collembola conducted on 75 publications dealing with urban
20 context.

21 The major points are the following: (1) Soil properties and landscape characteristics
22 influenced soil communities. The importance of landscape is also highlighted by the need of
23 connectivity between urban green spaces in order to allow dispersion of Collembola.
24 However, studies of Collembola communities in urban context are recent, offering little
25 hindsight to understand their assembly. (2) A gap of references values, complexities by a lack

26 of methods standardisation, is observable. Especially, knowledge on dispersion and biotic
27 interactions are still too rare. (3) Moreover, studies on temporal aspect in order to understand
28 better the colonisation processes are almost absent of the corpus.

29

30

31 **Keywords (4-6):** Urban soil, soil biodiversity, assembly rules, dispersal, habitat, biotic
32 interactions

33

34

35 **1. Introduction**

36 Protecting biodiversity in the coming decades is a major challenge as the global assessment
37 report on biodiversity and ecosystem services has estimated that around 1 million animal and
38 plant species are threatened by extinction (IPBES, 2019).

39 Representing only 3% of the Earth's surface (MEA 2005), urban environments have long been
40 neglected by ecological and biological sciences. Until 1995, only approximately one hundred
41 publications in ecology focused on the urban environment. Today, urban ecology papers
42 account for 14% of all ecology papers (Barot et al., 2019). This interest is due in particular to
43 the increase in societal issues related to the city due to (i) the city is the living environment for
44 the majority of the Earth's inhabitants. Since 1950, the urbanization process has been
45 undergoing a change that accelerated in the 1990s with the increase in urban population; (ii)
46 urban ecosystems must be multifunctional. Cities, which are very "mineral", must evolve to
47 become multifunctional and resilient in order to meet the new needs of ever-increasing
48 numbers of city dwellers; and (iii) the urban environment condenses multiple environmental
49 problems such as greenhouse gas emissions, air, water and soil pollution and urban waste
50 management (Liu et al., 2014). The emergence of these societal issues is reflected in the

51 promotion of a more present nature in cities, which must provide the multiple services
52 necessary for the proper functioning of cities. In a context of biodiversity erosion, we can
53 wonder to what extent the multiplication and diversification of urban green spaces can impact
54 biodiversity. Preliminary results showed that the effects of urbanization on biodiversity vary
55 according to taxonomic groups, environmental conditions and socio-economic contexts (Liu
56 et al., 2014). However, some authors seem to agree on several findings: urbanization modifies
57 the biodiversity of organisms present in cities. In terms of taxonomic diversity, an increase as
58 well as a decrease along an urbanization gradient can be observed between groups
59 (McKinney, 2008). In terms of composition, urban biodiversity is made up of native and
60 exotic species, often generalist and synanthropic, and remnants of less tolerant species that
61 may disappear (Shochat et al., 2006). These conclusions were drawn as a result of studies on
62 birds, plants and more recently epigeal arthropods (e.g. Marzluff, 2019; Sukopp, 2008).

63 However, urban soil biodiversity is largely under-studied. To neglect soil biodiversity - or
64 subterranean biodiversity - is to neglect a quarter of global taxonomic diversity (Decaëns et
65 al., 2006). This compartment is often neglected because of its lack of visibility and the
66 difficulties inherent in its study, which often gives it the title of third biotic frontier - after the
67 canopies of tropical forests and abysses - or black box (André et al., 1994).

68 Among soil organisms, Collembola, that belong to the mesofauna (0.1 at 2 mm), are known to
69 perform major functions in soils: organic matter decomposition, micro-aggregation and
70 population regulation (Hopkin, 1997; Rusek, 1998). In addition, their great diversity and
71 abundance in soils makes it possible to evaluate effect of environmental factors on their
72 community in different urban habitats. Finally, contrary to larger soil organisms such as
73 earthworms, they are present even in soils of low depth such as soils of green roofs.

74 In this context, the objective of this study was to draw a state of Collembola communities in
75 cities in order to draw conclusions on the part of biodiversity of urban soils and to guide

