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One green roof type, one Technosol, one ecological community

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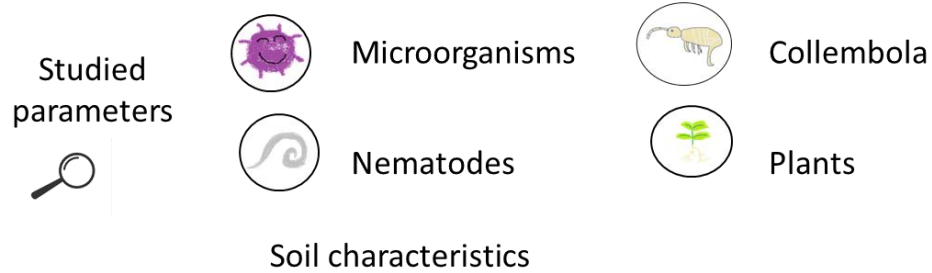
Abstract

Green infrastructures play a key role in the functionality and resilience of urban ecosystems. The physical, including thickness, chemical and biological properties of the Technosols of green infrastructures on rooftops are highly variable, leading to more or less favourable conditions for soil biodiversity. The aim of this study was to investigate the abundance and diversity of bacteria, fungi, nematodes, collembola and plants communities in relation with abiotic parameters of Technosols on 12 productive and extensive green roofs of the Paris region (France).

Results showed that green roofs harboured a high level of abundance and diversity from microorganisms to micro and mesofauna. Microbial biomass ranged between 16.3 and 419.8 $\mu\text{g DNA g}^{-1}$, with a predominance of bacteria, nematodes represented 820-60 700 individuals per kg of soil and between 1000 and 60 700 collembolan were present per m^2 of soil. A total of 13 986 bacterial OTU (Operational Taxonomic Unit), 33 559 fungal OTU, 47 Collembola species, 28 nematodes families, 16 cultivated plant species and 48 spontaneous plant species was identified on all the green roofs studied. Microbial, animals and plants communities were significantly different between the two types of green roofs. Productive and extensive rooftops represent contrasted habitats, which can strongly influence the soil biota. Any voluntary action to enhance soil biodiversity in cities would need to take-into-account both soil properties and the landscape around.

Keywords: urban agriculture, extensive green roofs, productive green roofs, soil biodiversity, plants

Graphical abstract



Highlights

- Soil biodiversity and plants communities have been investigated on 12 productive and extensive green roofs inside the Paris region (France)
- Green roofs harbour higher abundances and diversity of Collembola than forest or agricultural soils
- Green roofs harbour higher microbial biomasses than forest or agricultural soils
- Only productive green roofs harbour higher abundances of nematodes than forest or agricultural soils
- Productive and extensive rooftops present contrasted communities (abundance and diversity)

1 **1. Introduction**

2 Due to the development of urban areas and related environmental issues (e.g. soil sealing, air,
3 water and soil pollution, habitat fragmentation, heat island), the urban ecosystem has been the
4 subject of new societal expectations in the last years with an increasing necessity to
5 reintegrate nature into the city (Bratman et al., 2019; Cheverry and Gascuel, 2009). Nature in
6 the city has so far been mostly associated with vegetation and with its recognized role in the
7 landscape and as a component of the green belt network (Arnould et al., 2011). The evolution
8 of knowledge and awareness allows nowadays considering green infrastructures as a whole,
9 considering both the soil and above- and below-ground biodiversity and to highlight their
10 importance in the functioning of urban ecosystems. Indeed, green infrastructures play a key
11 role in the functionality and resilience of urban ecosystems, in particular through the
12 ecosystem services they provide (e.g. food production, regulation of the water cycle and
13 floods, carbon storage and climate regulation, biodiversity support) (Luederitz et al., 2015;
14 Tzoulas et al., 2007). Thus green infrastructures should temper negative environmental
15 impacts of rapid urbanization (Pataki et al., 2011) and impact positively the biodiversity in
16 urban areas (Uy and Nakagoshi, 2008). Urban ecosystems, from simple supports for
17 buildings, will be recognized as supports for several ecosystem services.

18 Because of the scarcity of space and land pressure in the city and the availability of large roof
19 surfaces, the development of green infrastructures on the roofs of buildings is a promising
20 development. Green infrastructures on buildings offer additional space and corridors to
21 enhance biodiversity in cities (Mayrand and Clergeau, 2018) as island habitats for urban
22 biodiversity, and thus participate to the conservation of ecological networks, the so-called
23 “green and blue infrastructures”. Green infrastructures on rooftops can fulfill different
24 functions, from food production (productive green roofs) to ornamental (extensive green
25 roofs) purposes. Green roofs have been also recognized for their better energy efficiency for

26 building and reduced rain runoff over conventional roofing (Li and Yeung, 2014). Initiatives
27 have gain local supports and institutional supports and cities authorities. Since 2014, the city
28 of Paris, through its "Parisculteurs" call for initiatives, aims to develop the place of nature in
29 the city, by attracting new farmers, creating social links and employment, and raising
30 awareness of good eating habits, notably through the implementation of rooftop urban
31 agriculture. The role of green roofs in biodiversity supporting, and its drivers, are very poorly
32 known nowadays, particularly in the case of productive green roofs (Lin et al., 2015).

33 Substrates of green roofs, that we can consider as soils, are composite and man-made, that
34 involve in some cases the use of urban waste (Molineux et al., 2009) and can be named
35 Isolatic Technosols (IUSS Working Group WRB, 2014). The soils of green infrastructures on
36 rooftops -more or less thick- are characterized by a high variability in their physical, chemical
37 and biological properties, which varies greatly according to the aesthetic and/or productive
38 functions of the rooftop that could impact positively or negatively the soil biodiversity
39 (Rumble and Gange, 2013). For example, extensive green roofs have mostly esthetic values
40 and a role in water regulation whereas productive green roofs have moreover functions of
41 food productions or educational services. We need to better address the direct and indirect
42 roles of these soils and their above- and below-ground biodiversity in ecosystem functioning
43 and services in order to be better considered in the management of nature areas into cities. In
44 a recent review, Guilland et al. (2018) outlined the importance of making new studies as
45 urban soils are still very little studied with only a few studies characterizing the biodiversity
46 of urban soils and theirs ecological and functional roles. Studies on productive and extensive
47 green roofs are even scarcer. Thus, biodiversity databases and repositories need to be enriched
48 with urban ecosystems information. A few studies described macroarthropods (Madre et al.,
49 2014, 2013) and Collembola (Rumble and Gange, 2013; Schrader and Böning, 2006) in green
50 roofs, with a high abundance of soil organisms and low species diversity but they did not

51 address simultaneously different groups of soil organisms nor interactions between the above-
52 and below-ground biodiversity. Recent studies showed for example an influence of soil
53 microbial communities on plant-pollinator interactions (Barber and Gorden, 2014).
54 However, without multi-taxon studies, we cannot be sure that all groups of soil organisms
55 respond in the same way to these infrastructures. Their different characteristics (e.g. size,
56 behaviour, colonisation pathways) may induce different responses to the roof type.

57 The objectives of this study were to i) describe the biodiversity of productive and extensive
58 green roofs through the study of soil and floristic biodiversity, ii) determine the key soil
59 parameters that condition the microbial, faunal and floristic biodiversity of green roofs, and
60 especially the water retention capacity, trophic and nutritional (e.g. content of organic matter)
61 as well as chemical (e.g. pH) characteristics of the Technosols and iii) study the co-
62 occurrence between the different soil organisms on the one hand and between soil organisms
63 and plants on the other hand. Understanding the drivers of the abundance and diversity of
64 microbial and faunal communities should make it possible to propose how to optimize
65 biodiversity in cities through the design and implementation of management of green roofs.

