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## Soil biota in boreal urban greenspace : Responses to plant type and age

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# 1 **Soil biota in boreal urban greenspace: responses**

## 2 **to plant type and age**

3

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29 **Key words:** Microbial biomass (PLFA), Urban greenspace, Nematodes,

30 Earthworms

31

## 32 **Abstract**

33

34 Plant functional type influences the abundance and distribution of soil biota.  
35 With time, as root systems develop, such effects become more apparent. The  
36 relationship of plant type and time with the structure and abundance of soil  
37 microbial and invertebrate communities has been widely investigated in a  
38 variety of systems. However, much less is known about long-term soil  
39 community dynamics within the context of urban environments. In this study,  
40 we investigated how soil microbes, nematodes and earthworms respond to  
41 different plant functional types (lawns only and lawns with deciduous or  
42 evergreen trees) and park age in 41 urban parks in southern Finland. As non-  
43 urban controls we included deciduous and evergreen trees in 5 forest sites. We  
44 expected that microbial biomass and the relative abundance of fungi over  
45 bacteria would increase with time. We also expected major differences in soil  
46 microbial and nematode communities depending on vegetation: we  
47 hypothesized that i) the presence of trees, and evergreens in particular, would  
48 support a greater abundance of fungi and fungal-feeding nematodes over  
49 bacteria and bacterial-feeding nematodes and ii) the fungi to bacteria ratio  
50 would be lowest in lawns, with deciduous trees showing intermediate values.  
51 In contrast to our predictions, we showed that old deciduous trees, rather than  
52 evergreens, supported the highest fungal abundances and fungal-feeding  
53 nematodes in the soil. Consistent with our predictions, microbial biomass in  
54 urban park soils tended to increase with time, whereas – in contrast to our  
55 hypotheses – fungal-feeding nematode abundance declined. Even in the oldest  
56 parks included in the current study, microbial biomass estimates never  
57 approximated those in the minimally managed natural forests, where biomass  
58 estimates were three times higher. Anecic earthworm abundance also  
59 increased with time in urban parks, whereas abundances of fungal-feeding,  
60 plant-feeding and omnivorous nematodes, as well as those of epigeic and  
61 endogeic earthworms remained constant with time and without any distinct  
62 differences between urban parks and the control forests. Our findings highlight  
63 that although urban park soils harbor diverse soil communities and

64considerable microbial biomass, they are distinct from adjacent natural sites in  
65community composition and biomass.

66

**67 Highlights**

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- 69• In cities, soil communities under different plant types diverge
- 70 increasingly with time
- 71• Microbial biomass associated with deciduous trees increases with park
- 72 age
- 73• Earthworm biomass increases with park age
- 74• Adjacent non-urban sites maintain a greater microbial biomass than
- 75 urban parks

## 761. Introduction

77

78Urbanized areas are rapidly expanding at the expense of natural habitats.  
79Urban green spaces, including public parks, assume a pivotal role as surrogates  
80for these lost natural environments. These green spaces provide a vast array of  
81ecosystem services (Costanza et al., 1997; Bolund and Hunhammar, 1999)  
82including carbon and nitrogen sequestration (Raciti et al., 2011; Setälä et al.,  
832016), storm water interception and purification (Valtanen et al., 2015),  
84biodiversity and climate regulation (Bolund and Hunhammar, 1999). These  
85ecosystem services depend strictly on the soil, and in turn on the soil biota  
86hosted therein.

87       Soil microbes and invertebrates are directly linked to biogeochemical  
88processes that take place in the soil and thus promote a variety of soil-derived  
89ecosystem services (Lavelle et al. 2006; Balser and Firestone, 2005; Blouin et  
90al., 2013 Ledin, 2000; Haritash and Kaushik, 2009). Yet, the abundance and  
91distribution of soil biota are often directly linked with the distribution of plant  
92species, and indirectly to soil properties that are modified by the plants  
93(Wardle et al., 2004) over time (Bardgett et al., 2005). Although the  
94successional trajectories of soil communities in relation to plant type and soil  
95characteristics over time have been widely investigated in, e.g., primary  
96(Ohtonen et al., 1999; Doblas-Miranda et al., 2008; Brown and Jumpponen  
972014) and secondary succession (Pižl, 1992; Maharning et al., 2009), much less  
98is known about these dynamics in urban park soils.

99       The linkage between plant functional types and soil microbial and  
100invertebrate communities has received substantial interest in contemporary  
101soil- and ecosystem ecology (Orwin et al., 2010; Thomson et al., 2010). There is  
102also a growing body of literature describing soil biota in urban parks  
103(microbes: Baxter et al., 1999; Xu et al., 2014; Ramirez et al., 2014; Hui et al.  
1042017a, b; nematodes: Pavao-Zuckerman and Coleman 2007; Amossé et al.,  
1052016; earthworms: Steinberg et al., 1997; Smetak et al., 2007; Amossé et al.,  
1062016). In a nutshell, these studies collectively provide evidence that  
107urbanization can substantially change in soil microbial and faunal  
108communities. Yet, there is a paucity of studies that simultaneously account for

109 different trophic groups in large and well-replicated experimental designs  
110 within the context of urban ecosystems.

111 Plant species identity is linked to the quantity and quality of inputs  
112 provided to the soil, either via litter deposition or through root exudates, which  
113 in turn are largely responsible for the composition of soil microbial (Grayston  
114 et al., 1998; Bardgett and McAlister, 1999; Marschner et al., 2004), nematode  
115 (Ilieva-Makulec et al., 2006) and earthworm communities (Curry, 2004). Whilst  
116 plants that produce labile, nitrogen-rich litter, such as grasses, herbs and  
117 deciduous trees often support bacterial-dominated soil microflora, plants  
118 producing more recalcitrant litter, such as evergreens, more commonly  
119 support fungal-based soil food webs (Wardle et al. 2004). Evergreen trees are  
120 adapted to low nutrient availability and thus have leaves with low nutrient  
121 contents (Kattge et al. 2011). In contrast, deciduous broadleaf trees have  
122 higher foliar nutrient content (Kattge et al. 2011) with *Tilia cordata* and *Acer*  
123 *platanooides* particularly in particular producing high quality litter (Aerts and  
124 Chapin 2000, Hobbie et al. 2014). Moreover, soil acidification promoted by  
125 evergreen trees (Setälä et al. 2016) is also associated with the prevalence of  
126 fungi over bacteria (Bååth and Anderson 2003). Finally, the quantity of root  
127 exudates, in boreal systems, tends to be higher in evergreen trees than  
128 deciduous trees (Gower et.al 2001), suggesting that evergreen trees may  
129 allocate a higher percentage of net primary productivity to, i.e. ectomycorrhizal  
130 fungi than do deciduous trees. Such plant-associated distinctions in soil  
131 microbial communities are reflected in the relative proportions of bacterial-  
132 and fungal-feeding fauna (Trofymow and Coleman, 1982; de Vries et al., 2013).  
133 This is particularly interesting as fungal-based food webs are characterized by  
134 slow nutrient cycling and a high capacity to retain nutrients, whereas bacterial  
135 dominated food webs are characterized by high nutrient turnover and nutrient  
136 leaching (de Vries et al., 2006; de Vries et al., 2012). Consequently, the ratio  
137 between fungi and bacteria in the soil is crucial when considering fundamental  
138 ecological processes such as the rate of organic matter decomposition  
139 (Coleman et al., 1983; Wardle, 2002; Moore et al., 2005; Paterson et al., 2008)  
140 and thus carbon and nutrient sequestration.

141 The type and availability of plant-derived resources can also change  
142 during plant community succession (Berendse, 1990; Knops and Tilman,  
143 2000). As soil organic matter (OM), C and N accumulate over time, so too do the  
144 biomasses of soil microbes (Zak et al., 1990; Ohtonen et al., 1999), nematodes  
145 (Háněl, 2010) and earthworms (Pižl, 1992). Changes in microbial abundances  
146 are not only quantitative, but also qualitative. For instance, the relative  
147 abundance of fungi over bacteria tends to increase with time (Ohtonen et al.,  
148 1999; Zeller et al., 2001; Bardgett and Walker, 2004). Furthermore, temporal  
149 changes in the fungal to bacterial ratio during succession are often also  
150 mirrored by changes in the ratio of fungal feeding to bacterial feeding  
151 nematodes (Brzeski, 1995; Ferris and Matute, 2003; Háněl, 2010). Only a few  
152 studies have investigated such successional trajectories of soil biota in urban  
153 parks (Smetak et al., 2007; Amossé et al., 2016; Hui et al., 2017a, b).