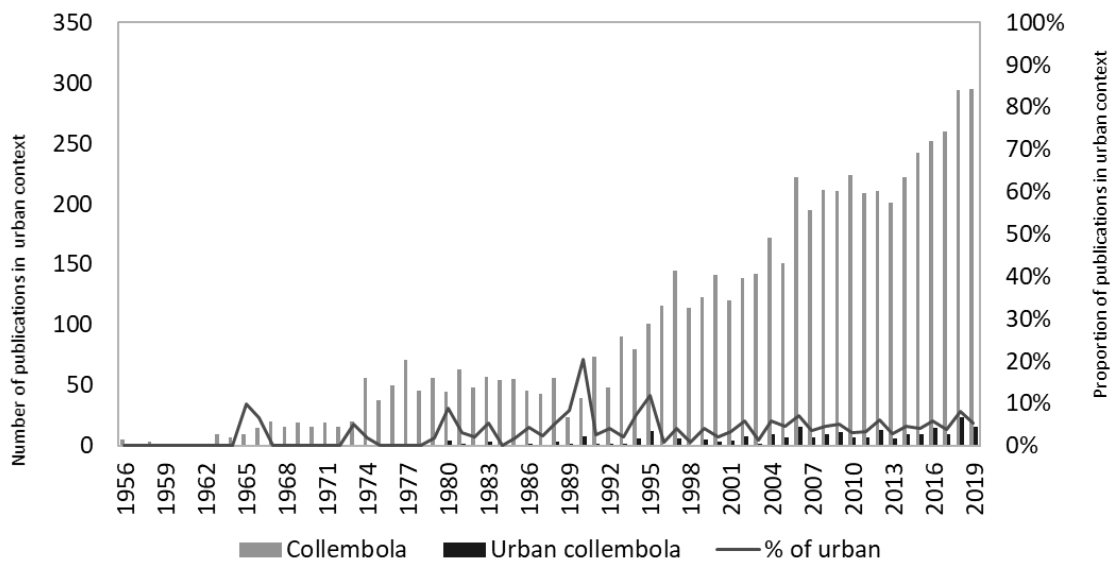
76 future research. In order to understand the provision of biodiversity service and the
77 functioning of ecosystems, it is necessary to understand the determinisms of biodiversity
78 distribution at different scales. Also, the synthesis is divided in three parts articulated within
79 the conceptual framework of filter theory (Lortie et al., 2004). We therefore selected three
80 questions: (i) how do Collembola arrive in the city (capacities and means of dispersal)?, (ii)
81 what are the links between the biodiversity of Collembola and habitat characteristics (e.g.
82 reference to ecological niches)? and (iii) What are the relationships between Collembola and
83 other organisms (interactions, co-occurrences)?

84

85 **2. Bibliometric methods and analysis**

86

87 The research focused on urban Collembola was conducted in April 2021 in ISI web of
88 Knowledge among all database offered. Key words selected for topic were: “(collembol* or
89 springtail*) and (urban* or city or cities or technosol* or anthroposol*). As showed in Fig.1,
90 the first studies concerning urban Collembola communities appeared between the 60’s and the
91 80’s, and were more regular only from the 90’s. This concurs with the development of urban
92 ecology (Liu et al., 2014; Young and Wolf, 2006) and other ecological urban soil studies
93 (Guilland et al., 2018). Nowadays, the proportion of publications dealing with urban
94 Collembola represents around 4-5% of the total number of publications dealing with
95 Collembola. These figures are of the same order of magnitude as those highlighted by
96 Guilland et al. (2018) for the biology of urban soils, confirming that urban soil organisms are
97 still poorly studied and unevenly between taxa.



98

Figure 1 : Number of publications dealing with Collembola since 1956; light grey bars: number of publications dealing with Collembola; black bars: number of publications dealing with Collembola in a urban context and dark grey line: proportion of publications in a urban context

99

100 172 articles came out of the query. A first selection was applied on the base of titles
 101 and abstracts to keep papers that mention soil Collembola communities in an urban habitat,
 102 their dispersal capacity towards or within cities or interactions with other organisms in urban
 103 soils. Thus, papers describing a new species or solely evaluating physiological responses were
 104 excluded. Finally, 75 publications were gathered as a corpus for analysis (S1, S2). From each
 105 article, information concerning study location, land-use, sampling methods as well as
 106 abundance, density, richness and species composition was collected. The access was restricted
 107 to the abstract for 22 articles: 17 were not published in English and 5 were not accessible,
 108 limiting the available information. Thus the in-depth analysis of the results was carried out
 109 only on 53 articles.

110 A disparity was observed in the geographic origin of the studies. Indeed, 51% of them
 111 were conducted in Europe and 26% in Asia (n=75). Rare works were recorded in Africa,
 112 South America and Oceania while they host distinctive and probably endemic species (Culik
 113 and Filho, 2003; Hopkin, 1997; Janion-Scheepers et al., 2015). As the vast majority of the

114 unavailable papers were from Asia and more precisely from China (17 out of 22), Europe
115 represents 66% of the publications of the reduced corpus (n=53).