66 We hypothesised that the Technosols characteristics of productive green roofs will favour soil
67 biodiversity but not vegetation diversity compared to extensive green roofs due to differences
68 in edaphic constraints and management. Productive greens roofs being usually deeper and
69 richer in organic matter due to organic waste used in their construction (Grard et al., 2015,
70 2018) should favour soil biodiversity, especially detritivorous organisms. In contrary, we
71 supposed that, as both green roof types have different purposes, plant diversity could be
72 influenced by practices, as previously reported in gardens such as plants removed by
73 gardeners (Kendal et al., 2012). Indeed, plant diversity is controlled in productive green roofs
74 by targeted planting and by weeding control. It is also necessary to keep in mind that, if plants

75 are mostly chosen for food production or ornamental values, no voluntary introduction of
76 soil organisms are conducted.

77

78 **2. Materials and Methods**

79 **2.1. Studied sites**

80 We selected 12 rooftops (ca 35 m above ground) located in the dense urban environment of
81 the Paris region (Ile-de-France, France), six extensive green roofs and six productive green
82 roofs (Table 1). According to the “Green Roofing Guideline”, these green roofs were
83 classified according to three criteria: Technosol’s depth, main function of the roof and
84 presence/absence of an irrigation systems (The Roof Greening Working Group, 2002).
85 Extensive green roofs were characterised by a thin layer (8 to 10 cm-depth) and coarse
86 substrate (typically pozzolan), were not irrigated and mostly covered with ornamental
87 succulent species (*Sedum sp.* mostly). These species were introduced initially at green roofs
88 construction. Others plants species can thus colonize the green roofs. Productive green roofs
89 were characterized by grown vegetables covering more than 50% of their surface area, a thick
90 layer of Technosol (20 to 30 cm of depth) and high organic matter contents (presence in the
91 Technosols of compost, spent mushroom substrate, shredded wood, potting soil).

92 Extensive and productive green roof surface areas were *circa.* 390 m² and 270 m².

93 **2.2. Sampling methods**

94 Soil biodiversity samplings and vegetation identification were carried out in April 2017. In
95 each green roof, six plots of 25x25 cm were randomly located in the area covered by
96 vegetation (i.e. excluding paths or impervious surface), at least 1 m from the roof border to
97 avoid edge effects for vegetation identification and for invertebrates sampling.

98 For each green roof, final representative soil samples (600 g) were composed of 5 soils sub-
99 samples (8 to 15 cm depth according to soil depth). This composite soil sample was used for
100 soil, nematodes and microbial analyses.

101

102 *2.2.1. Microbiological sampling and analysis*

103 From the composite soil sample of each plot, an homogenized aliquot of soil was sieved at 4
104 mm and 50 g of soil were sent to the Genosol platform (Dijon) to be lyophilized and stored at
105 -40°C for further molecular analyses.

106 **Molecular microbial biomass**

107 Microbial DNA was extracted from 1 g of lyophilized soil subsamples using the procedure
108 described in Plassart et al. (2012). Briefly, soil samples were homogenized in 1 ml of
109 extraction buffer [100 mM Tris, pH8; 100 mM EDTA; 100 mM NaCl; 1% (w/v)
110 polyvinylpyrrolidone; 2% (w/v) sodium dodecyl sulphate] and glass beads for 3×30 s at 4
111 m.sec⁻¹ in a FastPrep ®-24 (MPBiomedicals, NY, USA). The samples were then incubated for
112 30 min at 70°C, and centrifuged at 7 000 g for 5 min at 20°C. After removing the supernatant,
113 proteins were precipitated with 1/10 volume of 3M sodium acetate prior to centrifugation (14
114 000 g for 5 min at 4°C). Finally, nucleic acids were precipitated by adding one volume of ice-
115 cold isopropanol. The DNA pellets obtained after centrifugation (14 000 g for 5 min at 4°C)
116 were washed with 70% ethanol. Soil DNA extracts were purified with a polyvinylpyrrolidone
117 spin column and a Sepharose 4B spin column. The quality and the integrity of the soil DNA
118 were checked by electrophoresis on 1% agarose gel. DNA was quantified by fluorescence
119 measurement of the Picogreen dye using a Quant-iT™ dsDNA Assay Kit (Invitrogen, USA).

120 **Molecular analyses of soil bacterial and fungal communities**

121 Quantitative real-time PCR were performed on extracted DNA to quantify 16S and 18S
122 rDNA gene sequences (Plassart et al., 2012), which led to the estimation of the fungal to
123 bacterial (18S/16S) ratios. For microbial diversity and composition analyses, banks of 16S

124 and 18S ribosomal sequences were prepared prior to sequencing by MiSeq technology (F479:
125 5' CAGCMGCYGCNGTAANAC 3' and R888: 5' CCGYCAATTCMTTTRAGT 3' for 16S
126 primers and FR1: 5' AICCATTCAATCGGTAIT 3' and FF390: 5'
127 CGATAACGAACGAGACCT 3' for 18S primers). Bioinformatics analysis of the sequences
128 was performed using the GnS-PIPE v1.17 (Tardy et al., 2015). In order to compare the data
129 sets efficiently and avoid biased community comparisons, the sample reads were reduced by
130 random selection closed to the lowest data sets (10 000 reads for 16S and 18S-rRNA gene
131 sequences respectively for each soil sample). The retained high-quality reads were used for
132 taxonomy-based analysis using similarity approaches.

133

134 2.2.2. *Nematode sampling and identification*

135 Aliquots of the composite soil samples (one per plot) from each green roof were pooled in a
136 single sample of 300 g of wet soil for the analysis of nematodes (no replicate and no sieving).
137 Nematodes were analysed by extraction, quantification and taxonomic identification at the
138 level of the nematode family according to NF/ISO 23611-41 by the ELISOL laboratory.

139

140 2.2.3. *Collembola sampling methods and identification*

141 For each of the six plots by green roofs, undisturbed soil cores (5 cm depth, 6 cm diameter)
142 were sampled from the topsoil. Collembola were then extracted from soil samples using a
143 high-gradient McFadyen extractor for one week according to NF/ISO 23611-2 and identified
144 at the species level using available dichotomous keys (Gisin, 1943; Hopkin, 2007).

145

146 2.2.4. *Plants identification*

147 All spontaneous vascular plants, i.e. those growing and reproducing without human assistance
148 (Bossu et al., 2014) and cultivated plants were identified at the species level using

149 identification keys (Machon and Motard, 2012; Mamarot et rodriguez, 2014) in each of the
150 six plots of 25x25 cm per roof type. Their relative abundance was estimated using the Braun-
151 Blanquet cover-abundance scale and then transformed to the ordinal scale. The discrimination
152 of species between cultivated and spontaneous plants was difficult due to the lack of
153 information about plantations during the green roofs installation. We assumed that the species
154 that had resisted over time were species able to colonize extensive roofs. Even if some species
155 of *Sedums sp.* could have been initially planted, we considered all *Sedums sp.* as spontaneous
156 species in this study due to the high age of extensive green roofs.

