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

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ABSTRACT

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

1. Introduction

Urbanized areas are rapidly expanding at the expense of natural habitats. Urban green spaces, including public parks, assume a pivotal role as surrogates for these lost natural environments. These green spaces provide a vast array of ecosystem services (Costanza et al., 1997; Bolund and Hunhammar, 1999) including carbon and nitrogen sequestration (Raciti et al., 2011; Setälä et al., 2016), storm water interception and purification (Valtanen et al., 2015), biodiversity and climate regulation (Bolund and Hunhammar, 1999). These ecosystem services depend strictly on the soil, and in turn on the soil biota hosted therein.

Soil microbes and invertebrates are directly linked to biogeochemical processes that take place in the soil and thus promote a variety of soil-derived ecosystem services (Lavelle et al., 2006; Balser and Firestone, 2005; Blouin et al., 2013 Ledin, 2000; Haritash and Kaushik, 2009). Yet, the abundance and distribution of soil biota are often directly linked with the distribution of plant species, and indirectly to soil properties that are modified by the plants (Wardle et al., 2004) over time (Bardgett et al., 2005). Although the successional trajectories of soil communities in relation to plant type and soil characteristics over time have been widely investigated in, e.g., primary (Ohtonen et al., 1999; Doblas-Miranda et al., 2008; Brown and Jumpponen, 2014) and secondary succession (Pižl, 1992; Maharning et al., 2009), much less is known about these dynamics in urban park soils.

The linkage between plant functional types and soil microbial and invertebrate communities has received substantial interest in contemporary soil- and ecosystem ecology (Orwin et al., 2010; Thomson

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et al., 2010). There is also a growing body of literature describing soil biota in urban parks (microbes: Baxter et al., 1999; Xu et al., 2014; Ramirez et al., 2014; Hui et al., 2017a, b; nematodes: Pavao-Zuckerman and Coleman, 2007; Amossé et al., 2016, 2016; earthworms: Steinberg et al., 1997; Smetak et al., 2007). In a nutshell, these studies collectively provide evidence that urbanization can substantially change in soil microbial and faunal communities. Yet, there is a paucity of studies that simultaneously account for different trophic groups in large and well-replicated experimental designs within the context of urban ecosystems.

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

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

This study is part of a larger project that aims to shed light on the influence of divergent plant types on the physico-chemical and biological soil characteristics in urban parks of diverging ages. Our previous work has shown that plant type and park age are strong determinants of soil characteristics (Setälä et al., 2016, 2017) and soil microbial community composition (Hui et al., 2017a, b). However, the response of microbial biomass, a measure that strongly relates to the functional activity and capacity of soils, to plant type and park age remains unresolved. Moreover, in this study, we incorporate the microbial

consumer responses – key actors in providing soil-based ecosystem services and contributing to nutrient turnover (Wardle et al., 2004). We aim to investigate how park age and plant functional type affect the biomass of soil microbes and two important functional groups of soil fauna: nematodes and earthworms.

Given the clear effects that plant functional type and park age have on soil properties (see Setälä et al., 2016; Setälä et al., 2017) we tested the following hypotheses: plant functional type affects the soil food web so that i) evergreen trees producing recalcitrant litter promote an increase of fungal biomass over bacterial biomass and ii) deciduous trees. the lawn in particular, producing more labile litter, promote the establishment of bacterial biomass. Then we test iii) if changes in the soil microbial community also cascade up to higher trophic levels. We expect that higher densities of fungal feeding nematodes (compared to bacterial feeders) associate with evergreen trees and higher densities of earthworms associate with lawns and deciduous trees. Also, we test iv) whether time since park construction promotes changes in soil microbial and invertebrate community structure and abundance. We hypothesize that soil biota in old parks resemble natural communities more than in young parks. This is because the capacity of plants (especially trees) to modify soils is park-age dependent (Setälä et al., 2016, 2017) with young parks not having had the time to develop plant-soil interactions that are typical of natural forests.

2. Materials and methods

2.1. Study area

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

We selected 41 parks in the two cities and five additional control forests (see Setälä et al., 2016; Hui et al., 2017a for details). Parks of three ages were selected: young parks (between 7 and 15 years old), intermediate parks (ca. 50 years old) and old parks (> 100 years). Control forests, situated in the outskirts of the city of Lahti, are typified as unmanaged, conifer and linden dominated forests (> 80 years of age). Park size varied from one to several hectares. The selected parks were subjected to routine maintenance, including mowing (mowing residues not removed) and raking of tree leaves in the fall. However, the parks were not irrigated or commonly fertilized. Until the early 1990s, some of the older parks in the city of Lahti were occasionally fertilized - commonly with saltpeter (N, P, K, S), while some of the park lawns in Helsinki have received and still receive light refurbishment fertilization.

In each park we selected, where possible, three vegetation-types: deciduous (represented by *Tilia x vulgaris* 93% and *Acer platanoides* 7%) and evergreen trees (spruce, *Picea* sp. 43.3%, *Abies* sp. 20%, *Pseudostuga menziesii* 13.3%, *Pinus sylvestris* 13.3%, *Larix* sp. 10%) and a non-treed lawn with grass (including herbs such as *Trifolium pratense*, *Plantago major*). Lawn cover extended also under tree canopies. In some cases we selected parks including only deciduous trees and lawn or only evergreen trees and lawn. The control sites never had lawns, but deciduous (forest linden, *Tilia cordata*) and evergreen trees (Norway spruce, *Picea abies*) were always present at each site. In the parks, distance between

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