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One green roof type, one Technosol, one ecological community

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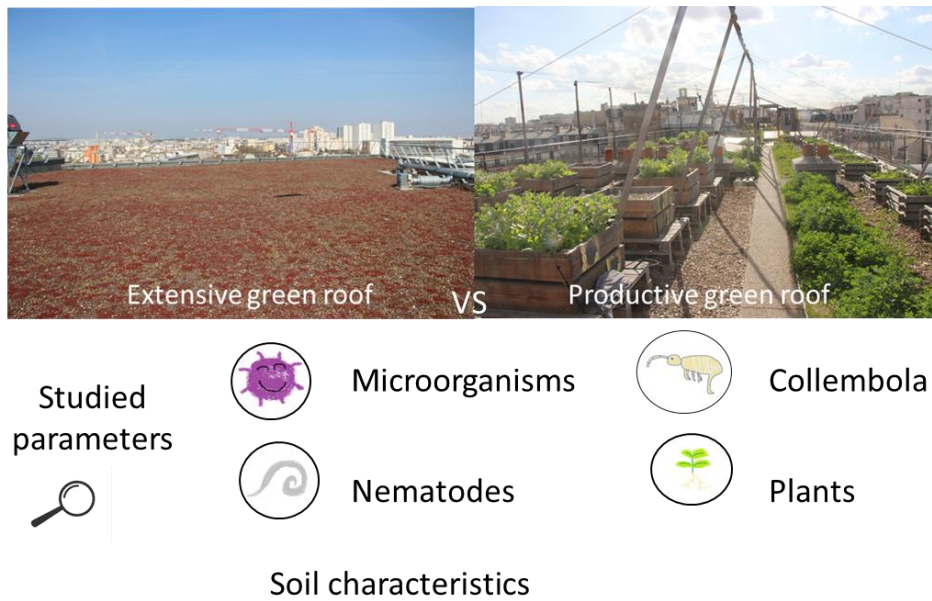
Abstract

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. Introduction

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

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

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

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

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

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

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

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

2. Materials and Methods

2.1. Studied sites

We selected 12 rooftops (ca 35 m above ground) located in the dense urban environment of the Paris region (Ile-de-France, France), six extensive green roofs and six productive green roofs (Table 1). According to the “Green Roofing Guideline”, these green roofs were classified according to three criteria: Technosol’s depth, main function of the roof and presence/absence of an irrigation systems (The Roof Greening Working Group, 2002). Extensive green roofs were characterised by a thin layer (8 to 10 cm-depth) and coarse substrate (typically pozzolan), were not irrigated and mostly covered with ornamental succulent species (*Sedum sp.* mostly). These species were introduced initially at green roofs construction. Others plants species can thus colonize the green roofs. Productive green roofs were characterized by grown vegetables covering more than 50% of their surface area, a thick layer of Technosol (20 to 30 cm of depth) and high organic matter contents (presence in the Technosols of compost, spent mushroom substrate, shredded wood, potting soil). Extensive and productive green roof surface areas were *circa.* 390 m² and 270 m².

2.2. Sampling methods

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

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

2.2.1. Microbiological sampling and analysis

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

Molecular microbial biomass

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

Molecular analyses of soil bacterial and fungal communities

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

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

2.2.2. *Nematode sampling and identification*

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

2.2.3. *Collembola sampling methods and identification*

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

2.2.4. *Plants identification*

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

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

2.2.5. *Soil sampling and physicochemical analyses*

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

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

2.3. **Community indices**

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

2.4. Statistical analyses

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

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

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

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

3. Results

3.1. Chemical and physical soil characteristics

Mean organic C contents were significantly lower in extensive roofs (7.8 g kg^{-1}) compared to productive roofs (21.0 g kg^{-1}) (Table 2). pH was slightly alkaline with values ranged from 7.3 (extensive roofs) to 7.6 (productive roofs). No significant difference was observed between green roof types for metal concentrations. Extensive green roofs retained significantly less water ($0.14 \text{ g H}_2\text{O g}^{-1}$ of dry soil) than productive ones ($0.75 \text{ g H}_2\text{O g}^{-1}$ of dry soil) at pF 2.3 and their bulk density was very low, but higher in extensive roofs (0.8 g cm^{-3}) compared to productive roofs (0.4 g cm^{-3}).