157

158 2.2.5. *Soil sampling and physicochemical analyses*

159 From the composite soil sample, an homogenized aliquot of soil from each green roof was air-
160 dried, disaggregated and sieved at 2 mm. Soil analyses were performed by the laboratory of
161 Paris city (AgiLIMS, France), according to the following standard methods: pH (NF ISO
162 10390), organic carbon (NF ISO 10694) and total metals (Cd, Cu, Pb and Zn; NF ISO 11466).
163 In addition, three undisturbed soil cores were sampled for bulk density determination (NF EN
164 13041). They were saturated with water for 24h and then placed on a suction table to
165 equilibrate at 20kPa corresponding to field capacity (pF2.3). The samples were then dried at
166 105°C to determine bulk density and soil water content at field capacity, i.e. the water holding
167 capacity (WHC).

168 Organic C and pH were selected as indicators of soil chemical fertility, bulk density and water
169 holding capacity as indicators of soil physical fertility and total concentrations of Cu, Ni, Pb
170 and Zn as indicators of metal contamination. These metals are often associated with human
171 activities in urban agriculture (Joimel et al., 2016).

172

173 **2.3. Community indices**

174 Microorganisms, nematodes, Collembola and plants communities were described by their
175 biomass, abundance or density (except for plants) and the total number of species per green
176 roof type. Additionally, we computed community indices for structure and composition based
177 on taxonomy and their relative abundance (species-based indices). We calculated the Shannon
178 and evenness indices for each green roof.

179

180 **2.4. Statistical analyses**

181 When indices did not match the basic assumptions of normality and homoscedasticity
182 required for parametric statistics (Wilk–Shapiro test at rejection level of $\alpha = 0.05$), we used
183 non parametrical one-way kruskal test to assess differences between the two types of green
184 roofs.

185 We analysed the effects of green roof type on species composition by performing a non-
186 metric multidimensional scaling (NMDS) for each taxonomic groups, using the Bray-Curtis
187 index, to explore dissimilarities between communities. Differences in species compositions
188 between green roof types were tested by a permutational analysis of similarities (ANOSIM)
189 (Clarke, 1993).

190 To study the co-variation between soil biological and selected soil abiotic parameters, a co-
191 inertia analysis was performed on two PCA: (i) one on soil chemical and physical parameters
192 (C, pH, bulk density, WHC, Cu, Cd, Pb, Zn) and (ii) one on biodiversity parameters
193 (abundances and species richness) of each taxonomic group. Co-inertia was chosen in order
194 to look on the co-structure of biological and physicochemical parameters.

195 All statistics were performed using R software version 3.2.2 (R Development Core Team,
196 2015), with “vegan” (Oksanen et al., 2014) and “ade4” (Dray and Dufour, 2007) packages.

197

198 **3. Results**

199 **3.1. Chemical and physical soil characteristics**

200 Mean organic C contents were significantly lower in extensive roofs (7.8 g kg⁻¹) compared to
201 productive roofs (21.0 g kg⁻¹) (Table 2). pH was slightly alkaline with values ranged from 7.3
202 (extensive roofs) to 7.6 (productive roofs). No significant difference was observed between
203 green roof types for metal concentrations. Extensive green roofs retained significantly less
204 water (0.14 g H₂O g⁻¹ of dry soil) than productive ones (0.75 g H₂O g⁻¹ of dry soil) at pF 2.3
205 and their bulk density was very low, but higher in extensive roofs (0.8 g cm⁻³) compared to
206 productive roofs (0.4 g cm⁻³).

207

208 **3.2. Community structures and composition**

209 *3.2.1. Microorganisms*

210 Microbial biomass ranged between 16.3 and 419.8 µg DNA g⁻¹ soil (Figure 1) and was
211 significantly higher in productive roofs (279.9 ± 29.3 µg DNA.g⁻¹ soil) than in extensive roofs
212 (111.3 ± 27.7 µg DNA g⁻¹ soil). Fungi/bacteria ratios varied from 3.2 to 13.9 and were lower
213 for the productive roofs (6.4 ± 1.3) than the extensive ones (8.8 ± 2.3). No significant
214 difference was observed between the two types of roofs concerning specific richness,
215 Shannon and evenness indices for bacteria and fungi (Table 3).

216 Microbial diversity was studied at the phylum, genera and OTU (Operational Taxonomic
217 Unit) scales. Twenty-eight bacterial phyla (apart from the categories "unknown" and
218 "unclassified") were identified and 16 among them were present in all soil samples. Thirteen
219 represented more than 0.5% of the total but 2 phyla were largely dominant: Proteobacteria
220 (39.9 and 38.8% in productive and extensive roofs respectively) and Bacteroidetes (35.3 and
221 31.1% in productive and extensive roofs respectively). Some phyla were only present in rare
222 samples (*Fusobacteria*, *TM6* et *Lentisphaerae*).

223 The same phyla were observed on both types of roofs but the hierarchy of phyla representing
224 less than 10% of the total was slightly different (Figure S1).

225 A total of 2031 bacterial genera was detected in all soil samples. Focusing on the 50 most
226 abundant genera in each sample (147 genera in total), the 10 000 sequences analysed
227 represented on average 89.8% of the diversity (87.3-91.6).

228 Dominant bacterial genera were similar between productive and extensive roofs. Some genera
229 were more abundant in one of the two roof types (greater than 0.5% in one roof and less than
230 0.5% in the other): *Anaerolinea*, *Halomonas*, *Desulfobulbus*, *Pseudomonas*, *Aquicella*,
231 *Arenimonas*, *Novosphingobium*, *Pseudoxanthomonas*, *Rhodobium*, *Chlorobium*,
232 *Altererythrobacter*, *Sorangium* in productive roofs and *Aeromonas*, *Sulfophobococcus*,
233 *Nitrosococcus*, *Nocardioides*, *Fluviicola*, *Solirubrobacter*, *Segetibacter* and *Niastella* in
234 extensive roofs.

235 A total of 13 986 different bacterial OTU (groups of sequences with 95% of similarities) was
236 quantified considering all soil samples, corresponding to means of 1377 ± 71 bacterial OTU
237 in productive roofs and 1410 ± 72 in extensive roofs. Seven and ten OTU were dominant
238 (>1%) in productive and extensive roofs respectively (including 5 common to both types of
239 roofs). They essentially belonged to 2 phyla (Bacteroidetes and Proteobacteria) in the 2 types
240 of roofs and the genera *Flavobacterium*, *Terrimonas*, *Bacteroides* (for OTU present in both of
241 roofs), *Sphingobacterium*, *Hyphomicrobium* especially in productive roofs and *Aeromonas*,
242 *Flavisolibacter*, *Sulfophobococcus*, *Pedomicrobium* in extensive roofs (Table S1).

243 The factorial map of the NMDS revealed marked differences between bacterial communities
244 between green roof types, along both axes 1 and 2 (Figure 2), and these differences were
245 significant (ANOSIM, $P < 0.001$).