154 This study is part of a larger project that aims to shed light on the  
155 influence of divergent plant types on the physico-chemical and biological soil  
156 characteristics in urban parks of diverging ages. Our previous work has shown  
157 that plant type and park age are strong determinants of soil characteristics  
158 (Setälä et al., 2016; Setälä et al. 2017) and soil microbial community  
159 composition (Hui et al., 2017a, b). However, the response of microbial biomass,  
160 a measure that strongly relates to the functional activity and capacity of soils,  
161 to plant type and park age remains unresolved. Moreover, in this study, we  
162 incorporate the microbial consumer responses – key actors in providing soil-  
163 based ecosystem services and contributing to nutrient turnover (Wardle et al.,  
164 2004). We aim to investigate how park age and plant functional type affect the  
165 biomass of soil microbes and two important functional groups of soil fauna:  
166 nematodes and earthworms.

167 Given the clear effects that plant functional type and park age have on  
168 soil properties (see Setälä et al. 2016; Setälä et al. 2017) we tested the  
169 following hypotheses: plant functional type affects the soil food web so that i)  
170 evergreen trees producing recalcitrant litter promote an increase of fungal  
171 biomass over bacterial biomass and ii) deciduous trees, the lawn in particular,  
172 producing more labile litter, promote the establishment of bacterial biomass.  
173 Then we test iii) if changes in the soil microbial community also cascade up to



174higher trophic levels. We expect that higher densities of fungal feeding  
175nematodes (compared to bacterial feeders) associate with evergreen trees and  
176higher densities of earthworms associate with lawns and deciduous trees. Also,  
177we test iv) whether time since park construction promotes changes in soil  
178microbial and invertebrate community structure and abundance. We  
179hypothesize that soil biota in old parks resemble natural communities more  
180than in young parks. This is because the capacity of plants (especially trees) to  
181modify soils is park-age dependent (Setälä et al. 2016, 2017) with young parks  
182not having had the time to develop plant-soil interactions that are typical of  
183natural forests.

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## 1862. Materials and Methods

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### 1882.1. Study area

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190The study was conducted in two municipalities in the boreal forest zone in  
191southern Finland; Helsinki metropolitan area (60° 10' 15'' N 24° 56' 15'' E, with  
192a population of ca. 1.4 million people) and Lahti (60° 58' 57'' N 25° 39' 41'' E,  
193population ca. 110 000). Winters are cold and wet, while rainfall is moderate  
194all year round. The annual mean temperature is 5.3°C in Helsinki and 4.5°C in  
195Lahti; the annual mean precipitation is 628 mm in Helsinki and 636 mm in  
196Lahti. Summer lasts for approximately 110-120 days, winter 135-145 days and  
197the temperature can span from -35 to +35°C (Finnish Meteorological Institute).  
198The Helsinki and Lahti regions are classified by NRCS (National Resource  
199Conservation Service) as having soils of primarily the Spodosol suborder.  
200However, all urban parks in the two cities are constructed and none showed  
201detectable signs of podzolisation at the time of sampling.

202 We selected 41 parks in the two cities and five additional control forests  
203(see Setälä et al., 2016 and Hui et al., 2017a for details). Parks of three ages  
204were selected: young parks (between 7 and 15 years old), intermediate parks  
205(ca. 50 years old) and old parks (> 100 years). Control forests, situated in the  
206outskirts of the city of Lahti, are typified as unmanaged, conifer and linden

207dominated forests (> 80 years of age). Park size varied from one to several  
208hectares. The selected parks were subjected to routine maintenance, including  
209mowing (mowing residues not removed) and raking of tree leaves in the fall.  
210However, the parks were not irrigated or commonly fertilized. Until the early  
2111990s, some of the older parks in the city of Lahti were occasionally fertilized -  
212commonly with saltpeter (N, P, K, S), while some of the park lawns in Helsinki  
213have received and still receive light refurbishment fertilization.

214 In each park we selected, where possible, three vegetation-types:  
215deciduous (represented by *Tilia x vulgaris* 93% and *Acer platanoides* 7%) and  
216evergreen trees (spruce, *Picea sp.* 43.3%, *Abies sp.* 20%, *Pseudotsuga menziesii*  
21713.3%, *Pinus sylvestris* 13.3%, *Larix sp.* 10%) and a non-treed lawn with grass  
218(including herbs such as *Trifolium pratense*, *Plantago major*). Lawn cover  
219extended also under tree canopies. In some cases we selected parks including  
220only deciduous trees and lawn or only evergreen trees and lawn. The control  
221sites never had lawns, but deciduous (forest linden, *Tilia cordata*) and  
222evergreen trees (Norway spruce, *Picea abies*) were always present at each site.  
223In the parks, distance between the two tree types was always greater than the  
224height of the nearest tree. Plant age was considered as coinciding with park  
225age, except for young parks, where ca. 10 year old saplings were planted at the  
226time of park construction. In order to have at least 10 replicates per park age  
227and plant functional type, we selected 41 urban parks, resulting in 91 sampling  
228locations as described by Setälä et al. (2016) plus five control forests with 10  
229additional sampling locations, totaling 101 sampling locations.

230

## 2312.2. Soil sampling and measurements for edaphic responses

232

233In urban parks, soils were sampled at the edge of the canopy projection of each  
234tree and in the middle of the lawn area (when present) in October 2014. In the  
235control forests, soils were sampled under the canopy projection of each tree in  
236May 2015. Samples were obtained using a metal corer that was sterilized in  
237ethanol between samples. At each sampling point, 3 subsample soil cores were  
238collected and then pooled. The soil from each sample was homogenized and  
239larger stones, roots and fresh or recognizable plant material removed. Samples

240for microbial analysis were stored in resalable plastic bags on ice in the field  
241and frozen at -20 °C in the laboratory. Soil pH was measured in a 1/5 (vol/vol)  
242soil/distilled water suspension. Soil was weighed and analyzed for percent  
243moisture by drying for 48 hr at 105 °C. Total carbon (hereafter C) and nitrogen  
244(N) were obtained by dry combustion at 1350 °C using a LECO CNS2000  
245Elemental Analyzer (0.07% C and 0.09% N detection limits) and reported as  
246percentage dry mass.

247

### 2482.3. Soil microbial analysis, PLFA

249

250Before analysis, the frozen samples were thawed at room temperature and  
251sieved through a 2 mm mesh to remove leaf litter, rocks, large particles and  
252roots. Then, part of the soil was freeze-dried and an aliquot of 4 g for urban  
253park soil and 2 g for forest soil was taken for phospholipid fatty acids (PLFA)  
254analysis. Fatty acids (FA) were extracted following a modified procedure as  
255described in Macnaughton et al. (1997), Bligh and Dyer (1959), Frostegård et  
256al. (1991) and White et al. (1979). The extraction was performed using a  
257Dionex ASE 350 machine (Thermo Scientific). Briefly, the samples were mixed  
258with diatomaceous earth and placed in the extraction vessels between two  
259cellulose filters prewashed in chloroform. FA were extracted with Bligh and  
260Dyer (methanol/chloroform/citrate buffer, 2/1/0.8 vol/vol/vol) at 80 °C and  
261the samples underwent two static cycles of 15 min each. Once FA acids were  
262extracted, chloroform and citrate buffer were added, for a final volume of  
263chloroform/methanol/citrate buffer of 1/1/0.9, vol/vol/vol. The extracts were  
264left overnight to separate the aqueous phase from the lipidic phase. The  
265supernatant was discharged and the lower phase collected, which was then  
266evaporated under a flux of N<sub>2</sub> at 40 °C. The resulting pellet was suspended in  
267chloroform and applied to silica columns (Bond Elut LRC, Agilent). Chloroform,  
268acetone and methanol were applied in sequence to the column to separate  
269neutral lipids, glycolipids and phospholipids. The extracts were then dried  
270under N<sub>2</sub>. The phospholipid fraction so obtained was methylated and the fatty  
271acid methyl esters extracted with hexane/chloroform (4/1, vol/vol), dried  
272under N<sub>2</sub> and redissolved in 1 ml hexane. We used 19:0 (methyl

273nonadecanoate) as an internal standard. All the solvents used were of GC grade  
274and glassware was baked in an oven at 450 °C for 4 h prior to use.