3.2. Community structures and composition

3.2.1. Microorganisms

Microbial biomass ranged between 16.3 and $419.8 \text{ } \mu\text{g DNA g}^{-1}$ soil (Figure 1) and was significantly higher in productive roofs ($279.9 \pm 29.3 \text{ } \mu\text{g DNA.g}^{-1}$ soil) than in extensive roofs ($111.3 \pm 27.7 \text{ } \mu\text{g DNA g}^{-1}$ soil). Fungi/bacteria ratios varied from 3.2 to 13.9 and were lower for the productive roofs (6.4 ± 1.3) than the extensive ones (8.8 ± 2.3). No significant difference was observed between the two types of roofs concerning specific richness, Shannon and evenness indices for bacteria and fungi (Table 3).

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

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

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

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

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

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

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

(36.9% in productive roofs and 50.1% in extensive ones). Few differences were observed between productive and extensive roofs, and mainly for the 20% minority phyla.

Sixty-five fungal genera were present at least once in the soil samples and 34 were present in all samples. More than 50% of fungi were unknown or unclassified (Figure S4). The most prevalent fungal genus was *Lojkania* (11.5 in productive roofs and 24.4% in extensive ones). *Batrachochytrium* represented 8.9 and 7.0% in productive and extensive roofs respectively. Many genera were poorly represented (42<0.1%).

A total of 33 559 different fungal OTU was quantified considering all soil samples, corresponding to means of 1359 ± 164 fungal OTUs in productive roofs and 1434 ± 170 in extensive ones. Thirteen and nine OTU were dominant (>1%) in productive and extensive roofs (Table S2). Some of them correspond to unknown fungi. Others were Ascomycota (*Hypocrea*, *Verticillium*, *Leptosphaeria*, *Lojkania*, or unclassified), Basidiomycota (unclassified) and Chytridiomycota (*Batrachochytrium*).

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

3.2.2. Nematodes

A total of 28 nematodes families was present in the Technosol of the six productive and six extensive green roofs (Table 3, Table S3). The number of families varied from 5 to 18 taxa per roof. Total nematodes abundances in soil samples ranged from circa 820 to 60 700 individuals.kg⁻¹ and were significantly different between extensive and productive green roofs. No significant difference was showed for Shannon and Eveness indices.

The factorial map of the NMDS revealed marked significant differences in nematodes communities between green roof types, along both axes 1 and 2 (Figure 3, ANOSIM,

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

3.2.3. Collembola

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

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

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

4. Discussion

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

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

Microorganisms

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

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

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

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

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

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

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

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

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

Nematodes

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

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

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

Collembola

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

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

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

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

Plants

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

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

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

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

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

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

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

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

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

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

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

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

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

4.3. Synthetic approach

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

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

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

5. Conclusion

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

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

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

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The raw data of 16S and 18S sequencing were deposited to SRA under the following bioproject PRJNA726534 and analysed results with GnS-PIPE are available (<https://nextcloud.inrae.fr/s/8Ttr4sFDyPY3tDA>)

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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

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)	$\text{g H}_2\text{O.g dry soil}$	$0.14^b \pm 0.1$	$0.75^a \pm 0.4$
Cd	mg.kg^{-1}	$0.2^a \pm 0.3$	$0.4^a \pm 0.1$
Cu		$28.5^a \pm 20.0$	$41.1^a \pm 8.8$
Pb		$55.9^a \pm 42.0$	$56.2^a \pm 15.2$
Zn		$226.7^a \pm 202.2$	$251.2^a \pm 122.8$

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 (10 ¹⁰ 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 (10 ⁹ 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 (10 ³ 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 (10 ³ 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
Cultivate d plants	Total number of species	2	14
	Mean number of species	0.5 ± 0.5	2.8 ± 1.9
Spontann eous Plants	Total number of species	32	25
	Mean number of species	8.8 ± 5.0	5.3 ± 3.0

