





PRIMARY RESEARCH ARTICLE

Urbanization minimizes the effects of plant traits on soil provisioned ecosystem services across climatic regions

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Funding information

Academy of Finland, Grant/Award Number: 315987

Abstract

An increasingly urbanized world is one of the most prominent examples of global environmental change. Across the globe, urban parks are designed and managed in a similar way, resulting in visually pleasing expansions of lawn interspersed with individually planted trees of varying appearances and functional traits. These large urban greenspaces have the capacity to provide various ecosystem services, including those associated with soil physicochemical properties. Our aim was to explore whether soil properties in urban parks diverge underneath vegetation producing labile or recalcitrant litter, and whether the impact is affected by climatic zone (from a boreal to temperate to tropical city). We also compared these properties to those in (semi)natural forests outside the cities to assess the influence of urbanization on plant-trait effects. We showed that vegetation type affected percentage soil organic matter (OM), total carbon (C) and total nitrogen (N), but inconsistently across climatic zones. Plant-trait effects were particularly weak in old parks in the boreal and temperate zones, whereas in young parks in these zones, soils underneath the two tree types accumulated significantly more OM, C and N compared to lawns. Within climatic zones, anthropogenic drivers dominated natural ones, with consistently lower values of organic-matter-related soil properties under trees producing labile or recalcitrant litter in parks compared to forests. The dominating effect of urbanization is also reflected in its ability to homogenize soil properties in parks across the three cities, especially in lawn soils and soils under trees irrespective of functional trait. Our study demonstrates that soil functions that relate to carbon and nitrogen dynamics—even in old urban greenspaces where plant–soil interactions have a long history—clearly diverged from those in natural ecosystems, implying a long-lasting influence of anthropogenic drivers on soil ecosystem services.

KEYWORDS

boreal, city, plant–soil interactions, temperate, total carbon, total nitrogen, tropical

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1 | INTRODUCTION

Urbanization, representing one of the clearest examples of global change, is a large-scale, human-caused manipulation that serves as a 'natural experiment', which provides opportunities to investigate ecosystem processes and services (Niemelä, 1999; Pouyat et al., 2010). Across much of the globe, parks with their managed lawns and individually planted trees are a common component of urban greenspaces. In addition to their recreational and social values, urban parks and particularly their soils provide ecosystem services such as water purification, detoxification of harmful substances, storing organic matter (OM) and minimizing N leaching via N sequestration (Pouyat et al., 2010). These heavily managed soils are also influenced by plant community composition (Ossola et al., 2015; Pouyat, Pataki, et al., 2007; Vauramo & Setälä, 2010). Recent studies indicate that, given enough time, plant functional types (such as conifers, deciduous trees, grasses and herbs) in managed urban parks in the boreal biome differ in their ability to modify (i) soil physicochemical characteristics (Setälä et al., 2016); (ii) soil microbial communities (Francini et al., 2018; Hui et al., 2017); and (iii) storage of C, N and heavy metals (Setälä et al., 2016, 2017). These results support the hypothesis that, similar to natural systems (Wardle et al., 2004), plant–soil interactions in the urban milieu are sensitive to plant functional type and may impact an array of ecosystem services in human-modified urban soils. This is most easily seen in old parks (with trees >50 years old) where plant–soil interactions have been in place for long enough for plants to modify the soils beneath them, at least under boreal climatic conditions (see Setälä et al., 2016). The question remains as to whether the effects of various plant functional types on soil properties and functions are generalizable across the globe in other biomes with differing climates.

Vegetation is fundamental in controlling soil formation and the composition of soil food webs, as well as driving ecosystem processes and services carried out by the soil biota (Hobbie, 2015; Ponge, 1993, 2003; Wardle, 2002). Functional attributes (including functional types and traits, *sensu* Grime, 1974, 1998) of dominant plants fine-tune larger-scale vegetation effects and further modify the functioning of the plant–soil system (Wardle et al., 2004). For example, plant types that produce labile, easily decomposable litter affect the soil fungal to bacterial ratio differently than those that produce slowly decomposing, recalcitrant litter with resultant divergent carbon and nutrient dynamics in the system (Bardgett & Wardle, 2010; Wardle et al., 2004). Plant-driven effects on soil carbon and OM can be strong enough to regulate important soil derived processes/ecosystem services to mitigate adverse effects of humans on their environment at local and global scales (Wall et al., 2015). In urban greenspace systems, anthropogenic drivers strongly influence natural plant–soil interactions, and their impact on ecosystem services may overcome natural constraints that occur in more natural systems (see Groffman et al., 2014, 2017; Pouyat, Pataki, et al., 2007; Pouyat et al., 2010). This is because intensive land-use caused by humans radically alters natural soil formation and communities, leading to biotic and ecological homogenization (Groffman

et al., 2014; Jenny, 1941; McKinney & Lockwood, 1999). This, in turn, can lead to convergence (i.e. increased similarity) of functional responses not only within cities when compared to native systems but also across cities (McKinney, 2006; Pouyat et al., 2003). Whether homogenization of habitats and biota paves the way to convergence of soil characteristics and functions, and whether plant–soil interactions are disconnected from natural climatic factors and thus less dependent on plant control is not known. A better and global understanding of this aboveground–belowground relationship in the urban milieu will inform us if, and to what extent, anthropogenic drivers dominate natural ones and whether this control is climate dependent.

