



Contrasting homogenization patterns of plant and collembolan communities in urban vegetable gardens

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Abstract

Urban biotic homogenization is one of the foremost challenges for conservation of biodiversity in urban green areas. Urban gardening is a common practice in many industrialised and developing countries. The ability of urban vegetable gardens to support biodiversity, however, has yet to be studied in depth. To investigate the responses of flora and soil fauna to urbanization, we surveyed the taxonomic and functional composition of plant and collembolan communities, in addition to soil parameters, in 15 urban vegetable gardens across three large French cities. The vegetation was identified in six plots of 1 × 1 m in each urban vegetable garden and collembolan were extracted from one intact soil core sampled in the center of each plot (5 cm depth, 6 cm diameter). We found contrasting effects of urbanization on plants and Collembola biodiversity. The taxonomic and functional composition of the soil fauna was more similar within cities than among cities, which was driven by similarities in soil parameters. In contrast, plant communities were functionally similar among cities. Understanding the effects of urbanization on soil biodiversity could have implications for the management of urban ecosystems, in particular that of urban soils.

Keywords Urban soil · Soil biodiversity · Functional diversity; functional trait · Plant community · Urban biodiversity conservation

Introduction

As human activities worldwide have widely modified the abiotic environment, the resulting habitat homogenization has raised new concerns for biodiversity conservation, namely

biotic homogenization. Biotic homogenization refers to the process by which genetic, taxonomic or functional similarities of regional biota increase (Olden and Rooney 2006). It may occur through two non-mutually exclusive processes – together described as an “anthropogenic blender” (Olden 2006): a

Highlights

- Plant communities undergo homogenization in urban vegetable gardens
- Neither taxonomic nor functional homogenization of collembolan communities was found
- Soil parameters drive heterogeneity of the soil fauna in urban vegetable gardens

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replacement of native species by a limited set of widely successful exotic species, and a loss of local habitat or resource specialists in favour of common generalists. Multiple studies have revealed patterns of biotic homogenization in different regions of the world (see Baiser et al. 2012 and references therein), but not consistently so (Castro and Jaksic 2008). Despite sustained interest in the topic in the last two decades (Olden et al. 2016), the process of biotic homogenization and its implications for biodiversity conservation are far from resolved.

Whether or not one detects biotic homogenization depends to some extent on what dimension of biodiversity is considered. In fact, taxonomic homogenization does not necessarily imply functional homogenization, and vice versa (Olden 2006). Species assemblages might become both taxonomically and functionally more similar across locations when just a small set of widespread species take advantage of widely simplified ecosystems and fill the same few niches in various locations. Alternatively, if a regional species pool includes several functionally redundant species, functional homogenization may occur while local assemblages remain taxonomically dissimilar. There could even be functional homogenization and taxonomic differentiation, if distinct exotic species sharing similar traits establish in different locations. Taxonomic homogenization has so far received far more attention than functional homogenization (Olden 2006). Although both components of biotic homogenization are relevant for biodiversity conservation and ecosystem function, they do not provide the same information. Taxonomic homogenization points to an overall loss of species richness, while functional homogenization indicates a simplification of the whole ecosystem, which could eventually jeopardise the provision of ecosystem services. Thus, tackling biotic homogenization and its long-term consequences requires distinguishing and encompassing both taxonomic and functional dimensions of biodiversity.

Urbanization is considered an important potential driver of biotic homogenization (McKinney 2006). Indeed, urban areas play as major hubs for the introduction of exotic species, many of which benefit from high levels of disturbance to establish and spread, sometimes to the detriment of native species (McKinney 2006). Moreover, urbanization results in the destruction of natural habitats, thus causing the extirpation of species highly specialized to those habitats. Because remaining habitats are highly fragmented, profoundly altered, and frequently disturbed, ultimately urbanization only allows the persistence of a limited set of common, generalist species with broad ecological requirements and high tolerance to disturbance (McKinney 2008). Despite the recognition of the role likely played by urbanization, biotic homogenization in urban areas has received limited scrutiny and has remained largely focused on the flora (e.g. Kühn and Klotz 2006; Schwartz et al. 2006; Gong et al. 2013) and the avifauna (e.g.

Clergeau et al. 2006; Devictor et al. 2007; Luck and Smallbone 2011).

The effects of urbanization on biodiversity vary substantially across taxonomic groups (Olden 2006; McKinney 2008). Local species assemblages depend on a combination of ecological ‘filters’ (Keddy 1992; Weiher and Keddy 1999; Lortie et al. 2004): abiotic conditions, biotic interaction, and species dispersal. The importance of biotic versus abiotic filters is likely to depend on the taxa considered. In particular, because most animals can behaviourally achieve non-random dispersal into more suitable habitat patches, they may exhibit different responses to urbanization compared to plants, which may in turn influence patterns of biotic homogenization. Furthermore, the main pathways (i.e., deliberate vs. unintentional) for the introduction of exotic species differ among taxonomic groups, which may also influence patterns of biotic homogenization. Soil biota, despite playing a critical role in ecosystem functioning, have rarely been surveyed in urban areas (but see Magura et al. 2010; Horsak et al. 2013; Milano et al. 2018), and to the best of our knowledge never been checked for biotic homogenization. Urban soils are typically not well-structured, often form a heterogeneous mixture of in-situ soil and imported soil, may be nutrient-enriched through the addition of compost in gardens and parks, and may be polluted with various compounds such as heavy metals (Joimel et al. 2016). While contrasting climates may filter species assemblages that are taxonomically dissimilar among regions, greater similarities in urban soil conditions may on the other hand select plant and soil biota assemblages that are functionally similar across urban areas. Although extensive evidence shows tight links between belowground and aboveground components of biodiversity (Wardle et al. 2004), whether soil biota display the same patterns of biotic homogenization as their well-studied plant counterparts has yet to be assessed.

Urban areas typically form a mosaic of various habitat types, which differ in the degree to which they are subject to anthropogenic disturbances and management practices, and therefore in the biodiversity they can harbour. Gardens typically occupy a non-negligible fraction of the total surface of urban areas (19–27%, Perry and Nawaz 2008), yet they long received little attention compared to urban forests, wastelands, or large urban parks. In the last two decades, however, a significant body of research has highlighted how domestic gardens may contribute to preserve urban biodiversity (Goddard et al. 2010). Allotment gardens, in contrast, have remained largely overlooked (but see Borysiak et al. 2017; Cabral et al. 2017; Speak et al. 2015). Because allotment gardens usually have a function of food production, they require gardening practices that ensure low levels of competition from wild plants and of damage from wild herbivores, and still sustain a healthy ecosystem compatible with vegetable growth. This particular feature, together with their social

importance (including attitude towards nature) (Middle et al. 2014), and their growing popularity in both developed and developing countries (Guitart et al. 2012), makes allotment gardens a relevant place to assess biodiversity and patterns of biotic homogenization.