275 The samples were analyzed in a Shimadzu GCMSQP2010 Ultra with an  
276Agilent J&WDB23 column. The column oven temperature was set to 60 °C and  
277the injection temperature was 250 °C in splitless mode. MS ion source  
278temperature was 200 °C and the interface temperature was 250 °C. As  
279reference library we used the bacterial acid methyl ester (BAME) mix  
280(SigmaAldrich), while the Supelco 37 Component FAME mix (SigmaAldrich)  
281was used for calibration for PLFA biomass calculation. Peaks were cross-  
282checked against the NIST spectral library. A total of 29 PLFAs were identified.  
283Of the identified peaks, the following were considered to be of bacterial origin:  
284i15:0, 15:0, 17:0, 17:0cy (eubacteria); a15:0, i16:0, i17:0 (gram-positive  
285bacteria); 16:1 $\omega$ 9, 18:1 $\omega$ 7 (gram-negative bacteria). The PLFA 18:2 $\omega$ 6 was  
286considered to be mainly of fungal origin (Frostegård and Bååth, 1996). PLFAs  
287were expressed as  $\mu\text{g g}^{-1}$  soil dry weight. The totality of identified peaks was  
288used to investigate coarse microbial community changes, as explained in  
289section 2.5 below. The microbial to fungal (F/B) ratio was calculated as the  
290ratio of PLFA 18:2 $\omega$ 6 to bacterial PLFAs.

291

## 2922.4. Soil Fauna

293

### 2942.4.1. Nematodes

295

296Nematodes were collected in early June 2016 in Lahti, and in July-August 2016  
297in Helsinki. Similarly to the soil sampling, nematodes were collected at the edge  
298of the canopy projection of each tree and in the middle of the lawn (when  
299present) area. In the control forests, soils were sampled under the canopy  
300projection of each tree type. Each sample consisted of six pooled 5 cm diameter  
301soil cores of the uppermost 10 cm. The samples were pooled to make one  
302composite sample and immediately placed in plastic bags and stored in a  
303cooler. In the laboratory, the soil was gently mixed and 10 g (fresh weight) of  
304soil was used for nematode extraction. Nematodes were extracted for 48 h  
305without lights/heating following the wet funnel method described in Sohlenius

306(1979). Nematode feeding guilds were assigned following Yeates et al. (1993).  
307We calculated the nematode channel ratio (NCR) as described in Yeates (2003)  
308and the maturity index (MI) as in Bongers (1990). NCR is calculated as the ratio  
309of bacterial feeding (BF) to bacterial-feeding plus fungal-feeding (FF)  
310nematodes:  $BF/(BF+FF)$ , and is constrained to have values between 1 (totally  
311bacterial-mediated) and 0 (totally fungal-mediated) (Yeates, 2003). MI is the  
312sum of the relative abundance of each taxon multiplied by their colonizer-  
313persister (c.p.) value. The c.p. value of each family was assigned following  
314Bongers (1990, 1999). MI provides information on the degree of  
315environmental disturbance, with higher values indicating a less disturbed  
316environment.

317

#### 3182.4.2. Earthworms

319

320Earthworms were collected in August 2016 close to where soil microbes and  
321nematodes were sampled. We followed a modified version of the hot mustard  
322liquid method described by Gunn (1992). Each sample consisted of two (in  
323public parks) or four (in control sites) 25 × 25 cm frames irrigated with a hot  
324mustard liquid. The hot mustard slurry was prepared by mixing 15 g of hot  
325mustard powder (Colman's powder) in 100 ml of water, and then allowing it to  
326sit for at least 4 h. Immediately prior to sampling, the mustard slurry was  
327added to approximately 3.5 L of tap water in a watering can. This 3.5 L of  
328mustard water was applied to each frame over a span of 15–20 min. The  
329collected worms were immediately placed in tap water for some minutes, then  
330placed into plastic bags containing moist tissue paper, and stored in a cooler. In  
331the laboratory the earthworms were placed in a refrigerator and stored for 48  
332h to empty their guts. The worms were then identified, weighed and stored in  
3334% formaldehyde solution.

334

#### 3352.5. Data analysis

336

337Generalized linear mixed models (GLMM) were used to investigate the  
338relationship between our focal response variables (see below) and park age (a

339factor with three levels; young, intermediate, old), plant functional type (a  
 340factor with three levels; evergreen, deciduous, lawn), soil pH, % soil C, % soil N,  
 341C/N ratio, soil OM, and % soil moisture. Our response variables were: total  
 342microbial biomass (PLFA), PLFA fungal/bacterial ratio, PLFA fungal marker  
 343(18:2 $\omega$ 6), PLFA gram-/gram+ ratio; nematode NCR ratio, BF nematode, FF  
 344nematode, PF (plant-feeding) nematode, PO (predators and omnivores)  
 345nematode, anecic earthworm *Lumbricus terrestris* abundance and endogeic and  
 346epigeic earthworms (*Lumbricus rubellus*, epigeic; *Allolophora caliginosa*,  
 347endogeic; *Octolasion cyaneum*, endogeic - collected in one sample only;  
 348*Allolophora chlorotica*, endogeic - collected in one sample only; *Dendrobaena*  
 349*octaedra*, epigeic). These GLMMs did not include the control forest samples in  
 350Lahti. Response variables were log or square-root transformed, when  
 351necessary, to satisfy assumptions of normality. In the GLMM analysis, city was  
 352considered a random effect, with park identity nested within city. We  
 353performed a stepwise model selection procedure by removing insignificant  
 354predictor variables, one at a time, if their p-values were greater than 0.05 and if  
 355the AIC subsequently decreased. However, park age and vegetation functional  
 356type were always retained in the final model, irrespective of significance. Then,  
 357we compared the control forest with old parks in Lahti, using ANOVA, with  
 358park age and vegetation functional type (and their interaction) as factors.  
 359Lawns were excluded from this analysis. Finally we evaluated whether FF  
 360nematodes, BF nematodes and NCR were correlated, respectively, with PLFA  
 36118:2 $\omega$ 6, bacterial PLFA and the PLFA fungal/bacterial ratio, using Pearson  
 362correlation.

363       Microbial (based on the relative abundance of PLFA biomasses) and  
 364nematode community structures were assessed using nonmetric  
 365multidimensional scaling analysis (NMDS). The earthworm community was  
 366dominated by one species, resulting in low species richness and deemed  
 367unsuitable for NMDS. For the NMDS analysis we used Euclidean distances for  
 368PLFAs and Bray-Curtis distances for nematodes. The “envfit” function was used  
 369to assess the significance of the relationship between these communities and  
 370the environment (factors: city, park age, plant functional type; abiotic  
 371parameters: pH, % soil C, % soil N, C/N ratio, soil OM, % soil moisture). To test

372our specific hypotheses, NMDS analyses were performed on three different  
373datasets; i) we included all park samples to evaluate the effects of plant  
374functional type and park age on microbial and nematode communities; ii) we  
375included only trees belonging to intermediate and old parks to focus on  
376differences mediated by tree type; iii) we included only old deciduous and  
377evergreen trees in Lahti parks and control forests in order to specifically  
378explore differences between urban parks and natural forest. R scripts and data  
379are provided as supplementary material (Supplementary material, S1-S25).

380 All statistical analyses were performed in R version 3.2.1. (R Core Team,  
3812015), using the packages *vegan* (Oksanen et al. 2007), *lme4* (Bates et al.  
3822014), *nmle* (Pinheiro et al. 2007) and *car* (Fox et al. 2011).