246 A high proportion of fungi belonged to unknown or unclassified phyla (44.4% in productive
247 roofs and 33.5% in extensive roofs) (Figure S4). Ascomycota was the dominant phylum

248 (36.9% in productive roofs and 50.1% in extensive ones). Few differences were observed
249 between productive and extensive roofs, and mainly for the 20% minority phyla.
250 Sixty-five fungal genera were present at least once in the soil samples and 34 were present in
251 all samples. More than 50% of fungi were unknown or unclassified (Figure S4). The most
252 prevalent fungal genus was *Lojkania* (11.5 in productive roofs and 24.4% in extensive ones).
253 *Batrachochytrium* represented 8.9 and 7.0% in productive and extensive roofs respectively.
254 Many genera were poorly represented (42<0.1%).
255 A total of 33 559 different fungal OTU was quantified considering all soil samples,
256 corresponding to means of 1359 ± 164 fungal OTUs in productive roofs and 1434 ± 170 in
257 extensive ones. Thirteen and nine OTU were dominant (>1%) in productive and extensive
258 roofs (Table S2). Some of them correspond to unknown fungi. Others were Ascomycota
259 (*Hypocrea*, *Verticillium*, *Leptosphaeria*, *Lojkania*, or unclassified), Basidiomycota
260 (unclassified) and Chytridiomycota (*Batrachochytrium*).
261 The factorial map of the NMDS revealed marked differences between fungal communities
262 between green roof types, along both axes 1 and 2 (Figure 2), and these differences were
263 significant (ANOSIM, $P < 0.001$).

264

265 3.2.2. *Nematodes*

266 A total of 28 nematodes families was present in the Technosol of the six productive and six
267 extensive green roofs (Table 3, Table S3). The number of families varied from 5 to 18 taxa
268 per roof. Total nematodes abundances in soil samples ranged from circa 820 to 60 700
269 individuals.kg⁻¹ and were significantly different between extensive and productive green
270 roofs. No significant difference was showed for Shannon and Eveness indices.
271 The factorial map of the NMDS revealed marked significant differences in nematodes
272 communities between green roof types, along both axes 1 and 2 (Figure 3, ANOSIM,

273 P<0.001). On average, trophic groups of nematodes were mostly composed by bacterivorous
274 (51% in productive green roofs and 80% in extensive green roofs) followed by phytophagous
275 in productive green roofs (35%) or omnivorous and carnivorous in extensive green roofs
276 (12%). Two productive green roofs presented phytoparasites. In terms of frequency, the
277 families *Plectidae* (100%), *Tylenchidae* (100%), and *Cephalobidae* (100%) were also always
278 present on both types of roofs. The most frequent families specific on productive roofs were
279 *Rhabditidae* (100%), *Anguinidaeditylenchus* (83%), *Apelenchoidi* (83%) and
280 *Neodiplogasteridae* (83%). The species most frequently observed on extensive roofs was
281 *Qudsianematidae* (67%).

282

283 3.2.3. Collembola

284 A total of 47 Collembola species was identified in the topsoil of the six productive and six
285 extensive green roofs (Table S4). The number of species varied from 9 to 20 species per roof.
286 The total Collembola density in topsoil ranged from circa 1 000 to 235 600 individuals.m⁻².
287 No significant difference was observed for Shannon and Evenness indices for Collembola
288 between green roof types.

289 The factorial map of the NMDS revealed marked differences in Collembolan communities
290 between the two green roof types, along both axes 1 and 2 (Figure 3), and these differences
291 were highly significant (ANOSIM, P<0.001). Productive and extensive roofs had similar
292 frequencies of *Proisotoma notabilis* (Schaeffer, 1896) (100%) and *Protaphorura armata*
293 (Tullberg, 1869) (71%). Some species were specific to green roof types. *Megalothorax*
294 *minimus* (Willem, 1900) and *Proisotoma minuta* (Tullberg, 1871) were the most frequently
295 observed species on productive green roofs (71% for both) while *Bourletiella hortensis*
296 (Fitch, 1863) and *Sminthurinus aureus* (Lubbock, 1862) were present on extensive green
297 roofs (100% and 86% respectively).

298

299 3.2.4. *Plants*

300 A total of 16 cultivated plant species and 48 spontaneous plant species was identified in the
301 six productive and six extensive green roofs (Tables 3, S5, S6). The total number of plant
302 species was not significantly different between green roofs on average. Cultivated plant
303 species were mostly vegetables such as lettuce (present on 50% of productive green roofs) or
304 onion (33%), cucumber, radish, chard (17%) and herbs. Parsley and other herbs were also
305 present exceptionally in extensive green roofs. Concerning spontaneous species, *Cerastium*
306 *glomeratum* Thuill was present in 50% of productive green roofs but was absent in extensive
307 green roofs. The most frequent species, belonged to genus *Sedum*, were present in all
308 extensive green roofs (6 different species), especially *Sedum album* L. (83%) and *Sedum*
309 *reflexum* L. (67%). Due to low frequency, no NMDS was performed on plants communities.

310

311 3.2.5. *Relationship with soil parameters*

312 In order to study the co-variation between soil chemical, physical and biodiversity parameters
313 in the 12 green roofs, we carried out a co-inertia analysis (Figure 4). The analysis showed a
314 high co-variation between biotic and abiotic parameters ($RV = 0.62$; Monte-Carlo
315 permutation test, $P = 0.003$). The two first axes explained 94% of the total inertia. Green roofs
316 were separated in two groups corresponding mainly to the two different types of green roofs
317 with the exception for the extensive roof n°6. Fertility parameters were higher in productive
318 green roofs whereas extensive green roofs presented a higher bulk density. Fertility
319 parameters and metal contents co-varied positively with biodiversity indices except for
320 spontaneous plants species richness. Abundances of microbial communities (bacteria and
321 fungi) and species richness and abundance of nematodes co-varied along the axis 1. Along the

322 axis 2, the species richness of bacteria, fungi and Collembola co-varied positively but
323 negatively with abundance of Collembola and species richness of cultivated plants.

324 **4. Discussion**

325
326

327 **4.1. Green roofs: a possible refuge for soil biodiversity, less for plants**

328

329 The first objective of this work was to have a better view of the biological patrimony of urban
330 soils, especially of green roofs by comparing productive and extensive roofs. Despite their
331 nature and artificial composition, our results showed that green roofs harbour a high level of
332 abundance and diversity from microorganisms to micro and mesofauna.

333

334 **Microorganisms**

335 Microbial molecular biomass in green roofs is higher compare to the average values observed
336 from more than 2000 French soils under grasslands (81 $\mu\text{g DNA g}^{-1}$ soil), forests (77 $\mu\text{g DNA}$
337 g^{-1} soil), crops (38 $\mu\text{g DNA g}^{-1}$ soil), vineyards and orchards (27 $\mu\text{g DNA g}^{-1}$ soil) and other
338 soils (gathering natural environments, urban parks...) (94 $\mu\text{g DNA g}^{-1}$ soil) (platform
339 GenoSol data – Gis Sol, 2015 in Briat and Job, 2017). These results are similar to those
340 described in the review by Guillard et al. (2018) where urban soils exhibit a higher microbial
341 biomass than agricultural soils (Chen et al., 2010; Enloe et al., 2015; Pavao-Zuckerman and
342 Coleman, 2005). However, Mc Guire et al (2013) observed higher microbial biomasses in
343 urban parks than in green roofs in New York City. These contradictory results could be
344 explain by the fact that urban soils include a wide variety of types of green spaces (parks,
345 gardens, sports fields, etc.) with contrasted characteristics. Our results showed a higher
346 microbial biomass on productive roofs than on extensive roofs These results could be
347 explained by higher organic carbon and clay contents and higher pH in productive roofs

348 (Table 2) as Horrigue et al (2016), showed that soil organic carbon and clay contents, altitude
349 and pH were the best explanatory variables of soil microbial biomass and explained 60% of
350 the variance for microbial molecular biomass by developing a statistical model.