In this study, we examined to what extent urban plant and soil biota assemblages were determined by climatic and/or edaphic conditions, and whether they were undergoing taxonomic and/or functional homogenization. We carried out a field study in 15 parcels of allotment gardens located in three large French cities with contrasting climates (continental, oceanic, and Mediterranean). Of all the taxonomic groups belonging to the soil fauna, we focused on Collembola because they have been highlighted as relevant bio-indicators of human activities (Cortet et al. 1999; Fiera 2009) and because they are critical for ecosystem functioning due to their position at the base of the food chain and their determinant role as detritivores for soil quality (Potapov and Tiunov 2016). Specifically, we hypothesised that communities might differ taxonomically between cities as a result of filtering from distinct regional pools of climatically suited species, but should not differ functionally because similar pressures associated with urbanization should select the same set of traits. In other words, we expected functional, but not taxonomic homogenization of both plant and collembolan communities.

Material and methods

Study gardens

We studied 15 urban vegetable gardens, representative in terms of variability of practices and environment, and situated in three French cities (five gardens per city). The 15 gardens were selected from a pool of 104 urban vegetable gardens previously surveyed for their physicochemical characteristics and gardening practices (Joimel 2015; Joimel et al. 2016). Gardens from this pool were chosen to assess the variability of gardens in different urban contexts under contrasting climates, thereby allowing the investigation of the variation in age, plot size and gardeners (Chenot et al. 2012). Within the pool of 104 gardens, the smaller group of 15 was selected according to three criteria: variability of urban practices (pesticides and use of rototiller), climate and size. Only gardens of between 100 and 200 m² were selected, to avoid the potentially confounding effect of garden size.

The main French climates were represented (Fig. 1). The Grand Nancy (Greater Nancy) area is located in north-eastern France, and is characterized by a semi-continental climate, with a strong temperature contrast between warm, humid summers and cold, snowy winters (min 6 °C – max 14.9 °C

monthly averages). Nantes is located in western France, close to the Atlantic Ocean, and is characterized by an oceanic climate, with moderate contrast between mild, rainy winters and cool, humid summers (min 8.3 °C – max 16.7 °C). Annual rainfall is low, but rainfall is regular throughout the year. Marseille is located in south-eastern France, on the Mediterranean coast, and is characterized by a Mediterranean climate, with warm, dry summers preceded and followed by two mild, wet seasons (min 10.8 °C – max 20.2 °C).

Collembola and plant sampling

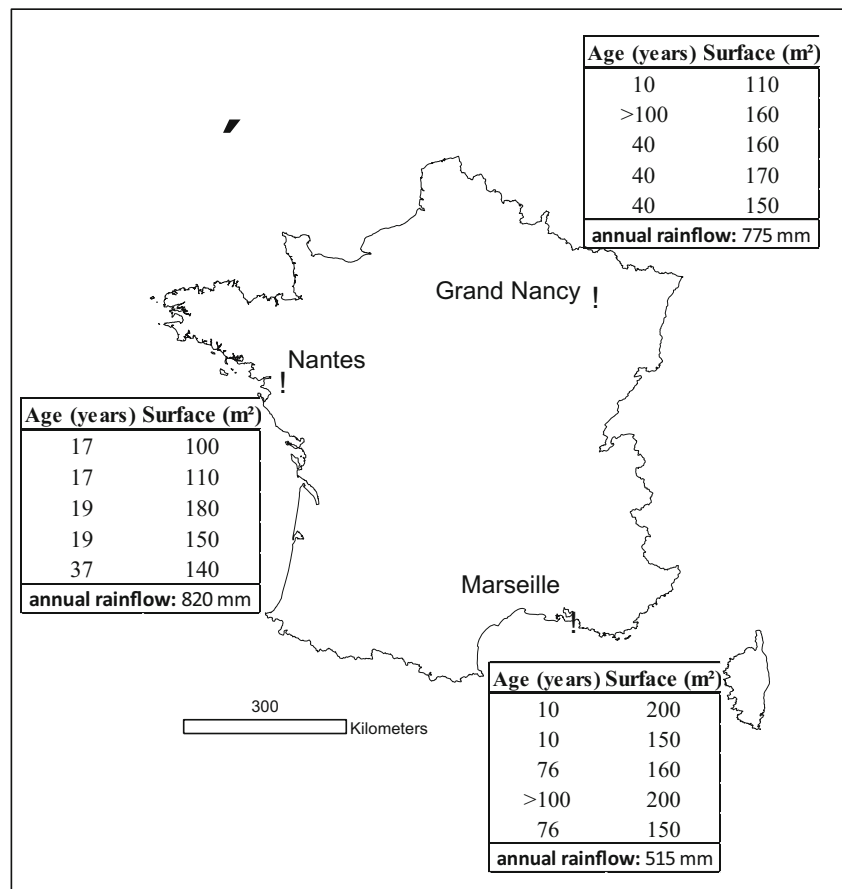
We made collections in three consecutive weeks in Spring 2013. In each urban vegetable garden, six plots of 1 × 1 m were randomly located in the area that was cultivated (i.e. excluding hedges or paths), at least 1 m from the border to avoid edge effects. In each plot, all spontaneous vascular plants, i.e. those growing and reproducing without human assistance (Bossu et al. 2014), were identified at species level using identification keys (Bonnier and de Layens 1986; Schauer and Caspari 2013) and their relative abundance was estimated using the Braun-Blanquet cover-abundance scale and then transformed to the ordinal scale.

In addition, one intact soil core was extracted from the centre of each plot (5 cm depth, 6 cm diameter). Collembola were then extracted from each soil core using a high-gradient McFadyen extractor for one week (ISO 23611-2 2006; Cluzeau et al. 2012). They were then identified to species level using dichotomous identification keys (Potapov 2001; Thibaud et al. 2004; Fjellberg 2007; Hopkin 2007). The taxonomic referential used for collembolan and plants was TaxRef (Gargominy et al. 2017).