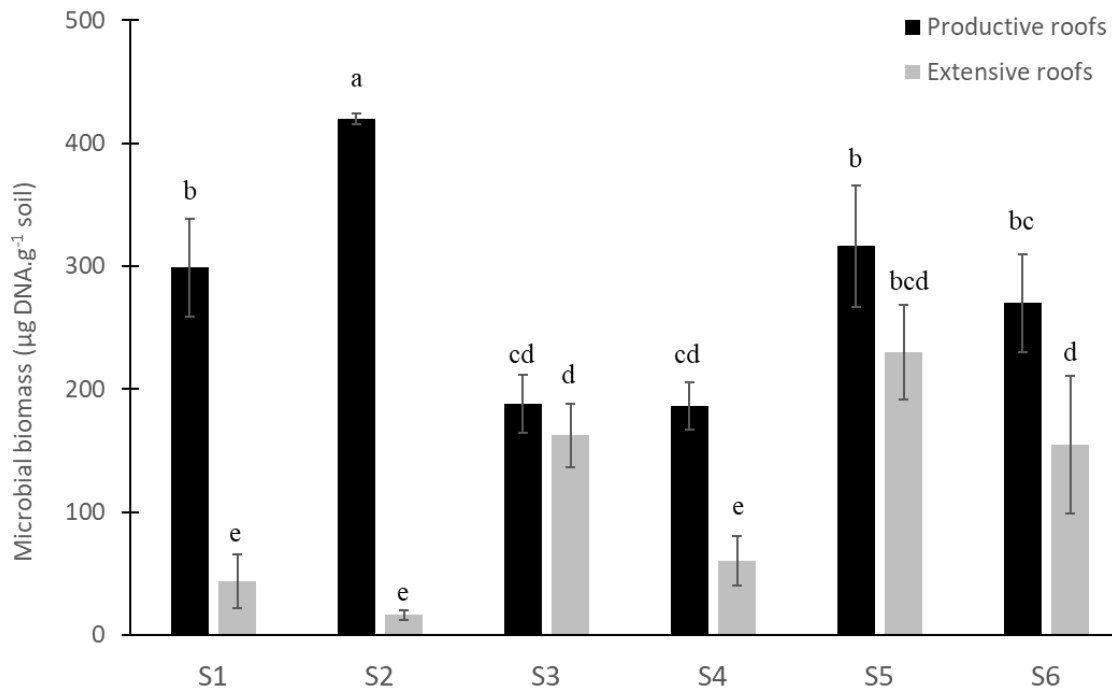


Figure 1. Microbial biomass in the 12 green roofs surveyed. Lower case letters indicate significant differences between green roofs type ($\alpha = 0.05$)

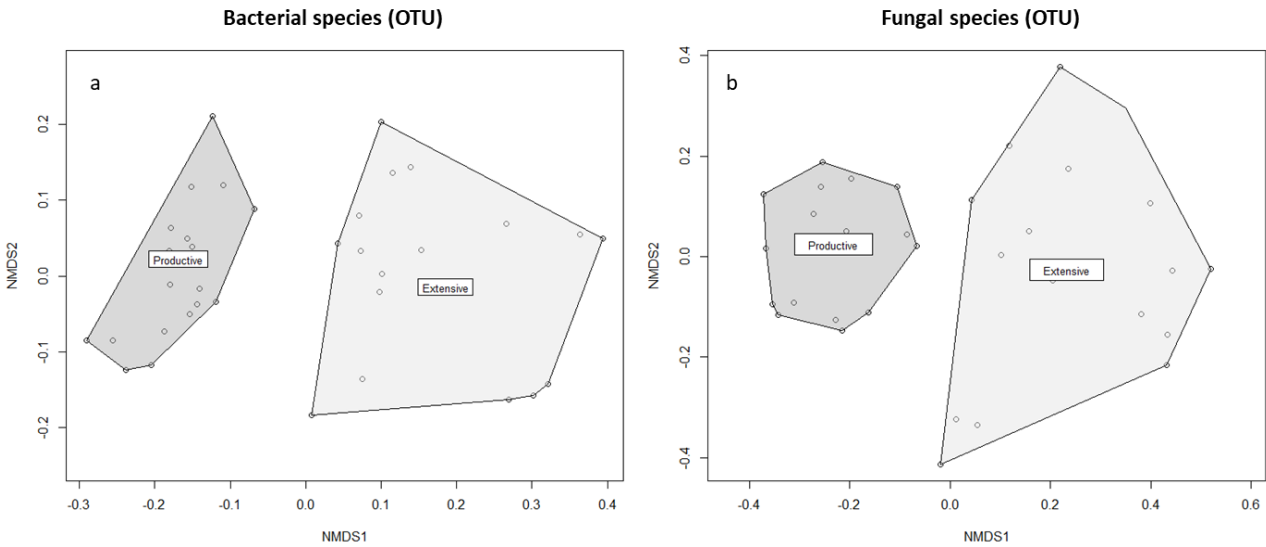


Figure 2. Graphic displaying the first two axes of the non-metric multidimensional scaling (NMDS) on bacterial (a) and fungal (b) composition (OTU) in green roofs.