351 Unlike fungi, bacteria were significantly more abundant in the soils of productive roofs than
352 in extensive roofs and led to 1.4 times lower fungi/bacteria ratios in productive roofs
353 compared to extensive ones. That indicated that productive roofs have a positive effect on the
354 bacterial populations. For comparison, in the study of Mc Guire et al. (2013), fungi/bacteria
355 ratios were of the same order and were lower in urban parks than in green roofs (5.3% vs
356 8.7% respectively).

357 Bacterial diversity is influenced by soil pH, soil texture and the quality of organic carbon and
358 is more important in alkaline, coarse-textured soils with low C/N (Constancias et al., 2015;
359 Terrat et al., 2018). Bacterial diversity is also influenced by land use, with lower levels of
360 biodiversity in grasslands and forests (2103 and 1897 taxa, respectively) than in cultivated or
361 vineyard soils (2181 and 2215 taxa, respectively) in soils from the RMQS campaign (Terrat et
362 al., 2018). These trends are the opposite of those observed for microbial molecular biomass,
363 where agricultural soils had a lower microbial molecular biomass compared to natural
364 environments (Dequiedt et al., 2011). Similarly, in green roof Technosols, we did not observe
365 a correlation between the microbial biomass (higher than in soils of the RMQS campaign) and
366 the bacterial diversity (lower than in soils of the RMQS campaign).

367 Green roofs also harbour a large diversity of fungi with an average number of OTU per roof
368 that was 10 times higher than those observed by Mc Guire et al. (2013) in green roofs of New
369 York. The comparison of taxonomic affiliations at the phylum and genera levels highlighted
370 differences in fungal diversity between our study and works of the Mc Guire et al. (2013).

371 Although the average level of bacterial and fungal diversity was similar in the two roof types,
372 the structure of the communities at the OTU scale was different, as shown by the NMDS

373 analyses. Soil abiotic characteristics such as concentrations of available nutrients and bulk
374 density may explain differences of communities between roofs (Mc Guire et al., 2013).

375 It is also noted that knowledge on the origin of microorganisms in green roofs remains low.
376 Maybe, the origin of substrate could play a major role and explain differences of results
377 between studies.

378 To summary, microbial characteristics of green roofs are different from soils with other land
379 uses. Furthermore soils of productive and extensive roofs differ both in the quantity of
380 microorganisms they harbour, especially bacteria, and in the type of microorganisms present,
381 with bacterial and fungal diversity specific to a roof type, due to soil characteristics.

382 Nematodes

383 The abundance of nematodes in extensive roofs was similar to those observed in cultivated
384 soils (1.10^4 to $1.3 \cdot 10^4$ individuals per kg of soil) (Cluzeau et al., 2012; Ponge et al., 2013). In
385 productive roofs, it was in contrast, higher than in soils with other land uses. Different studies
386 presented in the review of Guillard et al. (2018) reported a similar (Park, 2009) or a lower (Li
387 et al., 2011; Pavao-Zuckerman and Coleman, 2005) abundance of nematodes in urban soils
388 compared to agricultural soils in relation to heavy metals concentrations in soil.

389 Bacteriovorous nematodes dominated communities in green roof soils. Such results are
390 common in young constructed soils (Villenave et al., 2018) such as greens roofs (under the
391 age of 6 in our study). Young industrial Technosols are first dominated by bacteriovorous and
392 then by phytophagous nematodes (Cortet et al., 2013) that correlate with the higher bacterial
393 density. Guillard et al. (2018) reported that abundance of carnivorous and omnivorous
394 nematodes was low in urban soils and that the ratio between fungivorous and microbivorous
395 nematodes was significantly lower in urban environments than non-urban land uses,
396 indicating that organic matter decomposition was mainly ensured by bacteria (Ferris et al.,
397 2001).

398 In brief, nematodes communities are higher and different in productive compared to extensive
399 soils.

400

401

402 Collembola

403 The density of Collembola in green roofs was higher to those observed in agricultural (9810
404 ind.m⁻²) (Cluzeau et al., 2012) but also in some urban and industrial soils (Joimel et al.,
405 2017). For comparison, Rumble and Gange (2013) quantified a mean of 19.10³ individuals per
406 m² in extensive roofs. Guillard et al. (2018) explained the high abundance of Collembola in
407 green roofs by the absence of earthworms and the low abundance of predatory
408 macroarthropods such as spiders or ground beetles.

409 Despite their greater abundance in green roofs, several authors observed less diversity of
410 Collembola in green roofs compared to other urban soils such as parks, residential gardens,
411 lawns (Joimel et al., 2017; Rzeszowski et al., 2017; Santorufo et al., 2014) likely because of
412 habitat fragmentation. Nevertheless, in our study we identified 5 times more species than
413 Rumble and Gange (2013) in extensive roofs of London (6 species recorded). It could be due
414 to different origins of substrates in cities, especially compost which have been demonstrated
415 as a way of colonisation for Collembola (Joimel et al., 2018). Conversely, mean species
416 richness (12 and 14.5 in productive and extensive roofs respectively) was generally greater
417 than previous studies at regional scales comparing different land uses, ranging from 3.4 to 14
418 (Cluzeau et al., 2012).

419 While little significant differences in biodiversity levels were demonstrated between green
420 roofs, we observed a strong differentiation of communities as a function of green roof type as
421 shown by NMDS. *Parisotoma notabilis* is, as frequently reported in literature, the most
422 common species. Some Collembola species are specific to green roof types. Extensive green

423 roofs harbour epiedaphic Collembola as *B. hortensis* and *S. aureus* whereas eudaphic
424 Collembola are most present in productive ones, due perhaps to their ecological preferences.
425 The Collembola species identified in the green roofs were, for most of them, different from
426 those detected in extensive roofs by Rumble and Gange (2013) with the exception of
427 *Proisotoma minuta* but this species was in our case only detected in productive roofs.
428 To summary, green roofs harbour high level of abundances and diversity of Collembola with
429 strong differentiation of communities between productive and extensive roofs.

430

431 Plants

432 With only 65 species, green roofs were not the most favourable environments for the
433 establishment of native species, compared to poorly anthropised ecosystems which present up
434 to 600 species (Muratet et al., 2008).

435 In conclusion, few cultivated plant species have colonized the extensive roofs but in contrast,
436 spontaneous plants abundance was limited in productive roofs by the planting of vegetables
437 and weeding practices.

438

439 **4.2. Co-occurrence between organisms and links with green roofs** 440 **characteristics**

441

442 Soil physical and chemical characteristics are described to be major drivers of the abundance
443 and composition of plants and soil organisms, including in urban areas (e.g. Huot et al., 2018;
444 Milano et al., 2018; Santorufo et al., 2015).

445 In this study, the abundance and diversity of the different groups of organisms are differently
446 explained by soil parameters, especially for plants and soil organisms. Plants were mostly
447 correlated with bulk density whereas soil biodiversity was linked to metal contents and soil

448 fertility components (organic C, pH, water retention). Yet, previous studies have highlighted
449 the importance of soil characteristics including water availability and organic matter contents
450 for the assemblage of plant communities in urban soils (Dana et al., 2002). In cities, specific
451 constraints such as climatic conditions and human management of productive roofs can have
452 an impact on floristic diversity, in addition to soil characteristics (Joimel et al., 2019). We
453 showed that plant diversity was not correlated to soil biodiversity. Previous studies showed
454 contrasted results with absence (McGuire et al., 2013; Rumble and Gange, 2013) or presence
455 of a correlation in urban parks and green roofs. Rumble and Gange (2013) explained these
456 different results by the age of roofs, the diversity of plants, the climate or sampling season.
457 We may also propose that human management may have less effects on microbial diversity.