To assess the functional homogenization of plant and collembolan communities, we collected data for eight functional traits for Collembola and five for plants (Table 1). Some of these traits are related to reproduction (reproduction type, fruit type), dispersal (pollen vector, furcula length) or persistence (life form, strategy type). Strategy type is also an integrative trait, which provides information about their ability to survive in a more or less stressful environment.

Collembolan trait data were taken from the BETSI database (Biological and Ecological functional Traits of Soil Invertebrates – CESAB/FRB) (Pey et al. 2014a). Plant trait data were sourced from the BioFlor database (Trait Database of the German Flora: <http://www.ufz.de/biolflor>). Traits were split into attributes by a fuzzy coding approach (Pey et al. 2014b). Attributes were not always exclusive, but may present affinity scores for each trait of one functional trait. In the case of Collembola, such data transformation allows values to be computed for functional traits derived from a variety of

Fig. 1 Location and characteristics of the 15 urban vegetable gardens in France



sources, mainly arising from identification keys (such as Gisin 1943; Potapov 2001; Hopkin 2007).

Soil parameters

In each garden, twenty subsamples of cultivated topsoil (0–20 cm) were collected in autumn 2012 to cover the totality and heterogeneity of the cultivated area. All subsamples from a given garden were mixed and homogenized to obtain a single representative sample for that garden. Soil samples were then air-dried, disaggregated and sieved at 2 mm. Soil analyses were performed by a certified laboratory for soil analysis (Laboratoire d'analyse des sols-INRA, Arras, France), according to the following standard methods: total metals after HF dissolution (Cd, Cu, Pb and Zn; extraction HF; NF EN ISO 17294-2, NF ISO 22036), pH (NF ISO 10390), organic carbon (C) and total nitrogen (N) (NF ISO 10694), available phosphorus (P_{Olsen}) for plants (Olsen method; NF ISO 11263), particle size (silt, clay and sand, NF W 31–107) and cationic exchange capacity (Metson method, NF X 31–130). The ratio of C to N (C/N), Cationic exchange capacity (CEC), pH and P_{Olsen} were selected as indicators of soil chemical

fertility, particle size as an indicator of soil physical fertility and Cu, Ni, Pb and Zn total concentrations as indicators of metal contamination. These metals are often associated with human activities and are representative for toxic and/or nutritive elements (Joimel et al. 2016).

Diversity indices

Collembolan and plant communities were described by their species richness (mean number of species per plot). In addition, relative abundance data were used to calculate the Shannon diversity index and the evenness index for each plot.

Collembolan communities were described by their density in each plot (abundance per m²). To capture different facets of community functional trait-based diversity, we calculated four distance-based functional diversity indices and the community weighted mean (CWM) for each functional trait. Functional richness represents the volume of the functional space occupied by the community. Functional evenness corresponds to the regularity of the distribution of species abundance in this volume. Functional divergence is that observed in the distribution of abundance in this volume (Mason et al. 2005;

Table 1 List of collembolan and plant functional traits, and their respective attributes

	Trait	Attribute
Collembola	Body shape	Spherical; Cylindrical
		Body length
	0.5–1 mm	
	1–1.5 mm	
	1.5–2 mm	
	2–3 mm	
	3–4 mm	
	> 4 mm	
	Furcula length	Absent or vestigial furcula
		Reduced or short furcula
	Pigmentation	Long furcula
		Pigmented; Unpigmented
	Post-antennal organ	Absent; Present
Visual organ	Without ocelli	
	1 + 1 to 2 + 2 ocelli	
	3 + 3 to 5 + 5 ocelli	
Reproduction type	8 + 8 ocelli	
	Parthenogenetic; Sexual	
Scales	Present; Absent	
Plant	Life form (Raunkiaer system)	Geophyte
		Hemicryptophyte
		Therophyte
	Reproduction type	Sexually, by seed/spore; vegetatively
	Fruit type	Legume
		Capsule
		Nut
		Aggregate nutlets
		Silique
	Strategy type	Schizocarp
Competitor		
Ruderal		
Pollen vector	Stress-tolerator	
	Wind	
	Selfing	
		Insects

Laliberte and Legendre 2010). Functional dispersion is the mean distance from the barycentre of all species in this volume (Laliberte and Legendre 2010). CWM is the mean of trait attribute values weighted by the relative abundances of species bearing each value (Kleyer et al. 2012). Each possible attribute for each trait is considered as a variable. CWM values were gathered onto a single matrix for each taxonomic group (42 taxa × 18 CWM for plants, 53 taxa × 24 CWM for collembolan). Furthermore, in to measure beta diversity, we calculated the Jaccard dissimilarity between each pair of gardens among cities as: $A + B - 2J / (A + B - J)$, where A and B are the numbers of species that occur on either site, and J is the

number of species that occur on the two sites compared. The J distance ranges from 0 (100% similarity) to 1 (no similarity).

Data analysis

Neither taxonomic nor functional indices matched the assumptions of normality and homoscedasticity required for parametric statistics, so we used Wilcoxon Rank-Sum tests to assess differences in abundance, species richness, and indices of functional diversity between the three cities. To explore differences between cities in taxonomic and functional composition of collembolan and plant communities, we performed

non-metric multidimensional scaling (NMDS) using the Bray-Curtis dissimilarity index. To avoid auto-correlation in analysis of functional composition, only one attribute was used in the NMDS for binary attributes. Differences in species or trait assemblages between cities were tested by permutational analysis of similarities (ANOSIM). To evaluate the effects of soil parameters (C/N, pH, CEC, P_{Olsen} , Cu, Cd, Pb, Zn, silt, clay and sand content) on functional composition of plant and collembolan communities, these were fitted a posteriori to the NMDS space with generalized additive models (GAMs), using the restricted maximum likelihood estimation (REML) method (Marra and Wood 2011), as done by Milano et al. (2017). All statistics were performed using R software version 3.2.2 (R Core Team 2015), “FD” packages (Laliberté and Shipley 2011) and “vegan” (Oksanen et al. 2014).