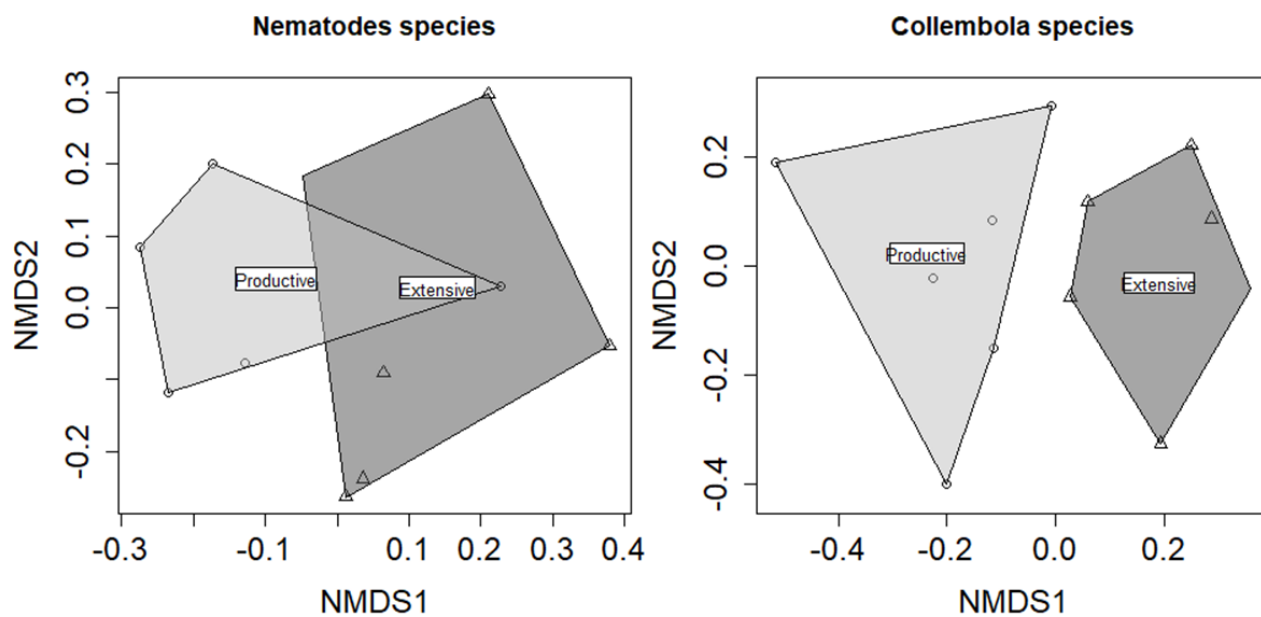


Figure 3. Graphic displaying the first two axes of the non-metric multidimensional scaling (NMDS) on nematodes and Collembola composition in green roofs.