116 Besides, aims and methods differed between the studies. A minor part of them, mainly from
117 China, was focused on describing the composition of urban soil fauna communities, giving
118 little insights about Collembola assemblages according to the three filters. The others tested
119 the effect of environmental parameters on the soil communities, providing results that can be
120 helpful in the understanding of Collembola responses to urban pressures. Among them, the
121 most tested parameters were soil characteristics, land-use and metal contaminations.
122 Differences in taxonomic levels were also noted in the restricted corpus (n=53) for which
123 50% of the publications dealt exclusively with Collembola species. The others were multi-
124 organisms studies and often used a wider taxonomic level such as arthropods orders
125 (microarthropods, invertebrates). Furthermore, several studies do not indicate mean species
126 richness, relative abundance per habitat or site or species composition but only a total number
127 of species or organisms in the study (e.g. Biffi et al., 2019; Rochefort et al., 2013). When
128 abundance values (number of individuals per mass of soil) were provided, they were
129 converted into density values (number of individuals per square meter), but a bias lies in the
130 variable depth of soil cores used that is not included in the conversion. Moreover, there was
131 no standardized method for sampling. Volume or surface of soil cores, number of replicates,
132 collection tools (pitfall traps or soil cores), extraction units, and seasons often vary between
133 studies, whereas they influence results (Lang, 2000; Querner and Bruckner, 2010; Santorufo
134 et al., 2014b).

135 Each publication was carefully read to determine if the study concerned habitat,
136 dispersal or biotic interactions. Whenever a habitat or environmental characteristics were
137 specified, the habitat was considered, which was the case in 89% of the papers (n=53). Biotic
138 interactions and dispersal ways were described much more rarely, 52% and 28% respectively

139 (n=53). The former was considered whenever Collembola were studied simultaneously with
140 other taxa, even though only nine studies really investigated interactions between organisms.
141 The latter was taken into account for each article that mentioned a way for Collembola to
142 move from a place to another.

143 There is no official or consensual classification to characterise urban green spaces (de
144 Groot et al., 2002) or urban soils which are often gathered on the term-of SUITMA (soils of
145 urban, industrial, traffic, mining and military areas (Joimel et al., 2016; Morel et al., 2014).
146 For the purpose of this study, we chose to address this classification through their function
147 within the city. We adapted the PPG17 guidelines of United Kingdom, which listed 17
148 distinctive types of green spaces predominantly focused on land uses. We added green roofs,
149 and removed habitats related to water land uses. In total 15 distinctive types of green spaces
150 were defined : (i) Parks & gardens: country, urban and local parks, public gardens, (ii) street
151 sides, rails, roads, (iii) Institutional grounds, (iv) Built-up areas residential land, (v) Industrial
152 and commercial sites, (vi) educational establishments, (vii) Outdoor sports facilities :
153 golfcourses, tennis, sport fields, (viii) Churchyards, cemeteries, burial grounds, (ix)
154 Brownfield land: quarries, wastelands, landfills, vacant and derelict land, (x) Community
155 green spaces: allotments, community gardens, urban farms, (xi) Horticultural establishments,
156 (xii) Natural & semi-natural green spaces: woodlands, forests, reserves, heathlands, grassland,
157 meadow, conservation land, (xiii) Avenue trees, (xiv) Agricultural land, farms, ranches, (xv)
158 green roofs and vertical forms.

159

160 **3. Dispersion and colonisation in urban environment**

161

162 Dispersion refers to the mobility or transport of organisms from a source location to a urban
163 habitat. Colonisation refers to the spatio-temporal dynamics in one habitat. The distinction
164 between dispersion and colonisation in the studied corpus is not always simple. We estimated

165 that only 10 articles dealt with Collembola dispersion and few articles treated it as a main
166 topic (e.g. Joimel et al., 2018; Rumble et al., 2018), illustrating the lack of knowledge in the
167 connectivity of the belowground communities in urban habitats. Concerning colonisation,
168 only three publications studied colonisation (Burrow et al., 2018; Rumble and Gange, 2013;
169 Santorufo et al., 2021).

170
171 Dispersion is one of the major drivers that rules assemblages patterns at a local or landscape
172 scale (Lortie et al., 2004; Zobel, 1997). Collembola are known to disperse in different ways
173 (Dunger et al., 2002). Dispersion may be the result of active (organism controlling the
174 locomotion leading to dispersal process) and passive (movement depending on external forces
175 such as wind, water currents or animals and materials used for the construction of Technosols)
176 mechanisms (Clobert et al., 2012), and concerns both airborne and soil organisms (Dunger,
177 1998). Although, their dispersion abilities are not well understood (Auclerc et al., 2009),
178 Collembola are supposed to actively disperse, probably in a range of few hundreds of meters
179 (Ponge, 2013). However, in urban context, experiments and insights about active dispersion of
180 Collembola is still absent from the published literature.

181 On the other hand several studies offer food to thought about how passive dispersion takes
182 place in urbanised landscape, especially the five articles concerning green roofs (Joimel et al.,
183 2018; Rumble et al., 2018; Rumble and Gange, 2013; Schindler et al., 2019; Schrader and
184 Böning, 2006). Indeed, in studying mechanisms behind dispersion, it has been shown that
185 Collembola are able to passively disperse those newly formed urban soils as they were present
186 in all the roofs substrates. Nevertheless Collembola diversity ranged from 6 (Rumble and
187 Gange, 2013) to 44 species (Joimel et al., 2018) in all sampled roofs. Questions then arise:
188 how did they get there and is it a one-off or a regular process?