Results

Geochemical parameters of urban vegetable garden soils

Mean pH was mostly neutral with values comprised between 6.8 and 7.9, and was significantly 16% higher in Marseille than in Nantes (Table 2). No significant differences were observed between cities for P_{Olsen} . Mean CEC was the 2.4 times lowest in Nantes (6.4) compared to the Grand Nancy Area (21.9), with significant differences between Nantes and the other two cities. For C/N, values ranged from 11.7 (Grand Nancy) to 15.3 (Nantes). On average, the highest soil metal concentrations were observed in Marseille (between 1.5 and 2.1 times higher than Nantes), except for Cu, which was

Table 2 Soil geochemical parameters (mean \pm standard deviation) in the 15 urban vegetable gardens surveyed (5 gardens per city)

Soil parameter	Unity	Grand Nancy	Marseille	Nantes
pH		7.4 ^{ab} \pm 0.1	7.9 ^a \pm 0.2	6.8 ^b \pm 0.6
P_{Olsen}	g kg ⁻¹	0.18 \pm 0.03	0.31 \pm 0.21	0.15 \pm 0.06
CEC	cmol kg ⁻¹	21.9 ^a \pm 10.2	13.4 ^a \pm 3.7	6.4 ^b \pm 1.9
C/N		11.7 ^b \pm 0.9	14 ^a \pm 1.3	15.3 ^a \pm 1.1
Cd	mg kg ⁻¹	0.3 \pm 0.1	0.4 \pm 0.2	0.2 \pm 0.1
Cu		34.1 \pm 6.4	48.2 \pm 22.0	93 \pm 128.0
Pb		52.2 \pm 23.4	62.3 \pm 26.2	43.1 \pm 4.8
Zn		138.1 \pm 38.8	154.4 \pm 90.4	71.7 \pm 10.0
Sand	%	21.1 ^b \pm 20.2	39.6 ^a \pm 18.6	71.2 ^a \pm 4.4
Silt		38.1 ^a \pm 10.4	29.2 ^{ab} \pm 10.1	20.4 ^b \pm 2.5
Clay		40.8 ^a \pm 22.3	31.2 ^a \pm 9.8	8.4 ^b \pm 2.3

Lower case letters indicate significant differences among cities (alpha = 0.05). P_{Olsen} available phosphorus, CEC Cationic exchange capacity, C/N organic carbon on total nitrogen, Cd Cadmium, Cu Copper, Pb Lead, Zn Zinc

higher in Nantes (between 2 and 2.7 higher than Marseille and Grand Nancy). However, none of the differences observed in metal concentrations were significant. Finally, concerning soil texture, Marseille exhibited mostly clay loam soils, Nantes had sandy loam soils, and Grand Nancy presented more varied soils, such as sandy loam, clay loam, silty clay, and clay soils.

Taxonomic composition of collembolan and plant communities

A total of 53 collembolan species belonging to 11 families were collected from urban vegetable garden topsoils (Table S1). The most abundant species in Grand Nancy were *Isotomurus palustris* (Müller, 1776) (16%) and *Isotomiella minor* (Schaeffer, 1896) (10%), which occurred in all five urban vegetable gardens, as did *Lepidocyrtus lanuginosus* (Gmelin, 1788) (7%). In Marseille, *Proisotoma minuta* (Tullberg, 1871) (23%) and *Ceratophysella gibbosa* (Bagnall, 1940) (8%) were the most abundant and frequent species, including *Protaphorura armata* (Tullberg, 1869) (7%) which occurred in each of the five urban vegetable gardens. In Nantes, the most abundant species were *Parisotoma notabilis* (Schaeffer, 1896) (12%), *Folsomia similis* (Bagnall, 1939) (9%), *Mesaphorura sp.* (8%) and *Oncopodura crassicornis* (Shoebbotham, 1911) (8%), but the most frequent species were *Desoria tigrina* (Nicolet, 1842) (6%), *L. lanuginosus* (4%), *P. notabilis*, *P. armata* (7%) and *Mesaphorura sp.* Only 17 species were found in all three cities, including three species present in 13 of the 15 gardens: *C. gibbosa*, *L. lanuginosus* and *P. armata*.

Total collembolan density in the soil samples ranged from ca. 5000 to 73,000 individuals m⁻² (Table 3). Species richness varied between 6 and 23 species per garden. The evenness was close to 1, with an average of 0.84. No significant differences in abundance, species richness, diversity, or evenness of collembolan communities were found between the three cities. At the city level, the mean Jaccard index calculated for collembolan communities across the five gardens of each city was 24% higher in the Grand Nancy Area (0.54) than in Nantes (0.67).

The factorial map of the NMDS revealed marked differences between the collembolan communities of gardens from the three cities, along both axes 1 and 2 (Fig. 2a), and these differences were highly significant (ANOSIM, $P < 0.001$). The effect of soil parameters were fitted a posteriori using the NMDS space revealed only significant GAMS based on P_{Olsen} and silt content ($P < 0.05$). These two parameters were correlated negatively with Axis 2 (P_{Olsen}) and 1 (silt) of NMDS and explained 86 and 77% of the deviance observed.

A total of 42 plant species were found in the urban vegetable garden, divided into 20 families (Table S2). Five species were common and frequent in urban vegetable gardens of all

Table 3 Taxonomic and functional diversity indices (mean \pm standard deviation) of collembolan and plant communities in the 15 urban vegetable gardens surveyed (5 gardens per city)

			Grand Nancy	Marseille	Nantes
Taxonomic diversity	Collembolan	Total number of species	28	32	37
		Mean number of species per garden	12.6 \pm 4.0	15.0 \pm 3.7	18.6 \pm 3.9
		Shannon diversity index	2.2 \pm 0.4	2.1 \pm 0.5	2.5 \pm 0.2
		Evenness index	0.9 \pm 0.1	0.8 \pm 0.1	0.9 \pm 0.1
		Density (individuals.m ⁻²)	16 10 ³ \pm 8 10 ³	34 10 ³ \pm 15 10 ³	39 10 ³ \pm 24 10 ³
		Jaccard distance index	0.5 \pm 0.1 ^b	0.6 \pm 0.04 ^{ab}	0.7 \pm 0.1 ^a
	Plants	Total number of species	19	26	23
		Mean number of species per garden	7.0 \pm 3.7	7.6 \pm 4.0	9.0 \pm 3.8
		Shannon diversity index	1.2 \pm 0.3	1.4 \pm 0.4	1.6 \pm 0.5
		Evenness index	0.7 \pm 0.1	0.7 \pm 0.2	0.8 \pm 0.1
		Jaccard distance index	0.7 \pm 0.1	0.8 \pm 0.1	0.7 \pm 0.1
Functional diversity	Collembolan	Functional richness	3 10 ⁻⁴ \pm 1 10 ⁻⁴	4 10 ⁻⁴ \pm 2 10 ⁻⁴	5 10 ⁻⁴ \pm 2 10 ⁻⁴
		Functional dissimilarity	0.2 \pm 0.01	0.2 \pm 0.02	0.2 \pm 0.01
		Functional divergence	0.9 \pm 0.06	0.8 \pm 0.04	0.8 \pm 0.03
		Functional evenness	0.7 \pm 0.1	0.6 \pm 0.1	0.6 \pm 0.1
	Plants	Functional richness	0.1 \pm 0.1	0.1 \pm 0.1	0.2 \pm 0.1
		Functional dissimilarity	0.2 \pm 0.1	0.2 \pm 0.1	0.2 \pm 0.1
		Functional divergence	0.8 \pm 0.2	0.7 \pm 0.2	0.6 \pm 0.1
		Functional evenness	0.5 \pm 0.1	0.7 \pm 0.1	0.6 \pm 0.1