383

384

### 3853. Results

386

#### 3873.1. Microbial biomass and community composition

388

389The GLMM models provided little evidence for systematic responses in PLFA-  
390based total microbial, bacterial and fungal biomasses (18:206) to plant  
391functional type or park age (Table 1, Fig. 1). Rather, these effects highlighted  
392interactions between park age and plant type: PLFA biomasses (total, bacterial,  
393fungal) were lowest under deciduous trees in young parks, yet highest under  
394deciduous trees in old parks (Fig. 1 a, b). Total microbial and bacterial  
395biomasses were mainly negatively correlated with the C/N-ratio (Table 1, Fig.  
3962a) and positively correlated with % soil C (Fig. 2b). The fungal marker  
397responded positively to % soil N (Table 1, Fig. 2c).

398 In old Lahti parks, total microbial and bacterial biomass  
399(Supplementary material, Table S26) of evergreen and deciduous tree soils was  
400about a third lower than in control forests (total microbial PLFA, age:  $F_{1,16} =$   
40115.18,  $p < 0.01$ ; bacterial PLFA, age:  $F_{1,16} = 76,74$ ,  $p < 0.01$  ). Within forests and  
402old parks, total microbial PLFA biomass did not differ under evergreen and  
403deciduous trees, but bacterial biomass was higher under deciduous ( $F_{1,16} = 5.13$ ,  
404 $p = 0.03$ ) than evergreen trees. Fungal biomass (Supplementary material, Table

405S26) showed an interaction between land use type (control forest vs. urban  
406park) and tree type ( $F_{1,16} = 5.13$ ,  $p = 0.03$ ): fungal biomass was similar among  
407deciduous trees in forest and parks, whereas under evergreens it was  
408substantially higher in forests than in parks.

409 The PLFA-based fungi/bacteria (F/B) ratios suggest that, regardless of  
410park age and plant type, all soils were bacteria dominated (Fig. 1c). However,  
411the relative proportion of fungi over bacteria was higher under deciduous trees  
412than evergreen trees and lawns, regardless of park age (Table 1, Fig. 1c). None  
413of the measured soil parameters (Supplementary material, Table S26)  
414correlated with the F/B-ratio, and the F/B ratio among old parks and forests  
415did not differ (Table 1).

416 The ratio between gram-/gram+ bacteria did not respond to park age or  
417to vegetation type, and did not differ between control forests and old Lahti  
418parks. However, the gram-/gram+ ratio correlated positively with soil pH  
419(Table 1, Fig. 2d).

420 Relative abundances of PLFAs were used in NMDS analyses to  
421investigate changes in the soil microbial communities in parks and control  
422forest. Although microbial biomasses responded, we observed distinct changes  
423in community composition only when the following datasets were analyzed; i)  
424all plant types and park ages and ii) control forest and old deciduous and  
425evergreen vegetation types in Lahti. When all plant types and park ages were  
426included in the NMDSs, plant functional type had no effect on the soil microbial  
427community composition in urban parks (Fig. 3, panel 1). However, park age  
428influenced the composition of these communities ( $R^2 = 0.06$ ,  $p = 0.02$ ) (Fig. 3,  
429panel 2). The soil microbial communities also differed ( $R^2 = 0.11$ ,  $p = 0.01$ )  
430between the two cities. Environmental variables – primarily % soil C ( $R^2 = 0.14$ ,  
431 $p < 0.01$ ), % soil N ( $R^2 = 0.12$ ,  $p < 0.01$ ), the C/N-ratio ( $R^2 = 0.08$ ,  $p = 0.02$ ) and  
432soil OM ( $R^2 = 0.07$ ,  $p = 0.02$ ) – correlated with the soil microbial community  
433composition in the parks.

434 Comparing natural forest to deciduous and evergreen trees in old parks  
435in Lahti showed that plant functional type clearly influenced ( $R^2 = 0.14$ ,  $p =$   
4360.04) the soil microbial communities (Fig. 3, panel 5). However, the soil



437 microbial community did not differ among old parks and control forests (Fig. 3,  
438 panel 6).

439

440 3.2. Nematodes

441

442 Bacterial and fungal feeding nematodes were more abundant under evergreen  
443 trees than under lawns (Table 1). However, while the abundance of bacterial  
444 feeders declined with park age, fungal feeders did not differ across park age  
445 classes. The abundance of bacterial feeders declined with park age and  
446 positively correlated with soil % soil C (Table 1). Fungal feeders negatively  
447 correlated with soil OM (Table 1). Plant feeders and omnivorous nematodes,  
448 although not responding to plant type or park age, positively correlated with  
449 soil OM and the C/N ratio (Table 1). When forests were compared with old  
450 parks in Lahti, bacterial feeding nematodes were more abundant ( $F_{1,16} = 7.06$ ,  $p$   
451  $= 0.01$ ) under evergreen trees than under deciduous trees in old parks and  
452 control forests, while the other groups did not differ (see supplementary  
453 material, Table S26).

454 Plant type affected the nematode channel ratio (NCR) ( $F = 4.89$ ,  $p =$   
455  $0.01$ ). However, lawn and evergreen or deciduous and evergreen did not differ  
456 (Table 1, Fig. 4a), but rather, the differences can be attributed to those between  
457 deciduous trees and lawn. NCR negatively correlated with soil OM in the soil  
458 (Table 1). The NCR did not differ between old parks and control forest in Lahti.  
459 The maturity index (MI) showed a significant interaction between plant type  
460 and park age: when considering only deciduous trees, MI had the lowest values  
461 in young and old parks and highest values in intermediate parks (Table 1, Fig.  
462 4b). MI also positively correlated with the soil C/N-ratio (Table 1). MI was  
463 higher ( $F_{1,16} = 7.92$ ,  $p = 0.01$ ) in old Lahti parks than forest controls (see  
464 supplementary material, Table S26 ).

465 We observed no relationships (Pearson correlations) between (i) the  
466 fungal marker and fungal feeding nematodes, (ii) bacterial biomass and  
467 bacterial feeding nematodes, and (iii) the PLFA fungal/bacterial-ratio and NCR.

468 The NMDSs revealed that nematode communities depended neither on  
469 plant functional type nor park age (Fig. 3, panels 7, 8). Park age did, however,

470 have an effect when deciduous and evergreen trees in old and intermediate  
 471 parks were compared (Fig. 3, panel 10) ( $R^2 = 0.63$ ,  $p < 0.01$ ). Forests had  
 472 distinct ( $R^2 = 0.48$ ,  $p = 0.01$ ) nematode communities compared to old Lahti  
 473 parks (Fig. 3, panel 12). When all park samples were included in the analysis, %  
 474 soil C was an important determinant of nematode community structure ( $R^2 =$   
 475  $0.07$ ,  $p = 0.04$ ). However, when only evergreen and deciduous trees in  
 476 intermediate and old urban parks were investigated, only soil moisture  
 477 correlated with nematode community structure ( $R^2 = 0.15$ ,  $p = 0.04$ ). Soil  
 478 characteristics seemed to strongly control soil nematode communities (Fig. 1  
 479 panels 11, 12) when forests were compared to old parks, with only deciduous  
 480 and evergreen trees included in the analysis (moisture:  $R^2 = 0.61$ ,  $p < 0.01$ ; pH:  
 481  $R^2 = 0.56$ ,  $p < 0.01$ ; OM:  $R^2 = 0.39$ ,  $p = 0.01$ ; % soil C:  $R^2 = 0.39$ ,  $p = 0.01$ ; % soil N:  
 482  $R^2 = 0.33$ ,  $p = 0.02$ ; C/N-ratio:  $R^2 = 0.57$ ,  $p < 0.01$ ). Nematode community  
 483 compositions differed among the two cities when the comparison was made  
 484 between all parks ( $R^2 = 0.13$ ,  $p < 0.01$ ) and when deciduous and evergreen  
 485 trees in old and intermediate parks in Helsinki and Lahti were included in the  
 486 analysis ( $R^2 = 0.19$ ,  $p = 0.04$ ).

487

## 488 3.3. Earthworms

489

490 GLMM results of the anecic earthworm *Lumbricus terrestris* showed that its  
 491 biomass positively correlated with park age (Table 1), with the highest  
 492 biomasses in intermediate and old parks (Supplementary material, Table S2).  
 493 Plant type was not associated with *L. terrestris* biomass. *L. terrestris* correlated  
 494 negatively with soil OM content (Table 1). The *L. terrestris* biomass did not  
 495 differ between old parks and control forests in Lahti.