458

459 Secondly, a strong co-variation between biodiversity and soil characteristics was observed
460 that allowed to distinguish the two types of green roofs. The studied soil characteristics
461 reflected the green roofs functions, either productive or ornamental. Technosols of the studied
462 productive green roofs were rich in organic matter, even higher than other urban agricultural
463 soils such as vegetable gardens (Joimel et al., 2016). In contrast, Technosols of extensive
464 green roofs were among the urban soils with the lowest fertility. The studied green roofs had
465 low concentrations in metals compared to those classically observed in urban soils (Joimel et
466 al. 2016). Results showed that some indicators such as abundance of Collembola and species
467 richness of nematodes were rather influenced by soil fertility parameters and others such as
468 abundance of microorganisms and nematodes or diversity of microorganisms and Collembola,
469 by metal contents. Some of these results are consistent with the literature while others are
470 more unexpected. Indeed, many studies reported the effects of soil pH, organic carbon and
471 metal contents on Collembola (Joimel et al., 2019; Santorufo et al., 2015) and
472 microorganisms (Hui et al., 2012; Huot et al., 2018; Wang et al., 2017) in non-urban soils.

473 The distribution of molecular microbial biomass at the scale of France was mainly explained
474 by the soil physico-chemical characteristics (Dequiedt et al, 2011). Concerning nematodes,
475 results from Villenave et al. (2018) showed that the high organic matter content of Technosols
476 and its positive effect on bacterial populations, ensured nematode colonization and
477 progressive diversification. Soil fauna such as Collembola is also correlated to physical
478 parameters related to porosity and aggregation because they preferentially live in air-filled
479 soil pores (Wall et al., 2013). Moreover, the correlation we observed between metal contents
480 and biodiversity was positive, contrary to previous studies (Fountain and Hopkin, 2004),
481 which we explain by the low concentrations of trace metals in the roof top soils. Finally, no
482 relation between abundance and diversity of the different groups of soil organisms was
483 observed.

484 The relationships between organic matter and biodiversity, with generally a higher diversity
485 in productive green roofs, which present the higher contents in organic matter, are in line with
486 the conclusion that organic matter content is likely to be the key for successful biodiversity
487 colonisation (Villenave et al. 2018).

488 Substrate characteristics were also shown to have an influence on the development of the
489 plant cover, especially in extensive green roofs (Emilsson, 2008).

490 Our statistical analyses did not take into account difference of soil depth. It is necessary to
491 note that thickness is different between green roofs: 8 to 10 cm-depth for extensive green roof
492 and 20 to 30 cm-depth for productive green roofs. Previous studies demonstrated that depth
493 soil could influence soil organisms such as nematodes (Hafeez et al., 2012). However, these
494 conclusions were drawn from deeper Technosols (85 cm) and did not differentiate the first
495 layer (0-15 cm). Moreover, in this study, the soil layers of the green roofs were homogenous
496 and then comparable. So, it is possible that in our case the depth does not play a role in the

497 observed groups. However, the depth may play a role for other taxonomic groups such as
498 earthworms.

499 To summary on this part, the physical and chemical characteristics of Technosols play a
500 major role in the pattern of soil biodiversity observed in our study.

501 **4.3. Synthetic approach**

502 The responses of each studied taxonomic group to the green roofs type were synthetized in a
503 radarplot (Fig. 5). Productive green roofs exhibited, for each group of soil biodiversity, the
504 higher values of abundance and density. They also harboured a higher cultivated plants and
505 nematodes richness. In contrast, extensive green roofs had the higher values of diversity for
506 microorganisms, Collembola and spontaneous plants.

507 These results highlight the importance of considering different indicators (e.g. abundance *vs.*
508 diversity) and different soil organisms to answer a given question. Soil fauna, which usually
509 discriminate less land uses than microorganisms (Cluzeau et al., 2012), were very sensitive
510 here to the green roofs type.

511
512 In the present study, we only recorded the state of biodiversity at a given point in time.
513 Moreover, these Technosols are young soils and these findings will need to be re-examined in
514 the long term to investigate the sustainability of these systems. Colonization by organisms
515 from nearby environments may still be limited in young soils and could change over time and
516 contribute to an increase in biodiversity of older green roofs. In future studies, it would also
517 be important to carry out several sampling during the first stages of these young soils in order
518 to assess the biodiversity dynamics.

519

520 **5. Conclusion**

521 Green roofs provide habitats for biodiversity instead of impervious surfaces in the cities and
522 host in the first years a high abundance of soil organisms. But the characteristics of above and

523 below ground biodiversity vary in the different green roof types corresponding to different
524 Technosols with their own characteristics, depending on harsh conditions in extensive ones,
525 and human interventions in productive ones.

526 The contrasted abundance and composition of biotic communities between green roofs type
527 may impact on soil functioning.

528

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Table 1. Characteristics of 6 extensive and 6 productive green roofs

Site	Green roof type	City	Age (year of creation)	Technosol depth (cm)	Technosol composition
1	Extensive	Paris	3.5 (2014)	10	Pozzolan and compost
	Productive			21	Pozzolan and compost
2	Extensive	Paris	6 (2011)	8	Perlite, peat based substrate and pozzolan
	Productive		5 (2012)	30	Compost, spent mushroom substrate, shredded wood and crushed tiles and bricks
3	Extensive	Ivry	2 (2015)	-	-
	Productive			20	Compost, spent mushroom substrate, pozzolan and compost
4	Extensive	Nanterre	2 (2015)	10	Pozzolan, compost, crushed wood
	Productive			20 to 30	Peat based substrate, pozzolan, expanded clay balls and compost
5	Extensive	Paris	2 (2015)	8	Pozzolan and peat based substrate
	Productive			25 to 30	Spent mushroom substrate, crushed wood and compost
6	Extensive	Paris	3 (2014)	9	Pozzolan and peat based substrate
	Productive			20	Pozzolan, spent mushroom substrate and compost

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Table 2. Physical and chemical soil characteristics (mean \pm standard deviation) of extensive and productive green roofs surveyed. Lower case letters indicate significant differences between green roofs type ($\alpha = 0.05$)

Soil parameters	Unit	Extensive green roofs	Productive green roofs
pH	-	7.3 ^b \pm 0.25	7.6 ^a \pm 0.10
C	mg.kg ⁻¹	7.8 ^b \pm 6.5	21.0 ^a \pm 1.7
Density	g.cm ⁻³	0.8 ^a \pm 0.2	0.4 ^b \pm 0.2
Water holding capacity (pF 2.3)	g H ₂ O.g dry soil	0.14 ^b \pm 0.1	0.75 ^a \pm 0.4
Cd		0.2 ^a \pm 0.3	0.4 ^a \pm 0.1
Cu		28.5 ^a \pm 20.0	41.1 ^a \pm 8.8
Pb	mg.kg ⁻¹	55.9 ^a \pm 42.0	56.2 ^a \pm 15.2
Zn		226.7 ^a \pm 202.2	251.2 ^a \pm 122.8