Lower case letters indicate significant differences among cities (alpha =0.05)

the cities: *Poa annua* L., 1753 (87% of urban vegetable gardens), *Stellaria media* (L.) Vill., 1789 (80%), *Taraxacum officinale* F.H.Wigg., 1780 (67%), *Veronica persica* Poir., 1808, and *Convolvulus sepium* L., 1753 (53% for both). *Senecio vulgaris* L., 1753 and *Trifolium repens* L., 1753, were less frequent but common to all cities (33% and 27% of urban vegetable gardens respectively). Only 7 species were shared by the three cities and 28 species were present in only one city.

The number of plant species varied between 3 and 14 per urban vegetable garden (Table 3). The evenness was close to one with an average of 0.73. No significant difference was observed for any of the plant communities' structural indicators between the three cities. At the city level, the mean Jaccard index calculated for plant communities across the five gardens of each city was consistently high (0.73 on average) and no significant difference was found between the three cities.

The factorial map of the NMDS revealed variation in plant community composition between the three cities along both axes 1 and 2 (Fig. 2b) and these differences were significant (ANOSIM, $P < 0.05$). When soil parameters were fitted a posteriori to the NMDS space, only GAMS based on pH and Cu total content were significant ($P < 0.05$). These two parameters were correlated with Axis 2, negatively for Cu and positively for pH and explained 79% (Cu) and 55% (pH) of the deviance observed.

Functional composition of collembolan and plant communities

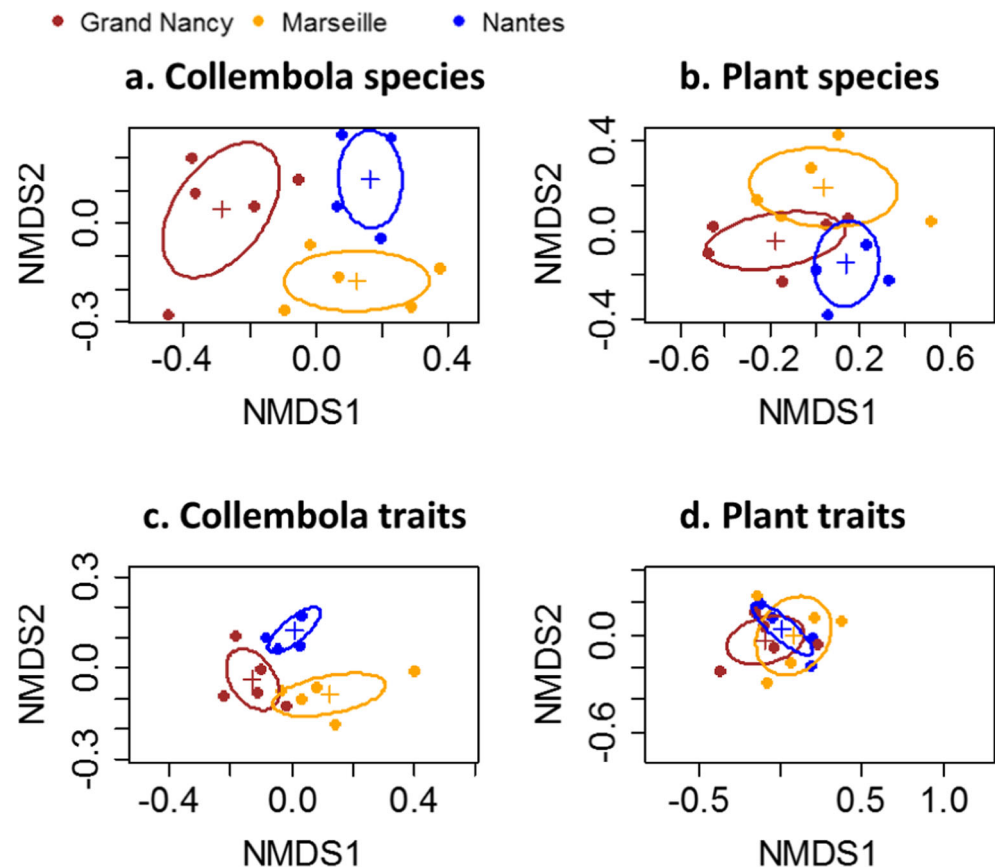
The functional structure of both collembolan and plant communities was not significantly different in distance-based functional parameters between the three cities (Table 3). Functional evenness was low: 0.5 and 0.7 for plants, and 0.6 to 0.7 for Collembola.

The functional composition of plant communities using the factorial map of the NMDS failed to reveal any substantial variation between the three cities along either axis (Fig. 2d). No significant discrimination between the three cities was found on the basis of functional traits (ANOSIM, $P > 0.05$). Concerning the effect of soil parameters fitted a posteriori to the NMDS space, only the GAM based on pH was significant ($P < 0.001$) and explained 89% of the deviance observed.

Plant communities in urban vegetable gardens were dominated by hemicryptophyte (54%) and/or therophyte life forms (37%). Plant reproduction was performed mainly by seed/spore (87%) and fruit types dominated by capsule fruits (44%) and nuts (44%). Vectors of dispersion were self (57%) and/or wind (35%). Strategy types for plants were mostly ruderal (64%) and/or competitor (31%).