189 Schrader and Böning (2006) already suggested that dispersion onto green roofs was a
190 dynamic process over time. They found significant differences in species composition

191 between young (<4 years) and old (>8 years) roofs, as the result of several communities
192 successions. This comforts the hypothesis that Collembola can reach green roofs even after
193 their construction. Rumble et al. (2018) observed a Collembola species (*Sminthurinus*
194 *trinotatus*) that was neither present in the original substrate or in *Sedum* plugs before planting.
195 The recent use of functional traits in urban Collembola assemblages studies brought some
196 insights to understand their dispersion in cities (Joimel et al., 2018). The study of dominant
197 traits revealed that Collembola of productive and extensive green roofs were characterized by
198 a small size, a parthenogenetic reproduction and the presence of ocelli and furcula. These
199 observations concerning mainly surface Collembola suggest that wind is the principal medium
200 for dispersion onto green roofs. Productive roofs also housed Collembola without ocelli and
201 furcula, which is in agreement with dispersion through organic matter supply. The
202 configuration of green roofs-fitted buildings probably act as vertical barriers and makes active
203 dispersion impossible.

204 Some results suggest that passive dispersion through human activities on a larger scale also
205 exists. An exotic species of Collembola, *Coecobrya tenebricosa*, has been collected in a
206 vivarium in Poland after being imported as food for frogs (Jaskuła et al., 2019). It is
207 reasonable to think that abiotic conditions would not enable this species to thrive and spread
208 in a territory so different of its native environment. Nevertheless acclimation to particular
209 habitats within the area of introduction might be possible. *Paranurophorus simplex* is thought
210 to be an Asian species but was found in hothouses in Paris (Delamare Deboutteville, 1947)
211 and hothouses and flower pots in Poland (Pomorski and Skarzynski, 1996) and Ukraine
212 (Shrubovych, 2002). *P. simplex* could have been imported through exotic plants collections
213 and thrived in the particular environment of hothouses. This dispersion way has been
214 highlighted by Rumble et al. (2018) with Collembola species brought on a green roof
215 substrate via *Sedum spp* plugs. Despite a lack of knowledge in the original distribution range

216 of many Collembola species (Hopkin, 1997), those insights suggest that global human transfer
217 activities may contribute to the large-scale dispersion of Collembola.

218
219 Sterzyńska et al. (2018) supported the idea that urban matrix can be an efficient barrier for
220 dispersion of Collembola as they observed less species in urban than natural habitats.
221 However, some publications demonstrated the success of Collembola to disperse in cities as
222 they are able to colonise constructed soils (Burrow et al., 2018; Santorufo et al., 2021). If the
223 distance between the urban habitat and the nearest large habitat area is short, wind dispersion
224 might be a more likely and frequent event (Querner et al., 2018). Dispersion processes may
225 compensate the negative effects of intense anthropisation (Rzeszowski, 2017); the presence of
226 hedgerows enhances abundance and diversity during colonisation process (Burrow et al.,
227 2018); close environment could play a role of source of Collembola for urban habitats
228 (Braaker et al., 2014; Schindler et al., 2019). Yet road network seems to decrease Collembola
229 abundance (Eitminavičiute, 2006) and close building or canopy cover are thought to modify
230 species composition (Ge et al., 2019; Milano et al., 2017).

231 Investigation about other means of dispersion like phoresy (transport of one organism by
232 another) or eggs transport need to be conducted and quantify the main source of collembolan in
233 urban habitat. Most of dispersal processes are stochastic passive processes and will depend of
234 urban habitat design and management (practices, high ground site, ...). In order to get to a
235 discerning comprehension of colonisation in urban Collembola communities, much work has
236 to be done.

237 A greater diversity of habitats such as parks, urban forests, domestic gardens, lawns and
238 their spatial arrangement in cities need to be considered to understand their role in the
239 connectivity and colonisation of soil organisms in the urban environment. Hence more works
240 are necessary to reveal patterns of assemblages, notably in heterogeneous habitats such as
241 cities where Collembola may display various responses to habitat fragmentation (Rantalainen

242 et al., 2008; Sousa et al., 2004) and land use history (Ponge et al., 2006). Finally, genetic
243 tools, that have been shown efficient to demonstrate the effect of landscape on connectivity
244 between soil populations (Dupont et al., 2017), should be considered for urban Collembola
245 communities studies even if these methods have yet to be refined for Collembola group.

246 Concerning the colonisation, in the corpus papers, a serious lack of data dealing with the
247 temporal dynamics of Collembola colonisation in urban habitats was noticed. As studies were
248 not conducted over several years, whether colonisation onto green roofs is continuous over
249 time is not known yet. Communities are thought to change, specialists replacing ubiquists
250 (Schrader and Böning, 2006) but they also could gone extinct as reduced flow of immigrants
251 due to urban constraints and can lead to a decrease in abundance and diversity (Rumble et al.,
252 2018). These evolutions are observed in the 4-years experiments of colonisation in
253 constructed Technosol (Santorufu et al., 2021).

