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# Collembola dispersion, selection, and biological interactions in urban ecosystems: a review

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## Abstract

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

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

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

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

## **1. Introduction**

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

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

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

## **2. Bibliometric methods and analysis**

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

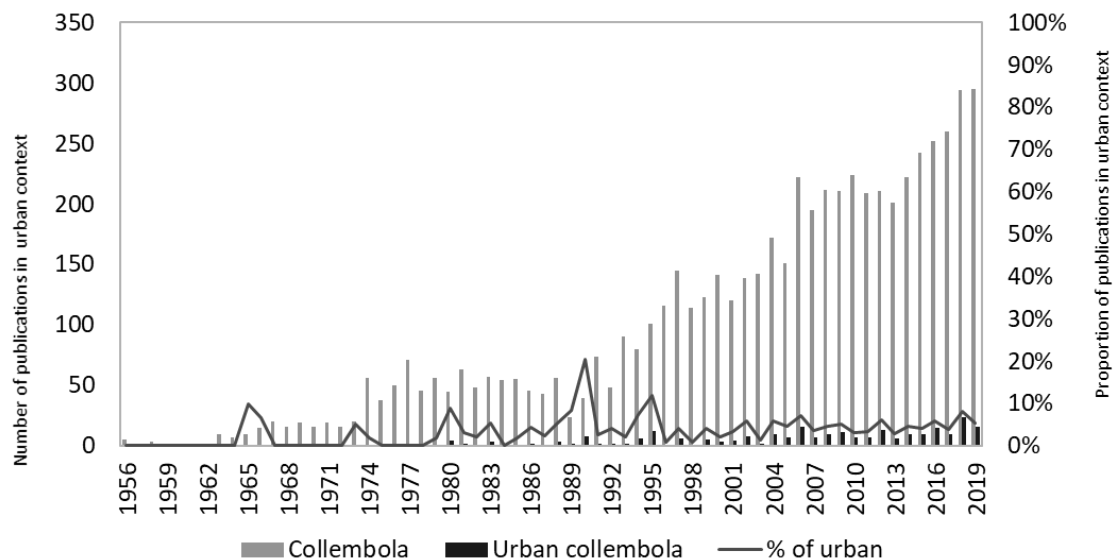


Figure 1 : Number of publications dealing with Collembola since 1956; light grey bars: number of publications dealing with Collembola; black bars: number of publications dealing with Collembola in a urban context and dark grey line: proportion of publications in a urban context

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

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

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

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

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

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

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

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

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



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

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

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

Schrader and Böning (2006) already suggested that dispersion onto green roofs was a 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

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

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

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

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

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

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

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

According to theoretical ecology, after a pool of species reaches a place through dispersal, habitat is the second filter that explains communities assemblages (Drake, 1990; Zobel, 1997). Several environmental factors can impact this filtering in soil communities: e.g. habitat type, soil local properties (Giller, 1996; Nielsen et al., 2010). Environmental conditions of each urban habitat could explain selection and survival of Collembola community. The effect of urban habitat on Collembola communities was by far the most studied factor among the corpus since only 6 articles did not include it in their reflections. Investigated sites within all studies (n=47) have been classified according to their function in the city (Tab.1). Although 12 on 15 different categories of habitats have been investigated among all papers, 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	%
<b>1</b>	Parks & gardens: country, urban and local parks, public gardens	35
<b>2</b>	street sides, rails, roads	23
<b>3</b>	Institutional grounds	0
<b>4</b>	Built-up areas residential land	23
<b>5</b>	Industrial and commercial site	8
<b>6</b>	educational establishments	0
<b>7</b>	Outdoor sports facilities : golfcourses, tennis, sport fields	2
<b>8</b>	Churchyards, cemeteries, burial grounds	0
<b>9</b>	Brownfield land: quarries, wastelands, landfills, vacant and derelict land	23
<b>10</b>	Community green spaces: allotments, community gardens, urban farms	15
<b>11</b>	Horticultural establishments	4
<b>12</b>	Natural & semi-natural green spaces: woodlands, forests, reserves, heathlands, grassland, meadow, conservation land	52
<b>13</b>	Avenue trees	4
<b>14</b>	Agricultural land, farms, ranches	6
<b>15</b>	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.

The lack of consensus on habitat typology, even for the better documented habitats, attempting to bring out general patterns of Collembola communities structural in response to habitats turned out to be complicated. In addition, a variety of indices are used (e.g. species diversity, families, QBS index, ratio) and not always comparable. Moreover, many publications do not give their raw values and rarely make taxonomic identifications on springtails. Values of density and species richness were specified in 26 and 24 studies respectively. Six different habitats, with their names provided by the authors, were characterized by at least two values by index and are presented in Tab. 2 to highlight the variability of the indices. The lowest and highest densities of Collembola were both found in lawns with 50 and over three millions ind/m<sup>2</sup> respectively (Eitminaviciute, 2006; Natuhara et 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:Santorufu 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:Santorufu et al., 2014, t:Sterzynska 1987

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

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

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

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

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

## **5. Biotic interactions between Collembola and between Collembola and other soil organisms**



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

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

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

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

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

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

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

## **6. Synthesis and future research**

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

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

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

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

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

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

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

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## Authors' contributions

**SJ**: idea for the article. **AJ, SJ**: literature search and data analysis. **AJ, SJ**: drafted the manuscript. **LVG** : critically revised the work.

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