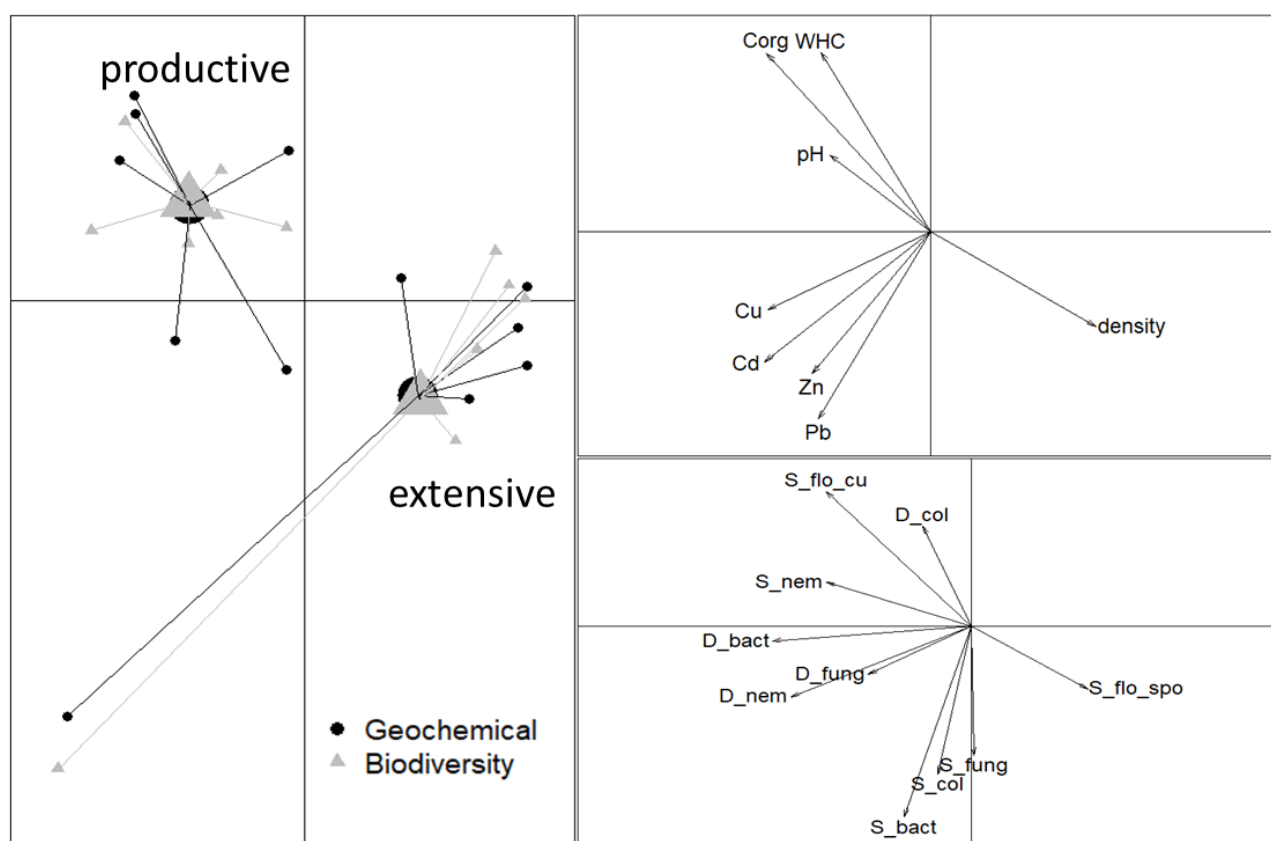


Figure 4. Co-inertia analysis of geochemical (circles) and biodiversity (triangles) parameters of the 12 green roofs. The biggest triangles and circles are barycenters. Corg : organic carbon; WHC : water holding capacity; Cd, Cu, Pb and Zn = Total metal contents; S: species richness for Collembola –Col-, spontaneous plants – flo_spo, cultivated plants – flo_cul, Fungi –fung- and bacteria –bact); Plant = plant and D_: abundance or density for each groups except for plants.

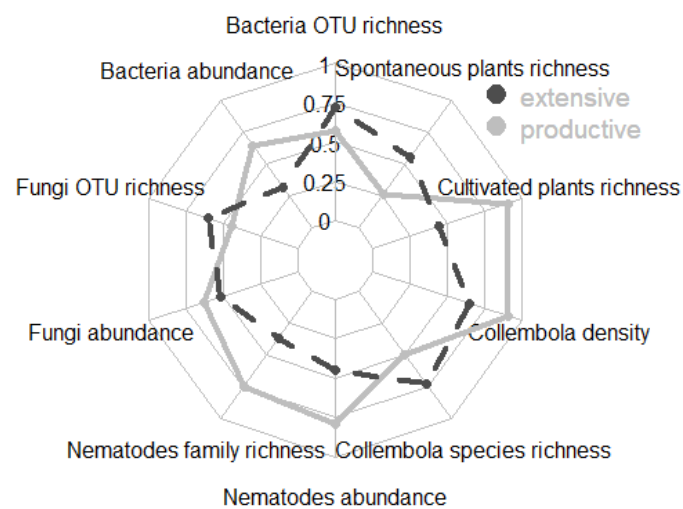


Figure 5. Radar plot illustrating mean abundance and diversity of microbial, faunal and plant groups according to the two types of green roofs. 0 corresponds to the minimal value and 1 to the maximal value recorded in green roofs from Paris and his region.