254

255

256 **4. Urban habitats and their characteristics**

257

258 According to theoretical ecology, after a pool of species reaches a place through
259 dispersal, habitat is the second filter that explains communities assemblages (Drake, 1990;
260 Zobel, 1997). Several environmental factors can impact this filtering in soil communities: e.g.
261 habitat type, soil local properties(Giller, 1996; Nielsen et al., 2010). Environmental conditions
262 of each urban habitat could explain selection and survival of Collembola community. The
263 effect of urban habitat on Collembola communities was by far the most studied factor among
264 the corpus since only 6 articles did not include it in their reflections. Investigated sites within
265 all studies (n=47) have been classified according to their function in the city (Tab.1).
266 Although 12 on 15 different categories of habitats have been investigated among all papers,
267 only 10 have been so in more than or equal to 3 different articles. It shows how scarce

268 knowledge about many urban habitats is, with a great disparity on the habitats studied. Indeed,
 269 several “natural-like” habitats such as urban forests (52%) and parks (35%) are quite well
 270 documented but with a wide diversity in each of the categories (surface, plant species...) and
 271 few, even no study, focus on very anthropised sites like cemeteries or public (institutional,
 272 educational) grounds.

Table 1: Distribution of habitats present in studies dealing with habitats as a filter of urban Collembola communities according to their function in cities

n°	urban land uses	%
1	Parks & gardens: country, urban and local parks, public gardens	35
2	street sides, rails, roads	23
3	Institutional grounds	0
4	Built-up areas residential land	23
5	Industrial and commercial site	8
6	educational establishments	0
7	Outdoor sports facilities : golfcourses, tennis, sport fields	2
8	Churchyards, cemeteries, burial grounds	0
9	Brownfield land: quarries, wastelands, landfills, vacant and derelict land	23
10	Community green spaces: allotments, community gardens, urban farms	15
11	Horticultural establishments	4
12	Natural & semi-natural green spaces: woodlands, forests, reserves, heathlands, grassland, meadow, conservation land	52
13	Avenue trees	4
14	Agricultural land, farms, ranches	6
15	green roofs and vertical forms	13

273
 274 Moreover, it was very difficult to classify certain studies because the name mentioned in the
 275 publication could correspond to several categories and no reference on the vegetation or the
 276 use of the site for example was precised. Among the problematic terms, lawn (brownfield or
 277 park?), garden (allotment or domestic garden?) or park (square or a residual forest?), were
 278 especially identified.

279 The lack of consensus on habitat typology, even for the better documented habitats,
 280 attempting to bring out general patterns of Collembola communities structural in response to
 281 habitats turned out to be complicated. In addition, a variety of indices are used (e.g. species
 282 diversity, families, QBS index, ratio) and not always comparable. Moreover, many
 283 publications do not give their raw values and rarely make taxonomic identifications on
 284 springtails. Values of density and species richness were specified in 26 and 24 studies
 285 respectively. Six different habitats, with their names provided by the authors, were
 286 characterized by at least two values by index and are presented in Tab. 2 to highlight the
 287 variability of the indices. The lowest and highest densities of Collembola were both found in
 288 lawns with 50 and over three millions ind/m² respectively (Eitminaviciute, 2006; Natuhara et
 289 al., 1994), but all habitats display large differences in minimal and maximal densities.

Table 2: Range of values of density, mean richness (mean number of species among sites of the study) and total richness (total number of species among all sites of the study) recorded in literature. N is the number of studies providing indices values. a:Eitminaviciute 2006, b:Natuhara et al., 1994, c:Shrubovych 2002, d:Milano et al., 2017, e: Fountain & Hopkin 2004, f:Huang et al., 2013, h:Rumble et al., 2018,i:Schrader & Böning 2006, j:Santorufo et al., 2015, k:Vincent et al., 2018, l:Joimel et al., 2017, m:Joimel et al., 2019,n: Sterzynska 1990, o:Joimel 2018, p:Devigne et al., 2016, q: Rzeszowski et al., 2017a, r: Rzeszowski et al., 2017b, s:Santorufo et al., 2014, t:Sterzynska 1987

Habitat	Density ($\cdot 10^3$)			Mean richness			Total richness		
	Min	Max	N	Min	Max	N	Min	Max	N
Lawns	0,05 ^a	3 398 ^b	9	2 ^b	32 ⁿ	5	33 ^q	64 ^f	7
Parks	0,331 ^c	36,5 ^d	8	7 ^d	37 ⁿ	2	13 ^s	64 ^t	9
Urban forests	4,95 ^e	268 ^f	6	3 ^b	21 ^f	5	21 ^e	70 ^c	3
Green roofs	11 ^h	88 ⁱ	4	5 ^h	14 ^o	3	30 ⁱ	44 ^o	2
Industrial	2,5 ^j	91 ^k	3	3 ^k	10 ^p	2	17 ^j	33 ^k	4
Gardens	7 ^l	73 ^m	3	6 ^m	33 ^l	3	28 ^m	41 ^l	4