In contrast, the functional composition of collembolan communities differed between cities. The factorial map of the NMDS revealed variation between the three cities along

Fig. 2 Graphic display of the first two axes of the non-metric multidimensional scaling (NMDS) on (a) collembolan and (b) plant species composition and (c) collembolan and plant (d) traits composition for each of the 15 urban vegetable gardens. Ellipses enclosing the five gardens for each city (with a confidence limit of 0.95), and the crosses represent the centroid



both axes 1 and 2 (Fig. 2c). This was observed on the basis of functional traits (ANOSIM, $P < 0.001$). The effect of soil parameters fitted a posteriori to the NMDS space (Fig. 3), using GAMS explained significantly ($P < 0.05$) respectively 42% (P_{Olsen}), 61% (Silt), 62% (C/N), 70% (CEC), 74% (Zn), 79% (Clay), 87% (pH), 89% (Sand) and 94% (Cd) of the deviance observed. Copper and Zn showed similar gradients correlated negatively with Axis 2 (Fig. 3d–e). Clay content, sand content and CEC showed similar gradients, although with opposite directions between clay content or CEC and sand content (Fig. 3g–i).

Variation of functional traits among cities indicated that the collembolan communities of Nantes exhibited more organisms without ocelli (36%), without furcula (20%) and a smaller size (25% between 0.5–1 mm) than those from Marseille (respectively 15, 8 and 9%) (Fig. 4). Moreover, more Collembola in Marseille exhibited a PAO (85%) and a smaller size (57% between 1 and 1.5 mm) than in Grand Nancy (10% between 3 and 4 mm).

Discussion

Our results showed that, in French urban vegetable gardens, no taxonomic homogenization was observed for either plants

or Collembola. Furthermore, although functional homogenization was observed for plants, this was not observed for soil Collembola. Several hypotheses, which are linked to the environmental filters, including soil properties and urbanization acting differently on both taxa, can explain these results.

Soil physical and chemical characteristics have been repeatedly reported as important drivers underlying variation in the composition of plant and collembolan communities, both in general and in urban areas in particular (Santorufio et al. 2015; Rzeszowski et al. 2017; Milano et al. 2018). Although we found differences in the composition of plant and collembolan communities from one city to another, in the case of plants, this variation was unrelated to the soil parameters measured in each location. This finding is in contrast with previous studies on other land uses, which have highlighted the importance of soil characteristics for the assemblage of plant communities, e.g. in forests (Laughlin and Abella 2007; Bernard-Verdier et al. 2012). In urban areas, high levels of soil pollution may have an impact on the occurrence of species in novel anthropogenic habitats (Williams et al. 2009). The relationship with soil parameters and vegetation was demonstrated for compaction (Omar et al. 2018), as well as the water availability of urban soils (Dana et al. 2002) correlated to clay and organic matter contents. Syntheses of various studies about urban vegetation support the hypothesis

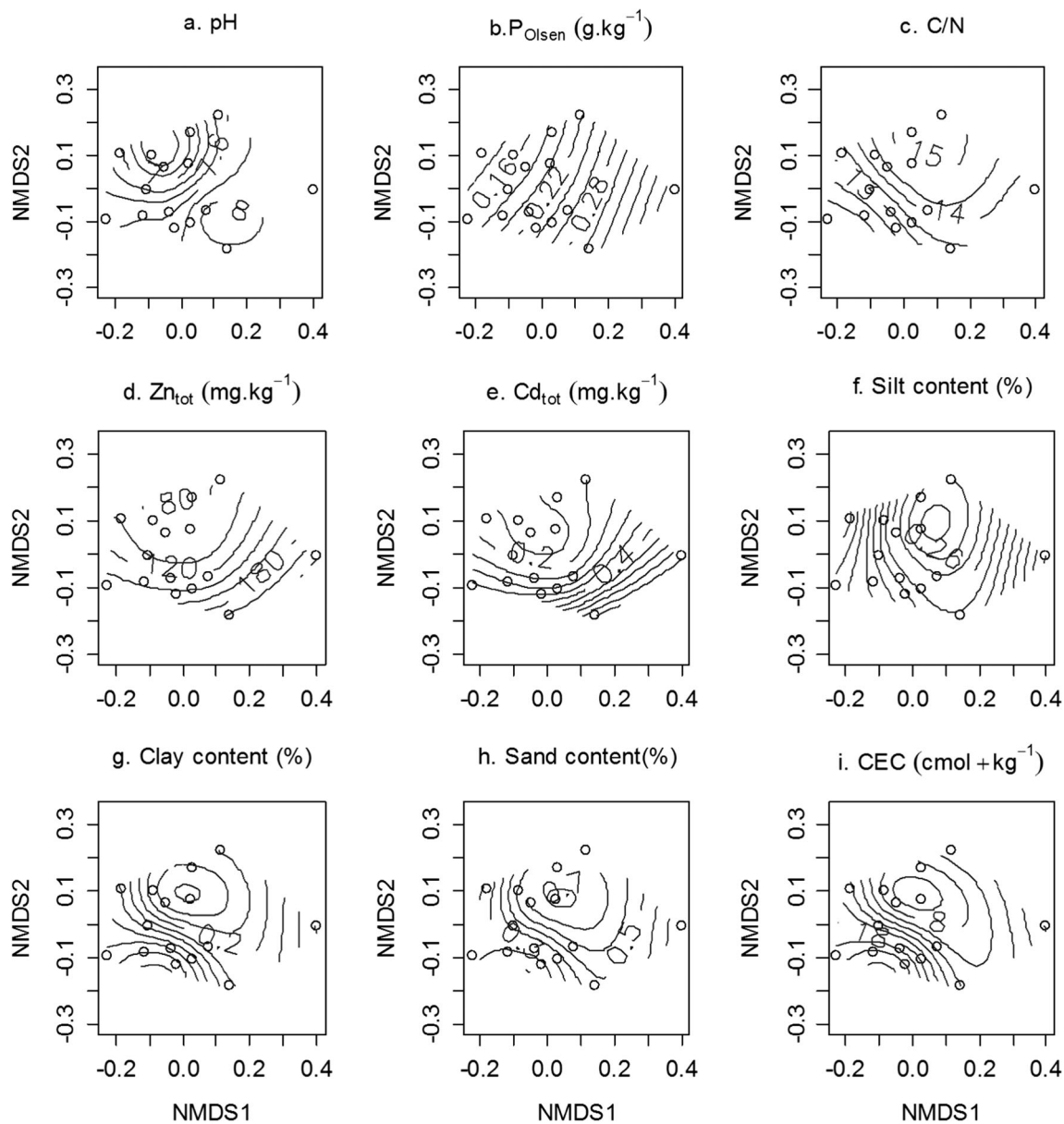


Fig. 3 Graphic display of soil parameters fitted a posteriori to the NMDS space of collembolan communities with generalized additive models (GAMs). Circles represents each urban vegetable gardens. Lines