496 The epigeic and endogeic earthworm biomasses responded to plant  
 497 type (Table 1), with highest abundances in lawns (Supplementary material,  
 498 Table S2). Here, soil pH negatively correlated with the biomass of earthworms  
 499 (Table 1). The biomass of these earthworm taxa did not differ between old  
 500 parks and control forests, nor between evergreen and deciduous trees in the  
 501 two habitat types.

502

503

**5044. Discussion**

505

5064.1. Effects of plant functional type on the soil biota

507

508 We hypothesized that different plant functional types – due to their  
509 documented divergent effects on soil characteristics and plant derived  
510 resources – will lead to changes in soil communities and the abundances of  
511 species and functional groups. Although overall communities were  
512 compositionally largely invariable, the biomasses and relative abundances of  
513 different microbial and nematode functional groups did respond to plant  
514 functional type.

515       Importantly, the PLFA-based F/B ratio was lowest in lawns, suggesting  
516 that bacteria dominated in lawn soils. Yet, to our surprise, soils under  
517 deciduous trees, and not evergreen trees, had the highest F/B and lowest NCR.  
518 NCR represents the relative abundance of bacterial feeders over fungal feeders,  
519 and thus mirrors the relative amount of bacteria over fungi in the soil (Yeates  
520 2003). In general, the relative amount of fungi over bacteria tends to be higher  
521 under deciduous and especially under evergreen trees than lawn. Thus, our  
522 data contrast those reported (e.g. Wardle et al., 2004). The reasons for this  
523 remain unclear, and given our data, we can only speculate. For instance, a  
524 higher amount of fine roots (Giardina et al. 2005) and decaying roots support a  
525 higher saprophytic fungal biomass (Hobbie 2006) in soil associated with  
526 deciduous trees than evergreen, which could explain why soils associated with  
527 old lindens showed such a high F/B ratio. Another important factor potentially  
528 explaining the similar F/B ratio under lawns and evergreen trees may be the  
529 continuous disturbance present in urban parks; in particular, soil compaction  
530 can lower the F/B ratio (Hedlund et al., 2003).

531       Our third hypothesis focused on plant type mediated changes in higher  
532 trophic groups, such as nematodes and earthworm. GLMM analyses focusing on  
533 microbial and nematode feeding guilds revealed clear responses to plant type,  
534 although in some cases the response was seemingly mediated largely through  
535 age and soil properties of the parks. Total microbial biomass, as well as

536 bacterial and fungal biomasses separately were highest under deciduous trees  
537 in old parks, whereas no such effect was detectable in younger parks. Bacterial  
538 feeding nematodes and fungal feeding nematodes were more abundant under  
539 evergreen and deciduous trees than under lawn. Nematode communities often  
540 vary according to vegetation, as a direct result of plant-provided resources and  
541 indirectly through changes in the quality and quantity of the microbial fauna  
542 controlled by plant litter and exudate production. The lower abundance of  
543 nematodes in lawns may be due to diminished predation/consumption by  
544 earthworms (Dash 1980), which were less abundant under trees than lawns.  
545 Moreover, Yates (1981) reported complementary dynamics between  
546 earthworms and bacterial feeding nematodes, suggesting that nematodes and  
547 earthworms can compete for resources, with both using microbial biomass as  
548 food. In line with other studies, total microbial and bacterial biomasses in this  
549 study were also positively correlated with % soil C. Soil % C was also  
550 correlated with nematode abundance (both FF and BF) and community  
551 structure. Taken together, this is a clear indication that, just as in non-urban  
552 soils, the availability of carbon is a key determinant of microbial and secondary  
553 consumer biomass in urban soils, but that the effects appear only over time.

554 Contrary to previous findings (Lauber et al. 2009; Hui et al. 2017a), the  
555 soil microbial (PLFA) community did not correlate with pH. In contrast, the  
556 gram-/gram+ ratio did. Even though these two groups are not strict functional  
557 groups, they responded differently to soil pH; and in agreement with previous  
558 studies, gram- bacteria were relatively more abundant at high pH (Wang et al.  
559 2016). Further, our results also corroborate Hui et al. (2017a), who showed  
560 that microbial communities (characterized with high throughput sequencing  
561 methods) in these urban parks were distinguished by plant functional types  
562 and correlated with % soil N and pH.

563

#### 564 4.2. Effects of park age on the soil biota

565

566 Our fourth hypothesis stated that time since the establishment of a park (park  
567 age as well as tree age) will drive changes in the soil microbial and invertebrate  
568 communities. Our previous study, conducted in the same parks, but using high

569throughput sequencing, showed that microbial communities differed  
570compositionally between young parks and old / intermediate parks (Hui et al.,  
5712017a). Consistent with those results, our NMDS analyses of microbial  
572communities separated old and intermediate parks from young parks. This  
573suggests that the soil microbial community reaches a stable structure between  
57410 and 50 years after park construction. Soil microbial community composition  
575in old parks overlapped with that in control forests. However, microbial  
576biomass was substantially higher in forests than in old parks. This is likely due  
577to frequent disturbances in the latter system (Pickett and Cadenasso 2009).  
578Malmivaara-Lämsä and Fritze (2003) reported that human soil trampling in an  
579urban boreal forest did not affect microbial community composition.  
580Accordingly, we also observed that microbial community composition of old  
581parks approximates the non-disturbed forest sites, albeit microbial abundance  
582is diminished in urban parks compared to forest sites. However, for logistical  
583reasons, we sampled the urban parks and control sites (forest) at different  
584times. Microbial biomass can change across seasons, with peaks in the spring  
585and autumn (Diaz-Ravina et al. 1995). Nevertheless, the control sites also had  
586higher soil OM and %C (Setälä et al. 2016) suggesting that the observed  
587microbial biomass differences are unlikely mere artifacts attributable to  
588different sampling times. In addition to biomass, microbial community  
589composition can be seasonally dynamic (Moore-Kucera and Dick 2008), but  
590despite such potential seasonal dynamics, the communities in control and  
591urban park sites overlapped.”.

592       Contrary to our expectations, the relative amount of fungi over bacteria  
593did not increase as a function of park age. Similarly, NCR, describing the  
594relative abundance of bacterial-feeding over fungal-feeding nematodes,  
595remained mostly invariant across all park age classes. In successional systems,  
596such as agricultural systems under restoration, the F/B ratio increases (Zeller  
5972001, Bailey 2002) as a result of changes in soil parameters (Zeller et al. 2001)  
598and reduced disturbance (Hedlund et al. 2003). However, in urban parks the  
599normal successional course is arrested and disturbance is continuous, possibly  
600preventing increases in the relative abundance of fungi. Disturbance may also  
601be the reason behind the invariant MI (Nematode Maturity Index) among the

602 parks of different ages. Interestingly, MI, which is regarded as a good indicator  
603 of ecosystem maturity, was higher in old parks compared with forest. In a  
604 study on the response of a riparian nematode community along a rural-urban  
605 transect, Pavao-Zuckerman et al. (2007) reported no differences in MI among  
606 sites, suggesting that the level of pollution was not high enough to influence MI.  
607 Also in our case, the levels of metal pollution were below ecologically relevant  
608 values (Setälä et al. 2017), but it is still unclear why MI values in forests are  
609 lower than in parks.

610 We were also unable to detect any shifts in the abundances of different  
611 nematode functional groups. Similarly to our speculations above, here too  
612 factors such as disturbance and litter removal may greatly contribute in  
613 altering resource availability to the soil biota, thus homogenizing these taxa  
614 across park ages. This could also explain the lack of response to plant traits and  
615 park age in plant-feeding nematodes, although plant root volumes likely  
616 increased substantially with time since park construction and establishment.

617 Nematode communities did respond to park age, but only in the  
618 rhizospheres of the two tree types; yet no changes in abundance with park age  
619 were observed. Nematodes can respond to changes in biotic and abiotic soil  
620 conditions (De Goede and Bongers 1994, Hanel 1995). Therefore, it is not  
621 surprising that we observed an age related shift in the nematode community  
622 only in association with trees, i.e. plant types which with time resulted in the  
623 clearest soil property changes in our study parks (see Setälä et al., 2016), and  
624 not in lawns.