290
 291 A high variability was also observed between replicates within a same site: density can
 292 vary from none to hundred thousand individuals per square meter (Milano et al., 2017;
 293 Rumble and Gange, 2013). Specific richness is also highly variable between and within
 294 habitats, ranging from only two species in a lawn (Natuhara et al., 1994) to 37 in a park
 295 (Sterzynska, 1990). When total richness is considered, disparity again occurs. Less than 20
 296 overall species were sampled in parks (Santorufo et al., 2014a) and in industrial sites

297 (Santorufu et al., 2015) and up to 70 overall species in urban forests (Shrubovych, 2002).
298 However it is obvious that urban sites can shelter enormous amounts of individuals (Huang et
299 al., 2013; Joimel et al., 2019; Natuhara et al., 1994). Besides species richness of urban lawns,
300 parks and forests can reach similar levels as non-anthropogenic sites (Joimel et al., 2017;
301 Ponge et al., 2003). This concurs with findings arguing that habitat type in urban area does not
302 always influence abundance or species richness, emphasising that biogeographic processes
303 may be of greater significance (Joimel et al., 2018; Sterzyńska et al., 2018). But these
304 conclusions need to be nuanced because i) as the classification is coarse, each category may
305 group sites with different structural characteristics and ii) in addition sampling methods and
306 season or habitat size vary from one study to another one and can impact results and make
307 comparisons between studies difficult (Querner and Bruckner, 2010; Santorufu et al., 2014b;
308 Yi et al., 2012). Thus provided figures (Tab.2) only broadly inform on Collembola community
309 indices adopted in urban habitats.

310 So if disparities between habitats exist, no general pattern concerning abundance and
311 richness seems to emerge. And the local characteristics might be more relevant to explain
312 Collembola urban assemblages (Sterzynska, 1987). Habitat structure can be spatially and
313 temporally defined (Byrne, 2007). Water content, pH, organic matter or nutrients content,
314 metal concentrations and presence or absence of a litter layer are the soil characteristics that
315 have been the most studied in relation to their effects on Collembola communities and they
316 are important drivers regarding their assemblages. Organic matter and water content – except
317 for anaerobic conditions - are almost always positively correlated with abundance, richness
318 and composition of Collembola (Ge et al., 2019; Islam et al., 2018; Milano et al., 2018, 2017;
319 Santorufu et al., 2015, 2014a). Soil pH and nutrients such as phosphorus and potassium seem
320 rather influence communities composition (Milano et al., 2018, 2017; Rzeszowski et al.,
321 2017). Soil concentrations of potassium and phosphorus can for instance be positively related

322 with the presence of *Pseudosinella alba* (Packard, 1873) and *Stenaphorura quadrispina*
323 (Börner, 1901) respectively and negatively with other species such as *Entomobrya nicoleti*
324 (Lubbock, 1868) or *Isotoma anglicana* (Lubbock, 1862; Rzeszowski et al., 2017). Metal
325 concentrations can have different types of impact on Collembola (Fountain and Hopkin, 2004;
326 Joimel et al., 2019; Vincent et al., 2018). Some studies showed that the presence of metals
327 even at high concentrations could not affect widespread species such as *P. minuta* (Milano et
328 al., 2017; Rota et al., 2015; Santorufo et al., 2015; Sterzyńska et al., 2018). However, high
329 metal concentrations could reduce Collembola abundance (Santorufu et al., 2014a, 2014b,
330 2012) or survival and reproduction (Fountain and Hopkin, 2004). Urban management
331 practices could also play a role in structuring Collembola communities. The presence of a
332 litter layer increases Collembola indices such as abundances or number of species (Milano et
333 al., 2017; Natuhara et al., 1994; Santorufo et al., 2014a). Too little work addressed the effect
334 of other management practices such as pesticide application or mowing to draw conclusions,
335 but they could also have an impact (Byrne and Bruns, 2004; Jensen et al., 1973; Rochefort et
336 al., 2013). Furthermore, habitat characteristics may evolve with time and these effects on
337 Collembola communities remain unknown. Pioneer studies showed that site history (i.e age
338 and previous land use) and long-term exposure to urbanisation may affect species community
339 and the number of Collembola species (Milano et al., 2017; Rzeszowski and Sterzyńska,
340 2016; Schrader and Böning, 2006).