represents values of each parameters; P_{Olsen} = available phosphorus, C/N = organic carbon on total nitrogen, Cd = Cadmium, Zn = Zinc

that urbanisation favours species with affinity to high-nutrient environments or alkaline soils (Williams et al. 2015). Also, a large subset of native plant species, which are able to colonize urban habitats, are common generalist species (Kowarik 2011). These species mostly have a broad ecological niche and could be less sensitive to soil quality, especially for comparison among cities. Unlike the plant communities, we found that the variation in collembolan community composition was significantly associated to soil geochemical parameters. Soil fertility parameters had a significant relationship between both collembolan community composition (species or trait) and soil texture, as well as to soil carbon content, irrespective of the city. Indeed it is well known that *Collembola* preferentially

live in air-filled soil pores (Wall et al. 2013) and thus may be influenced by textural and structural properties. These relations are also consistent with previous studies in forests or meadows (Fountain et al. 2008; e.g. Xu et al. 2009), which is in turn linked to the availability of nutrients such as nitrogen to collembolan community composition. Previous studies of urban lawn soils have also provided evidence that collembolan communities are influenced by both phosphorus concentration and pH (Rzeszowski et al. 2017). Some of the most frequently observed collembolan species in our study, namely *Parisetoma notabilis* and *Mesaphorura sp.*, have previously been shown to be negatively influenced by a high phosphorus content (Rzeszowski et al. 2017). Moreover, Santorufo et al.

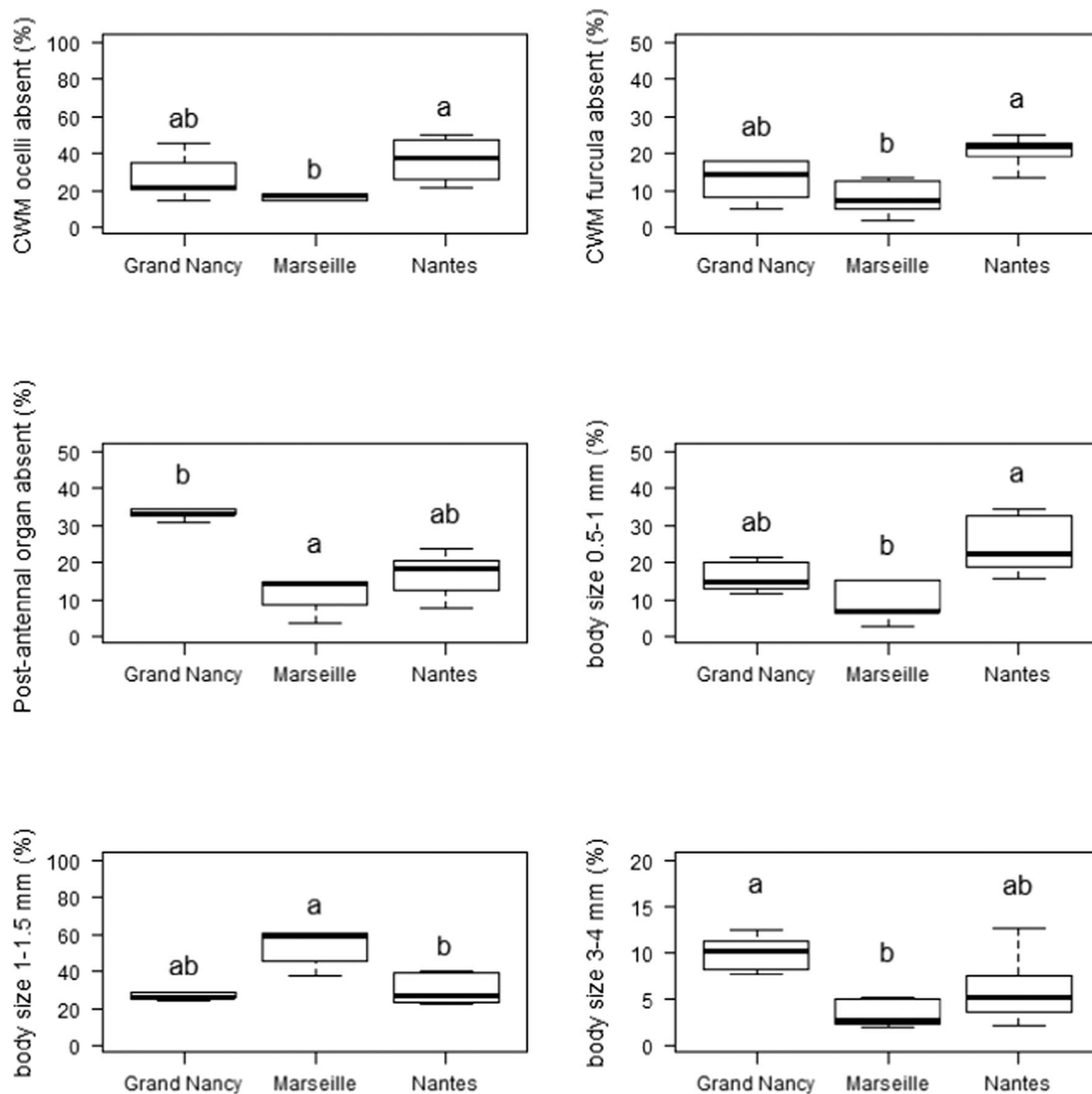


Fig. 4 Comparison between the three cities of attributes from functional collembolan traits: absence of ocelli, absence of furcula absent, presence of post-antennal organ and three body-size classes (0.5–1 mm, 1–1.5 mm

and 3–4 mm), weighted by the taxa-relative abundance of species (CWM). Lower case letters indicate significant differences between cities ($\alpha = 0.05$)

(2015) consider soil organic matter to be an important variation predictor in collembolan community composition in urban ecosystems and that organic matter could buffer some collembolan species against detrimental impacts of human activity. An important example of these detrimental impacts of human activity is soil contamination by metals demonstrated in urban areas such as urban vegetable gardens (Joimel et al. 2016). Indeed, the effects of metals on many *Collembola* species have been shown in several studies (Fountain and Hopkin 2004), thereby inducing a decrease both in biodiversity and in soil biological activity (Fountain and Hopkin 2004), or a shift in species or functional composition (Joimel et al. 2018). In this study, a significant relationship between functional collembolan community composition and soil metal contents (Cd and Zn) was again observed

(concentrations in mg kg^{-1} between 0.2–0.4 for Cd and 72–154 for Zn).