625 The nematode community was also extremely responsive when we  
626 compared old parks and control forest, responding in parallel with the  
627 microbial communities as reported in Hui et al. (2017a). The nematode  
628 community structure was also correlated with changes in the soil  
629 characteristics, which in turn were modified by the different plant functional  
630 type and time. Community composition correlated with changes in abiotic soil  
631 parameters, such as pH, C, N and soil moisture. Again, this shows that  
632 nematodes are sensitive indicators (Neher 2001) of temporally mediated  
633 changes in soil characteristics. Contrary to previous findings, nematode  
634 densities were similar in rural forests and in urban parks. Pouyat et al. (1994)

635 suggested that a decline in nematode populations in urban soils might be  
636 linked to higher heavy metal concentrations in urban soils. On the other hand,  
637 Ohtonen (1992) found no link between metal pollution and nematode density.  
638 It is possible that pollution, and in particular metal loads, in urban soils in  
639 Helsinki and Lahti were not extreme enough to affect the soil biota.

640 Abundance of the anecic earthworm *L. terrestris* was lowest in young  
641 parks, increased with park age and reached a plateau in intermediate parks.  
642 The low abundance of earthworms in young parks can be attributed to two  
643 factors: i) lack of time for earthworms to colonize newly constructed habitats,  
644 and/or ii) the inhospitality of the newly built park soil as a habitat. As  
645 resources such as C and N increase in our park soils (see Setälä et al., 2016), so  
646 too does earthworm biomass. Similar trends in urban parks were observed by  
647 Smetak et al. (2007). This can have important implications since earthworms  
648 can ameliorate negative soil characteristics, compensating for and even  
649 reducing soil compaction with time. It is interesting to note that epigeic and  
650 endogeic earthworms did respond to pH variation, being more abundant at low  
651 pH than at high pH. Earthworms are quite sensitive to pH (Edwards and  
652 Bohlen, 1996). However, variation in pH among parks and plant types was  
653 rather narrow (Setälä et al., 2016) and among the earthworm species that we  
654 recorded, *Lumbricus rubellus* and *Aporrectodea caliginosa* were more  
655 abundant. Considering that pH is highly correlated with park age (Setälä et al.,  
656 2016), the significant relationship between earthworm abundance and pH  
657 could also be interpreted as the result of a relationship between park age and  
658 earthworm abundance.

659

660

## 661 **Conclusions**

662

663 Our data show that microbial biomass in natural forests is much higher than in  
664 urban parks, irrespective of their age. Thus, the urban greenspaces  
665 investigated unlikely approximate ecosystem properties or functions of the  
666 surrounding non-urban areas. Yet, our study provides strong evidence that  
667 deciduous trees support a greater microbial biomass with time since urban

668green space establishment. Deciduous trees also had the highest relative  
669amount of fungi over bacteria in urban parks, that evergreen trees would  
670promote fungal rich soil microbial communities. Not only did microbial  
671biomass increase with age in urban parks, but so too did the abundance of  
672secondary consumers, such as earthworms. These data suggest that although  
673urban parks do not approximate natural forests, likely as a consequence of the  
674maintenance/disturbance regime they experience, the soil microbial and  
675invertebrate communities respond to vegetation and edaphic shifts over time.  
676Nevertheless, further studies are needed to assess the correlation and type of  
677ecosystem services provided by these trophic groups.

678

679

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681

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688

689

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## 1056 Figure and Table Captions

1057

1058 **Fig. 1** The effects of plant functional type and park age on a) total microbial  
1059 PLFAs, b) fungal PLFA (18:2 $\omega$ 6) and c) the PLFA fungal to bacterial ratio. Mean  
1060 values  $\pm$  SE are presented.

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1062 **Fig. 2** Relation between a) the C/N ratio and predicted values of total microbial  
1063 PLFAs, b) % soil C and predicted values of total microbial PLFAs, c) % soil N  
1064 and predicted values of fungal PLFA (18:2 $\omega$ 6) and d) pH and predicted values  
1065 of gram-/gram+ bacteria.

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1067 **Fig. 3** NMDS plots for bacterial (1-6, on the left) and nematode (7-12, on the  
1068 right) communities. Microbial communities were grouped by plant functional  
1069 type (1, 3, 5) and age (2, 4, 6), and nematode communities were grouped by  
1070 plant functional type (7, 9, 11) and age (8, 10, 12) under lawn, deciduous and  
1071 evergreen trees in young, intermediate and old parks. Significant effects ( $p <$   
1072 0.05) are indicated with a check mark in the upper panels and significant  
1073 vectors are shown in the NMDS plots.

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1075 **Fig. 4** The effects of plant functional type and park age on a) the nematode  
1076 channel ratio (NCR), and b) the nematode maturity index (MI). Mean values  $\pm$   
1077 SE are presented.

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1079 **Table 1.** GLMM results for PLFAs, nematodes and earthworms. For PLFAs the  
1080 response variables included total microbial PLFA, bacterial PLFA, fungal PLFAs  
1081 (18:2 $\omega$ 6, saprophytic fungi), fungal to bacterial ratio (fungi/bacteria) and gram + to  
1082 gram – ratio (gram+/gram-). For nematodes the response variables included  
1083 bacterial feeders, fungal feeders, plant feeders, predators and omnivorous, the  
1084 maturity index (MI) and the nematode channel ratio (NCR). For earthworms the  
1085 response variables were: *Lumbricus terrestris* and other earthworms. For each  
1086 variable we reported the coefficient, standard error and p-value. Significant effects  
1087 ( $p < 0.05$ ) are highlighted in bold and significant interactions are indicated with an  
1088 asterisk. Young evergreen trees are in the intercept.

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1090 **Supplementary material, Table S2.** Means ( $\pm$  1 SD) of the following PLFAs:

1091 total microbial, bacterial, fungal PLFAs (18:2 $\omega$ 6, saprophytic fungi),

1092 fungal/bacterial ratio, gram/gram+ ratio, nematodes: bacterial feeders, fungal

1093 feeders, plant feeders, predators and omnivores, maturity index (MI),

1094 nematode channel ratio (NCR), earthworms: *Lumbricus terrestris* and other

1095 earthworms, for the three different park ages (young, intermediate and old)

1096 and plant functional type (evergreen, deciduous, lawn). Values for Lahti old

1097 parks and control forest (evergreen and deciduous trees) are also presented.

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1122 Table 1. GLMM results for PLFAs, nematodes and earthworms. For PLFAs the  
 1123 response variables included total microbial PLFA, bacterial PLFA, fungal PLFAs  
 1124 (8:2ω6, saprophytic fungi), fungal to bacterial ratio (fungi/bacteria) and gram + to  
 1125 gram – ratio (gram+/gram-). For nematodes the response variables included  
 1126 bacterial feeders, fungal feeders, plant feeders, predators and omnivorous, the  
 1127 maturity index (MI) and the nematode channel ratio (NCR). For earthworms the  
 1128 response variables were: *Lumbricus terrestris* and other earthworms. For each  
 1129 variable we reported the coefficient, standard error and p-value. Significant effects  
 1130 ( $p < 0.05$ ) are highlighted in bold and significant interactions are indicated with an  
 1131 asterisk. Young evergreen trees are in the intercept.