341

342 **5. Biotic interactions between Collembola and between Collembola and other soil** 343 **organisms**

344

345 Biotic interactions can be understood at different scales, between Collembola
346 themselves and between Collembola and other soil organisms, but in all cases they have been
347 little studied in urban areas.

348 Concerning Collembola interspecific relations, while the dominance of certain species
349 among communities has been evidenced (Shrubovych, 2002; Sterzynska, 1987, 1987),
350 whether the presence of species can exclude or favour other ones is still obscure. But
351 Collembola are known to secrete pheromones involved in aggregation of individuals, either
352 inter or intra specific (Salmon et al., 2019), gathering up to millions of individuals. Their
353 interactions are proved to possibly be detrimental or beneficial depending on the species
354 (Theenhaus et al., 1999). Interactions between Collembola are complex and can vary
355 according to habitat (Christiansen et al., 1992), which raises interrogation to what extent
356 urban habitat affects those interactions and whether it induces a shift in community
357 composition.

358 Although half of publications of the selected corpus used a multi-taxa approach, only a
359 few addressed questions of trophic relations, competition, facilitation, or co-occurrence.
360 When several taxa were studied simultaneously, it was generally to evaluate the effect of an
361 environmental parameter on the overall soil fauna community (McIntyre 2000, Maisto 2017,
362 Mo 2018, Ge 2019). It is well established that Collembola interact with numerous other taxa
363 in different types of ways and habitats (Hopkins 1997). Many groups of the micro-flora and
364 fauna are part of their various diets, such as fungi, algae, bacteria and more rarely other
365 invertebrates (nematodes, rotifers and tardigrades). Collembola therefore play a crucial role in
366 soil communities structure, for instance by selectively eating certain fungi species or
367 regulating density of phytopathogens (Wardle 2006). Only two studies integrated both urban
368 Collembola and fungi in their investigations. Rumble and Gange (2013) found no correlation
369 between Collembola and arbuscular mycorrhizal fungi. It reinforces the hypothesis of a

370 selective diet for non-arbuscular fungi (Gange 2000). Moreover, Joimel et al. (2018) showed
371 that lead contamination can modify fungal communities. It could then have an impact on
372 Collembola diet, especially in urban habitats where contaminations are widespread.
373 Collembola are also preyed on by soil predators including spiders, acarian, myriapodes or
374 even some vertebrates (Thibaud 2010). Predator-prey interactions in soil have been shown to
375 display functional responses influenced by habitat structure and prey aggregation (Vucic-
376 Pestic 2010). However no work has been conducted in urban habitats for now.

377 Interactions between earthworms and Collembola have been the object of more
378 attention, but again very rarely in urban soils. Contrasted results were observed. Some
379 Collembola species seem to be preferentially present in soils richer in earthworms
380 (Wickenbrock 1997, Salmon 1999). An explanation could be that they feed on earthworm's
381 excrements and use their burrows to move and hide (Salmon 2004). Earthworms can impact
382 density, richness and species succession of Collembola communities (Dunger 2004, Mudrak
383 2012). Interactions between these two groups of soil organisms appear to depend on
384 community composition and how it impacts ecosystem processes is still to be discovered
385 (Grubert 2016). But some trade-offs may also exist. Schrader and Boenig (2006) think that the
386 absence of earthworms might favor the high densities of Collembola in green roofs substrates
387 where competition with earthworms does not exist. Joimel et al. (2018) also observed a higher
388 density of Collembola in Parisian urban farms soils where earthworms were absent.

389 Plants also appear to play a major role in the structure of Collembola communities.
390 Generally, Collembola diversity is positively linked with above plants diversity in cities
391 (Burrow 2017, Tresch 2019). As plants modify local soil properties (Qin 2019), it is possible
392 that a diversity of plants may offer for Collembola a variety of microhabitats or food
393 resources (e.g. by effect on microorganisms), explaining their higher abundance and richness
394 in more complex environments. Moreover, as mentioned above, when looking at sprout plugs

395 meant to be planted, differences can be observed in the Collembola species present in the plug
396 in function of the plant species (Rumble 2018). In return Collembola may provide nutrients to
397 plants with their excrements, their role in organic matter decomposition and improve their
398 growth through mycorrhizal stimulation (Gange 2000). These insights support the idea that
399 multiple feedback interactions exist between Collembola and plants, stressing the necessity to
400 incorporate reflections about selected plants in urban landscapes in order to favour long-term
401 viable soil communities. It should even be considered with great care as cities are hotspots for
402 the introduction of alien species (Cadotte 2017, Jäkel 2005) that could threaten local
403 communities by changing soil characteristics (Qin 2019), or introducing predators and
404 competitors (Jaskula 2019, Rowles 2019). Again, interactions between Collembola and
405 earthworms, plants and other soil dweller organisms deserve more interest, particularly in
406 constructed soils where their synergy could be very important in functional processes. These
407 biotic interactions can rapidly evolve and change biological interactions between Collembola
408 and the other organisms of macrofauna, especially in environments where dispersal can only
409 be achieved through voluntary inputs (e.g. compost for earthworms on roofs).