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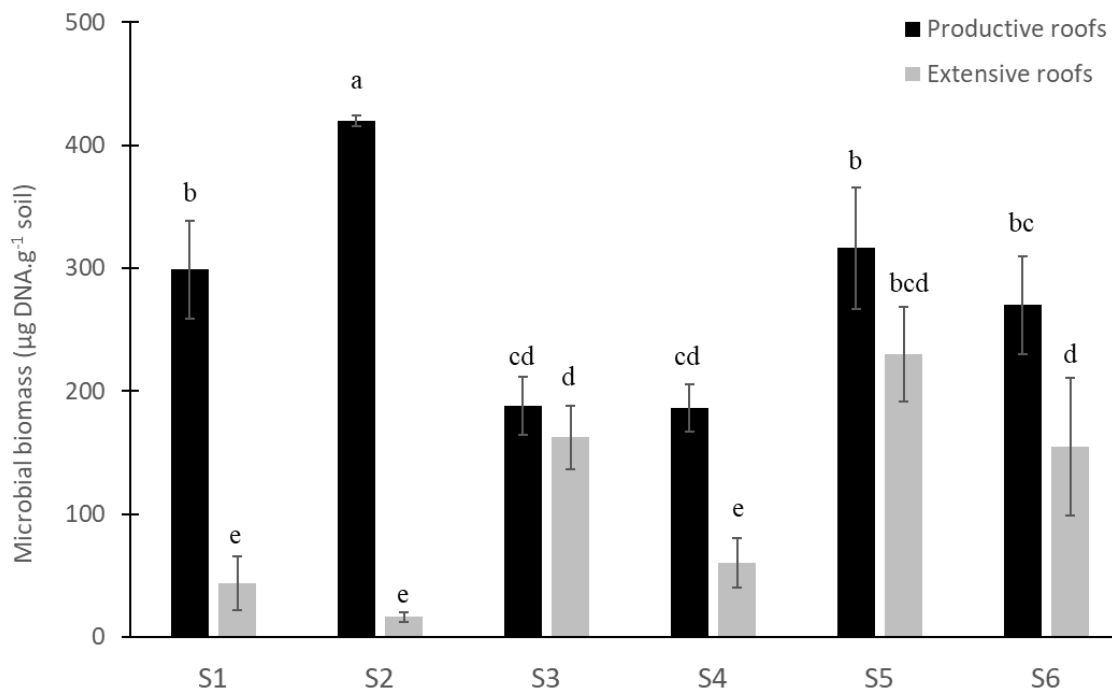
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Table 3. Taxonomic diversity indices (mean +/- standard deviation) of microbial, nematodes, collembolan and plant communities in the 12 green roofs surveyed. Lower case letters indicate significant differences among green roofs type (alpha = 0.05)

		Extensive (n=6)	Productive (n=6)
Bacteria	Total number of OTU	9003	8060
	Mean OTU richness	1410 ± 72	1377 ± 71
	Abundance (10¹⁰ copies of 16S.g⁻¹)	2.9 ^b ± 2.8	5.3 ^a ± 1.2
	Shannon diversity index	5.6 ± 0.2	5.6 ± 0.2
	Evenness index	0.8 ± 0.1	0.8 ± 0.1
Fungi	Total number of OTU	16 826	14 661
	Mean OTU richness	1434 ± 170	1359 ± 164
	Abundance (10⁹ copies of 18S.g⁻¹)	2.5 ± 2.1	3.2 ± 1.8
	Shannon diversity index	4.7 ± 0.4	4.8 ± 0.3
	Evenness index	0.6 ± 0.1	0.7 ± 0.1
Nematodes	Total number of families	18	27
	Mean number of families	8.3 ^b ± 2.7	13.3 ^a ± 3.4
	Abundance (10³ individuals.kg⁻¹)	13.2 ^b ± 22.9	33.9 ^a ± 14.8
	Shannon diversity index	1.5 ± 0.4	1.7 ± 0.6
	Evenness index	0.7 ± 0.2	0.7 ± 0.2

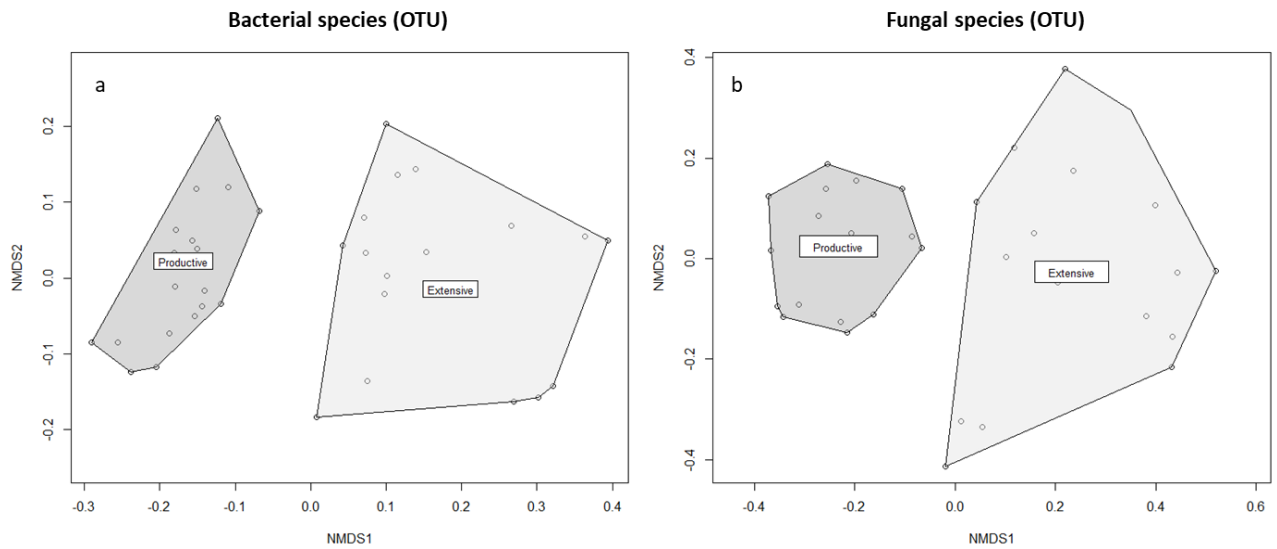
Collembola	Total number of species	36	33
	Mean number of species	14.5 ± 3.7	12.0 ± 3.5
	Density (10³ individuals.m⁻²)	31 ± 19	90 ± 78
	Shannon diversity index	2.0 ± 0.3	1.5 ± 0.7
	Evenness index	0.8 ± 0.1	0.6 ± 0.2
Cultivated plants	Total number of species	2	14
	Mean number of species	0.5 ± 0.5	2.8 ± 1.9
Spontaneous Plants	Total number of species	32	25
	Mean number of species	8.8 ± 5.0	5.3 ± 3.0