	variable	intercept	lawn	deciduous	intermediate	old	age x functional group	pH	% soil C
PLFAs	Total microbial PLFAs	6.821	0.041	0.040	0.081	0.068			0.064
		0.220	0.092	0.092	0.103	0.100	*		0.023
		<b>&lt;0.001</b>	0.447	0.437	0.791	0.675			<b>&lt;0.001</b>
	Bacterial PLFAs	5.951	0.091	0.007	0.060	0.046			0.070
		0.228	0.094	0.094	0.105	0.102	*		0.023
		<b>&lt;0.001</b>	0.336	0.942	0.565	0.655			<b>&lt;0.001</b>
	Fungal PLFAs	3.414	0.129	-0.156	0.248	-0.320			-0.162
		0.290	0.266	0.261	0.272	0.274	*		0.085
		<b>&lt;0.001</b>	0.627	0.549	0.362	0.243			0.056
	Fungi/bacteria	17.296	-4.994	8.044	-2.107	1.353			
		3.141	3.444	3.417	3.417	3.417			
		<b>&lt;0.001</b>	0.147	<b>0.019</b>	0.537	0.692			
	Gram-/gram+	0.327	0.007	0.037	-0.064	-0.133			0.105
		0.320	0.050	0.052	0.056	0.053			0.051
0.308		0.897	0.474	0.260	<b>0.018</b>			<b>0.040</b>	
Nematodes	Bacterial feeding	8.676	-2.038	-1.782	-2.121	-1.668			0.475
		2.279	0.847	0.832	0.860	0.852			0.218
		<b>&lt;0.001</b>	<b>0.016</b>	0.321	<b>0.013</b>	0.050			<b>0.029</b>
	Fungal feeding	5.58	-1.322	-0.245	-0.35	-0.761			
		0.963	0.492	0.485	0.55	0.548			
		<b>&lt;0.001</b>	<b>0.01</b>	0.612	0.524	0.165			
	Plant feeders	4.303	-1.030	-1.386	0.176	0.895			
		1.335	0.918	0.886	0.929	0.924			
		<b>&lt;0.001</b>	0.262	0.118	0.849	0.333			
	Predators and omnivorous	-0.082	0.161	0.770	0.770	-0.109			
		1.049	0.438	0.438	0.462	0.463			
		0.937	0.712	0.104	0.095	0.813			
	MI	0.550	0.209	0.090	0.033	-0.074			
		0.119	0.059	0.060	0.064	0.064	*		
<b>&lt;0.001</b>		<b>&lt;0.001</b>	0.134	0.600	0.246				

		0.418	0.008	-0.09	-0.084	-0.012			
	NCR	0.094	0.055	0.055	0.066	0.065			
		<b>&lt;0.001</b>	0.121	0.084	0.212	0.848			
Earthworms		1.920	-0.163	-0.242	1.452	1.097			-0.265
	<i>Lumbricus terrestris</i>	0.725	0.320	0.319	0.406	0.404			0.123
		<b>0.008</b>	0.611	0.448	<b>&lt;0.001</b>	<b>0.007</b>			<b>0.032</b>
	Other earthworms	3.657	0.794	0.433	0.160	0.368			-0.486
		1.355	0.190	0.196	0.226	0.217			0.200
		<b>0.007</b>	<b>&lt; 0.001</b>	<b>0.027</b>	0.480	0.090			<b>0.015</b>

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**Table 2** Means ( $\pm$  1 SD) of the following PLFAs: total microbial, bacterial, fungal PLFAs (18:2 $\omega$ 6, saprophytic fungi), fungal/bacterial ratio, gram/gram+ ratio, nematodes: bacterial feeders, fungal feeders, plant feeders, predators and omnivores, maturity index (MI), nematode channel ratio (NCR), earthworms: *Lumbricus terrestris* and other earthworms, for the three different park ages (young, intermediate and old) and plant functional type (evergreen, deciduous, lawn). Values for Lahti old parks and control forest (evergreen and deciduous trees) are also presented.

Variable		Young	SD	Intermediate	SD	Old	SD	Old Lahti	SD	Control	SD	
PLFA $\mu\text{g g}^{-1}$ soil dw	Total microbial PLFAs	Evergreen	380.09	132.83	526.96	208.32	417.16	93.44	318.82	64.09	842.19	319.05
		Deciduous	271.04	93.78	530.15	146.41	616.97	347.73	669.85	439.87	957.27	281.94
		Lawn	460.25	165.97	447.87	128.15	473.87	185.37				
	Bacterial PLFAs	Evergreen	172.85	66.11	223.54	88.39	181.19	50.83	160.42	46.90	799.71	306.51
		Deciduous	116.54	43.01	224.04	59.13	241.89	112.35	270.50	105.90	982.63	252.72
		Lawn	211.31	90.41	203.88	60.37	218.14	82.75				
	Fungal PLFAs	Evergreen	30.98	13.60	45.55	25.43	26.59	15.87	21.74	14.16	127.29	99.25
		Deciduous	24.65	9.00	48.12	28.67	111.03	125.14	141.06	156.35	127.97	100.76
		Lawn	34.26	12.77	23.88	11.22	26.16	16.65				
Fungi/bacteria	Evergreen	20.33	12.39	21.17	11.73	15.96	11.25	14.05	8.43	18.39	15.22	
	Deciduous	22.65	9.65	21.89	10.83	37.53	26.93	43.87	32.64	12.91	8.83	
	Lawn	18.76	8.98	11.88	5.29	11.83	4.55					
Gram+/gram-	Evergreen	2.98	0.45	2.77	0.31	2.49	1.02	3.07	1.02	3.14	0.83	
	Deciduous	3.35	0.79	2.70	0.44	2.68	0.53	2.78	0.57	3.53	0.62	
	Lawn	2.79	0.40	2.66	0.26	2.73	0.35					
Nematodes $10 \text{ g}^{-1}$ soil	Bacterial feeders	Evergreen	139	113	100	85	93	47	64	33	74	31
		Deciduous	106	84	51	60	85	73	34	30	38	6
		Lawn	79	83	78	63	49	51				
	Fungal feeders	Evergreen	25	23	18	14	12	12	11	10	40	53
		Deciduous	24	25	20	30	13	9	12	7	13	8
		Lawn	11	11	10	14	7	6				
	Plant feeders	Evergreen	63	63	54	55	86	67	68	36	45	27
		Deciduous	37	32	43	53	48	33	47	36	16	24
		Lawn	129	283	69	55	136	285				
Predators and omnivorous	Evergreen	9	8	12	9	7	11	4	4	19	15	
	Deciduous	15	15	14	9	10	9	12	12	18	18	
	Lawn	12	14	8	5	9	11					
MI	Evergreen	2.17	0.11	2.30	0	2.35	0.23	2.42	0.08	2.15	0.20	
	Deciduous	2.24	0.43	2.84	0.38	2.23	0.44	2.56	0.18	2.34	0.27	
	Lawn	2.37	0.44	2.43	0.64	2.54	0.46					
NCR	Evergreen	0.82	0.13	0.71	0.25	0.79	0.17	0.86	0.08	0.71	0.30	
	Deciduous	0.77	0.19	0.85	0.12	0.88	0.09	0.70	0.17	0.76	0.12	
	Lawn	0.88	0.12	0.88	0.10	0.87	0.10					
Earthworms $\text{g m}^{-2}$	<i>Lumbricus terrestris</i>	Evergreen	34	43	88	60	62	65	99	65	115	133
		Deciduous	15	32	63	49	66	67	102	77	97	100
		Lawn	27	30	54	67	43	37				
	Other earthworms	Evergreen	8	10	11	12	9	12	12	15	14	11
		Deciduous	9	13	19	32	19	13	25	13	50	48
		Lawn	16	16	36	44	35	40				