410

411 **6. Synthesis and future research**

412

413 This study, reviewing main data available about how urbanisation affects Collembola
414 used as bioindicators, has provided an initial overview (descriptive study) but it shows that,
415 although work has been developing increasingly in recent years, there is still a serious lack of
416 data to understand, explain and prioritise (i) the processes controlling the dispersion of
417 Collembola in urban soils and (ii) the relationships between Collembola and habitat
418 characteristics on the one hand (impact of abiotic factors) and Collembola and other soil
419 organisms on the other (impact of biotic factors).

420 Thus, in order to reconcile human activities and ecosystem functionality and to
421 contribute answering to the Sustainable Development Goal 11, "creating a more sustainable
422 future for cities and other urban communities" (FAO, ITPS, GSBI, CBD and EC, 2020), we
423 suggest some proposals for future research in urban soil biodiversity.

424 Concerning the methodology used, three points have been noticed: (i) the lack of
425 standardisation for sampling, collecting and extraction of Collembola; there is no standardized
426 methods and strategy making it difficult inter- and intra-habitat comparisons and creating
427 references values. We encourage following international standard ISO 23611-2 on sampling
428 and extraction of microarthropods with soil cores; (ii) No clear classification of urban
429 habitats; indeed confusions always reside between their type (e.g. forest, lawn), function (e.g.
430 recreational, ornamental, productive), spatial arrangement (proximity of roads, building
431 density) and their management (mowing, litter removal, chemical inputs). Moreover, behind
432 the same land use can hide a variety of soil types. As there is no common classification, we
433 propose to always specify the reference terminology used to classify the habitat. More details
434 on the different cited parameters could be also useful for future meta-analyses. These
435 parameters needs to include the presence of irrigation, connection to other soils or not (i.e.
436 height, above ground), soil depth and regular inputs of materials (e.g. compost) which directly
437 imply assumptions in main dispersion routes, selection and establishment processes of
438 Collembola community in urban habitat (iii) Density is not sufficient for highlighting
439 mechanisms underlying the assembly of communities. Species identification, which is only
440 present in less than half studies, is also necessary to better understand processes relatives to
441 homogeneisation and invasions by exotic species recorded in few studies. Moreover,
442 functional traits seem to be more widely complementary to allow comparison between various
443 cities, obtain a better global comprehension of assemblage processes, and soil functioning.
444 These functional approaches can be facilitated by the existence of many open databases that

445 provide data not only on Collembola but also on other soil fauna organisms (e.g. BETSI, Pey
446 et al. 2014). Direct measurements of functional traits on organisms can also be useful in
447 regions of the world where the taxonomy is less well known by offering an approach that
448 allows a finer understanding without the need for specific identification.

449 A second point noted in this review is the limited worldwide recovery. Moreover, an
450 international research in cities of varying sizes is necessary. In addition to new studies, the
451 diffusion of data published in the authors' native language to a wider audience could lead to a
452 rapid increase in global knowledge. Indeed, many data seems to be available in China and
453 Russia but the majority of non-English publications do not allow drawing conclusions.

454
455 Finally, concerning knowledge acquired on urban Collembola, studies are recent in
456 lines with all studies on urban soils, and make it possible to identify many areas of research to
457 be carried out: (i) increase the number of studies between the different habitat categories and
458 within each category ; (ii) Take into account management practices;; iii) Take into account
459 local conditions such as environmental conditions and soil properties (e.g. moisture, organic
460 matter, nutrients and metal contents) that may be responsible for the wide variability in the
461 structural responses of Collembola communities to the effect of habitat; (iv) Integrating
462 temporal evolutions; to understand the role of colonisation of urban habitats. Nowadays many
463 hypotheses are proposed, but none was verified. Specific studies must therefore be built in
464 order to understand precisely the mechanics of colonisation and dispersion of soil organisms
465 in cities; (v) Consider biotic interactions to better understand the functioning of urban soils
466 and be able to manage them in the long term; (vi) Take into account spatial organisation of
467 cities; Contemporary urbanization differs from former urbanization (Ramalho and Hobbs,
468 2012). Cities are larger, more rapidly urbanized, and more irregularly shaped (Batty, 2008;
469 Liu et al., 2014). Many questions therefore arise about the impact of the spatial organisation
470 within cities on the dissemination of soils organisms in cities. In order to answer these

471 questions, it seems necessary to set up *in situ* studies with varying soil types, heights,
472 obstacles or connectivity in order to monitor taxonomic and functional biodiversity indicators
473 over time: from installation to the eventual stabilisation of the community.

474

475

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479 **Authors' contributions**

480 **SJ**: idea for the article. **AJ, SJ**: literature search and data analysis. **AJ, SJ**: drafted the
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482

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