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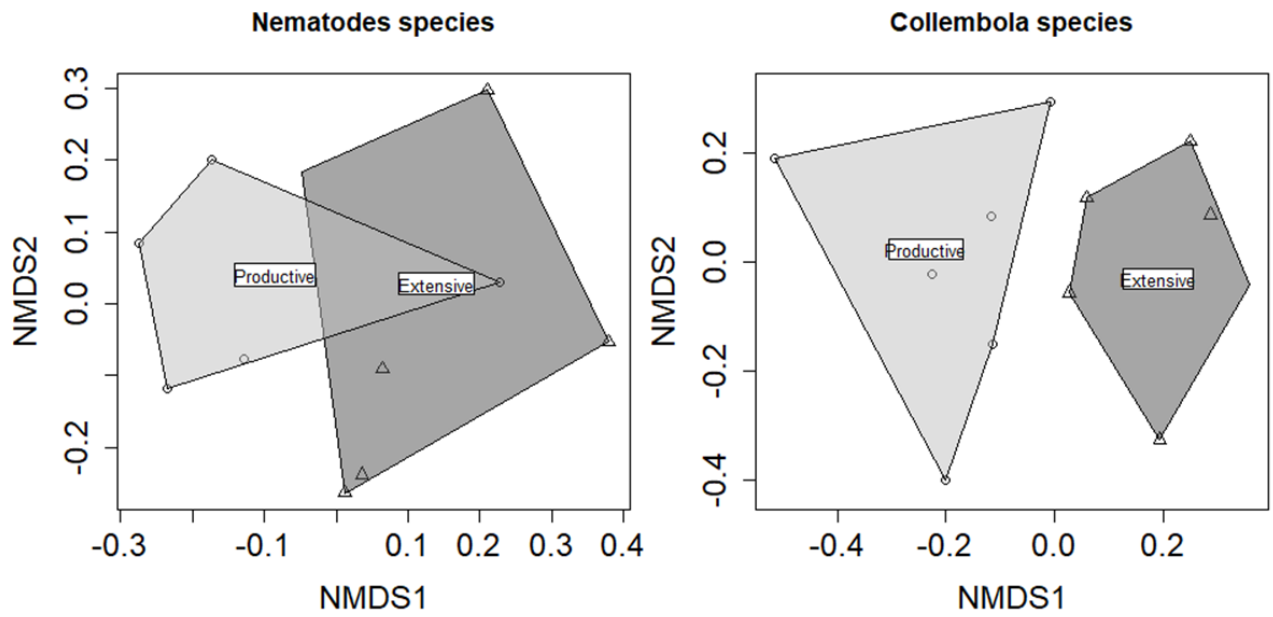


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797 **Figure 1.** Microbial biomass in the 12 green roofs surveyed. Lower case letters indicate
798 significant differences between green roofs type ($\alpha = 0.05$)
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803 **Figure 2.** Graphic displaying the first two axes of the non-metric multidimensional scaling
804 (NMDS) on bacterial (a) and fungal (b) composition (OTU) in green roofs.
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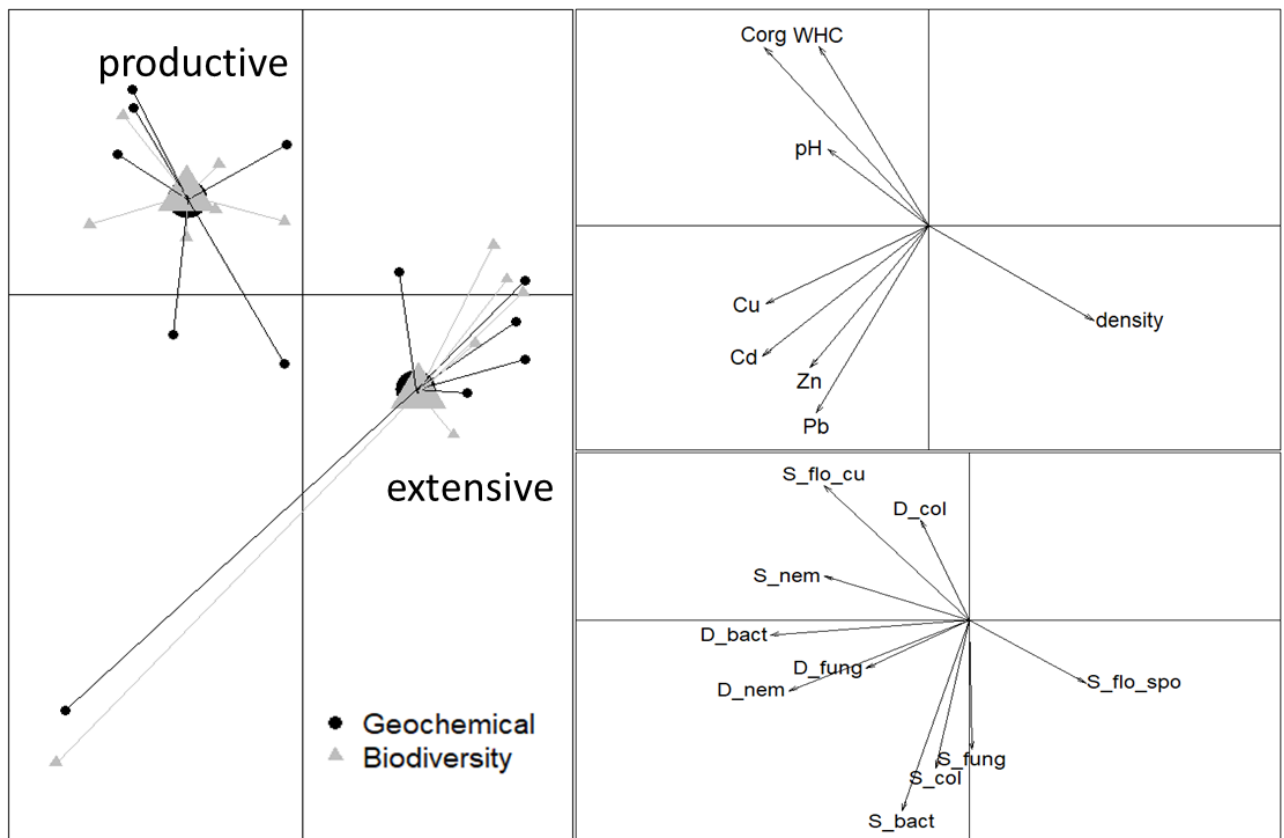


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808 **Figure 3.** Graphic displaying the first two axes of the non-metric multidimensional scaling

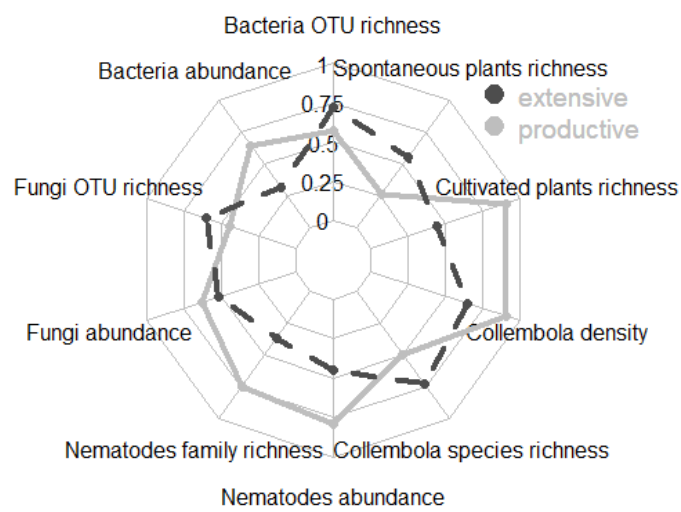
809 (NMDS) on nematodes and Collembola composition in green roofs.

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812 **Figure 4.** Co-inertia analysis of geochemical (circles) and biodiversity (triangles) parameters
 813 of the 12 green roofs. The biggest triangles and circles are barycenters. Corg : organic carbon;
 814 WHC : water holding capacity; Cd, Cu, Pb and Zn = Total metal contents; S: species richness
 815 for Collembola –Col-, spontaneous plants – flo_spo, cultivated plants – flo_cul, Fungi –fung-
 816 and bacteria –bact); Plant = plant and D_: abundance or density for each groups except for
 817 plants.
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 820 **Figure 5.** Radar plot illustrating mean abundance and diversity of microbial, faunal and plant
 821 groups according to the two types of green roofs. 0 corresponds to the minimal value and 1 to
 822 the maximal value recorded in green roofs from Paris and his region.
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