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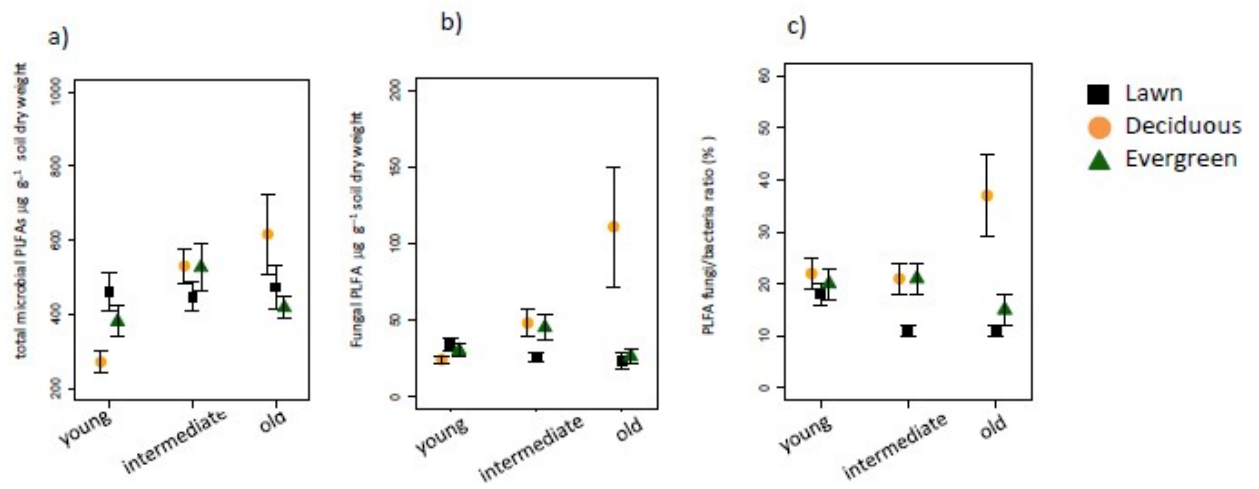
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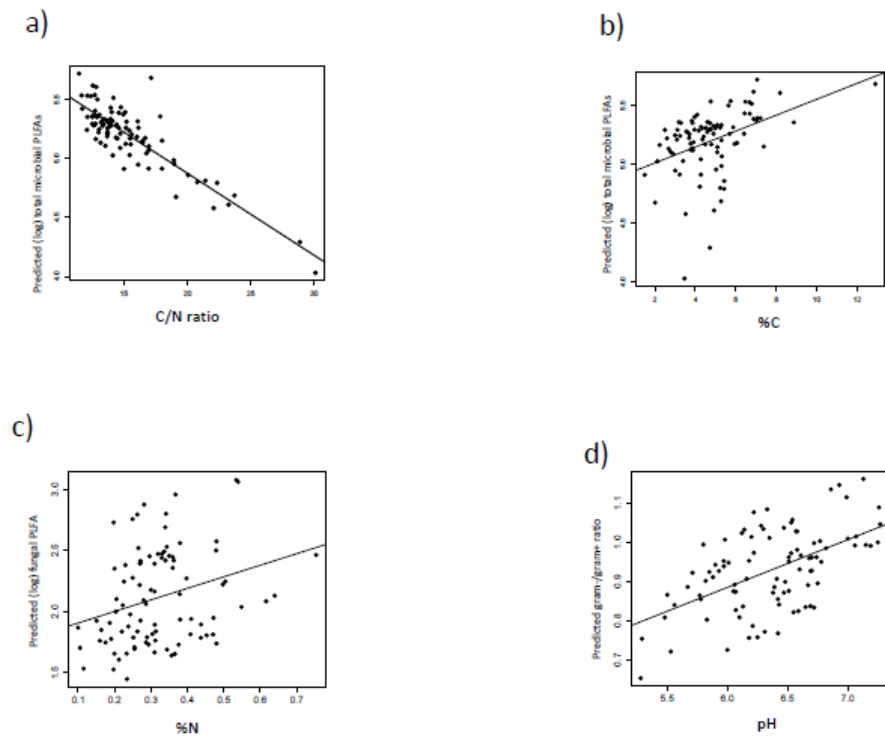
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1151 Fig 1.

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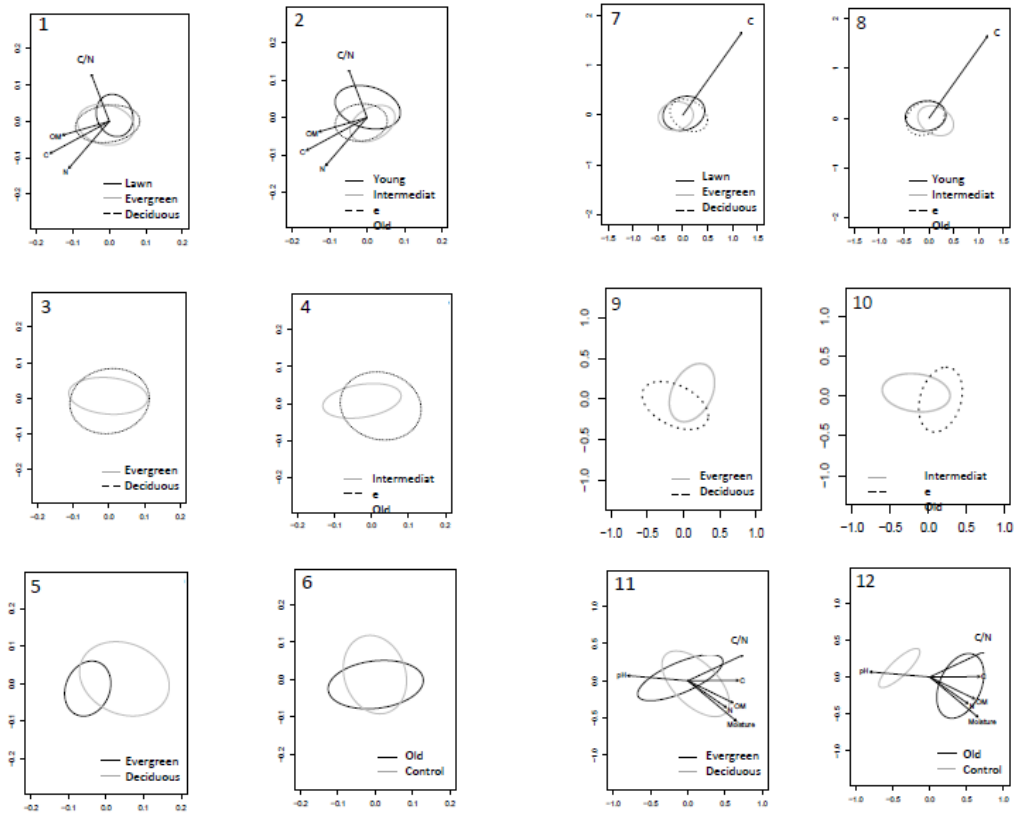
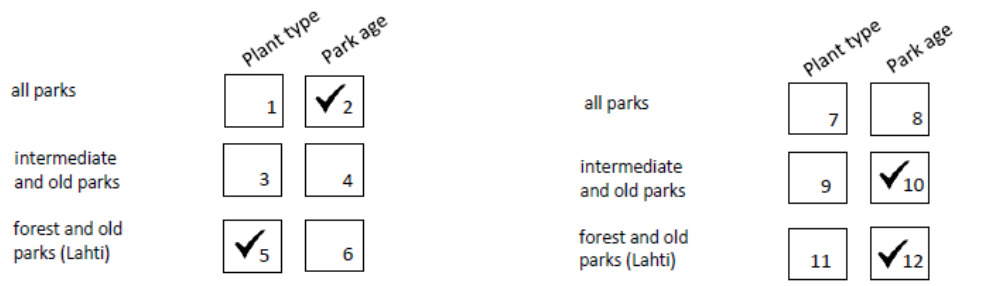
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1154 Fig 2.

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PLFAs

Nematodes

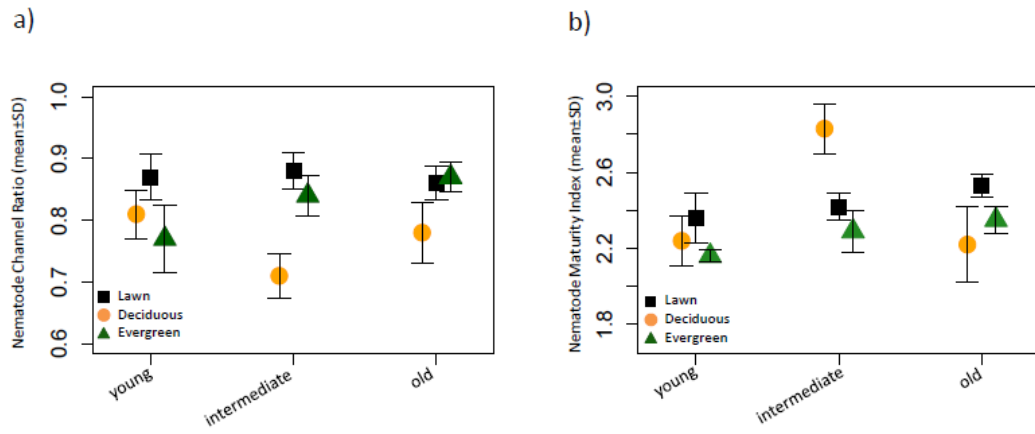


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1157 Fig. 3

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1161 Fig. 4

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