The biotic homogenization in urbanization processes can be induced by (i) the introduction and successful establishment of the same exotic species into different regions and (ii) the filtration of the same traits across different locations (McKinney and Lockwood 1999).

In our case, only three exotic plant species and no exotic collembolan species were identified. Even though the result for *Collembola* as to be interpreted with caution due to difficulties in assessing the native status of species, our results would suggest that the plant and collembolan communities in the gardens surveyed, have a very low exotic component. This finding contrasts with many previous studies focusing either on urban areas as a whole or on particular types of urban

green areas (Marco et al. 2008). However, none of these studies have been conducted in urban vegetable gardens, which present differences i.e. surface area or gardening practices, compared to other urban green areas. Yet, the impact of gardening practices on flora diversity have been clearly demonstrated (Marco et al. 2010) and could explain the lower exotic species colonization of urban vegetable garden than of other urban green areas. Whatever the reason, the low number of exotic species preclude this pathway for homogenization.

On the contrary, this study does show evidence of biotic homogenization for plants through filtering the same traits across different locations (i.e. functional homogenization). Although some plants (*Poa annua*, *Stellaria media*, *Taraxacum officinale*, *Veronica persica* and *Calystegia sepium*) and collembolan species (*Ceratophysella gibbosa*, *Lepidocyrtus lanuginosus* and *Protaphorura armata*) were frequently observed in all three cities, we did not find any taxonomic homogenization within or between cities, for either plant or collembolan communities. The selection of species, especially plants, could be more closely related to urbanization parameters related to habitat rather than soil characteristics. These parameters include landscape heterogeneity or fragmentation, urban heat islands or habitat disturbance (Kowarik 2011). The differentiated taxonomic communities between cities may reflect the influence of historical factors or garden management (Loram et al. 2008). The history of garden allotments varies from one city to another, leading to differences in garden morphology (hedges or not) and age (ranging from 10 to >100 years), and the sociological profile of gardeners (e.g. mostly male vs. gender-mixed, mostly pensioners vs. working-aged people). Both landscape heterogeneity around allotments and local gardening practices vary accordingly (Consalès 2004). While the former has been shown to influence the composition of plants communities in domestic gardens (Loram et al. 2008) and collembolan communities in urban parks (Milano et al. 2018), local factors (soil parameters, gardening practices) seem to override the effects of such larger-scale processes in allotment gardens, for collembolan communities.

For plant communities, we did detect significant functional homogenization and many of the plant species recorded, share a range of trait attributes which largely correspond to the typical suite of traits previously found in the urban herbaceous flora (Kleyer 1999; Knapp et al. 2012). These traits particularly enable dispersal and establishment in urban areas (Aronson et al. 2007). Specifically, plant communities in the gardens surveyed were dominated by species with a ruderal strategy, whereby plants can quickly colonize newly created gaps or vacant lots, e.g. following the demolition of a building or the removal of cultivated plants. In terms of Raunkiaer's life forms, we found a majority of hemicryptophytes, followed by therophytes. Hemicryptophytes are often associated with a higher tolerance to trampling (e.g. *Stellaria media*, *Taraxacum*

officinale, *Plantago major*) whereas therophytes are generally annual species, i.e. plants that survive in the form of seeds when conditions are unfavorable and that are able to complete their life cycle rapidly (Knapp et al. 2012), thus promoting the maintenance of populations in frequently disturbed areas. Finally, we found that self-pollination was the prevalent pollination system. While functional homogenization was in line with previous findings (Williams et al. 2015), the lack of taxonomic homogenization contrasts with previous studies (e.g. Gong et al. 2013; Bossu et al. 2014). Our results may simply reflect the complex, multi-scale nature of the biotic homogenization process: similar filtering acts in the three locations, resulting in functionally similar sets of species. However, because many species are functionally redundant in the global flora and the regional pools of species on which the selection operates differ between Nantes, Marseille and Nancy, the local sets of species in the gardens surveyed remain taxonomically distinct.

Concerning Collembola, we failed to detect any functional homogenization of communities among the three study cities. This is consistent with the lack of homogenization of urban carabid communities (Magura et al. 2010), but contrasts with homogenization reported for urban snail communities (Horsak et al. 2013), possibly because of differences in the underlying mechanisms (i.e. the addition of exotic species vs. the selection of common, generalist species).

Another parameter that could influence the taxonomy or functional composition of plant and collembolan species is the local climatic conditions that differ among the three cities studied. Many studies showed that factors such as water stress, luminosity or temperature have an influence on floristic compositions (Dana et al. 2002; Politi Bertoncini et al. 2012) or invertebrates (Smith et al. 2006) such as Collembola. Clearly, plants that prefer warmer and drier conditions may be excluded from Nancy, which has the more number of rainfall days in the year (124 days compared to 53 in Marseille and 119 in Nantes) and the lower minimum and maximum annual temperatures (6 and 14.9°C compared to 8.3 and 16.7 °C in Nantes and 10.8°C and 20.2°C in Marseille). On the contrary, with only 515 mm of annual rainfall in Marseille could induce a water stress for plants and Collembola compared to Nantes or Grand Nancy (respectively 820 mm and 775 mm). The water stress could select collembolan traits more adapted to these constraints as suggested by the high proportion of traits related to epedaphic species in Marseille (ocelli or furcula for example) compared to edaphic species in Nantes (no ocelli or furcula).

Conclusion

Urbanization is regarded as a prominent cause of biotic homogenization and accordingly, homogenization is considered

to be a major negative consequence of urbanization (McKinney 2006). However, urbanization does not always reduce native biodiversity (Magura et al. 2010), depending on the taxonomic group. Given the relatively high species diversity and abundances in urban vegetable gardens compared to nearby agricultural land uses (Joimel et al. 2017), we suggest that urban vegetable gardens could positively contribute to biodiversity conservation for some taxonomic groups, especially for those groups that are subject to multiple anthropogenic pressures in their original habitats. The effects of urbanization are, however, complex, as illustrated by the contrasting patterns of biotic homogenization we found for plants and for collembolan communities. The management strategy decided for urban green areas often relies exclusively on the expected response of aboveground biodiversity (plants, but also birds and mammals). As soil biota form an important component of the world's biodiversity and are critical for the provision of many ecosystem services, including those to cities (e.g. carbon cycle), we advocate for a much greater integration of belowground biodiversity into management schemes in urban areas.

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