Ecosystem services, such as the ability of soils to accumulate OM and retain nutrients, are generally controlled not only by plant type (Wardle et al., 2004) but also by the build-up of organo-mineral complexes (Cotrufo et al., 2013; Fry et al., 2018; Schmidt et al., 2011) in natural ecosystems. Recent evidence suggests that plant traits can control OM accumulation in urban greenspaces (Lu et al., 2021; Setälä et al., 2016), even when potential differences in organo-mineral complexes were not considered. In this study, we investigate the effects of vegetation that produce functionally dissimilar litters (recalcitrant vs. labile; hereafter referred to as vegetation type) on soil physicochemical characteristics across three locations that vary greatly in climate (i.e. in the boreal, temperate and tropical zones; referred to as climatic zone) and its vegetation. Our study system consists of young and old urban public parks that are strongly managed—but with no or negligible fertilizer addition or irrigation—and natural to semi-natural forest (as reference) within each of three cities (Lahti, Finland; Baltimore, USA; Singapore). In each of the three cities, we sampled soils from park lawns and at canopy edges of trees producing recalcitrant or labile litter, and from the same tree species in reference forests near the city (see Section 2). We divided our hypotheses into two groups (Figure 1a): those related to soil properties under vegetation types of varying ages in public urban parks across climatic zones (lower part of Figure 1a), and those comparing soils under vegetation types in old parks with reference sites (natural to semi-natural native forest in close proximity to the cities) across climatic zones (lower and upper parts of Figure 1a). These reference sites represent the original vegetation type of the region with minimal impacts of urbanization, including some management and climatic effects.

1.1 | Parks

First, we hypothesize that soils under trees producing recalcitrant litter (R; slow decomposition rate with higher accumulation of OM in the soil) will have higher concentrations of OM, carbon and nitrogen, compared to vegetation producing labile litter (L; faster decomposition) (see e.g. Cornwell et al., 2008; Figure 1a; $R > L$). However, we expect this controlling influence of vegetation type among climatic zones (Raich & Tufekciogul, 2000; Wisz et al., 2013) to diminish towards the tropics. This is because favourable climatic conditions in

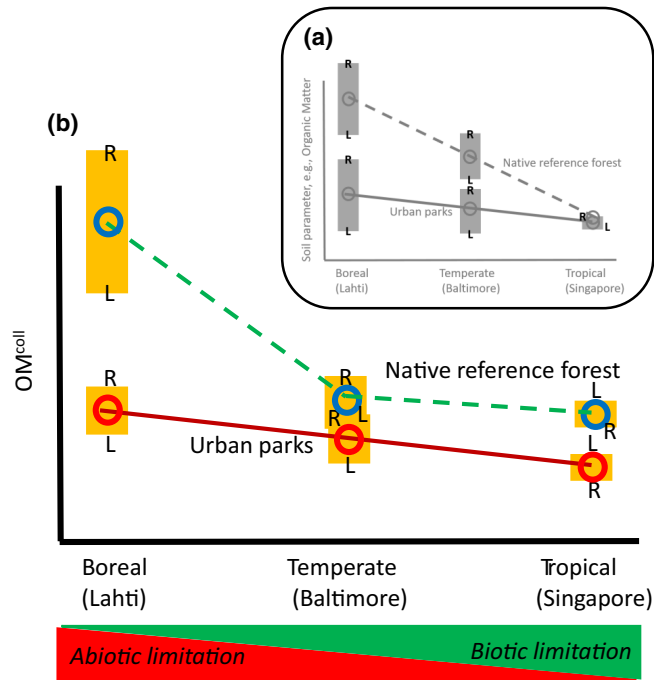


FIGURE 1 (a) Hypotheses tested in this study. Predicted responses of soil parameters (here organic matter) to biotic conditions (traits: plants producing recalcitrant [R] or labile [L] litter) along a climatic gradient (boreal, temperate and tropical). The dashed line represents the trend of a soil parameter in native soils (reference forests) along the climatic gradient whereas the solid line depicts the trend in soils in urban parks. The x-axis (boreal to temperate to tropical) relates to the degree to which the rate of decomposition determines the potential for organic matter (including total C and N) accumulation in the soil. (b) Summary of the main findings of this study. Note the narrowing of differences in soil properties underneath trees producing recalcitrant or labile litter (yellow bars), particularly in parks and in reference sites in the temperate and tropical zones. Additionally, differences between reference forests and parks narrowed in the temperate zone, but widened in the tropical zone. The grey and yellow boxes emphasize the expected and realized difference in the parameter value between trees producing recalcitrant and labile litter. The wedges below the graph illustrate limitations to biological activity

the tropics result in faster decomposition and thus a rapid loss of organic material irrespective of resource/litter type (Swift et al., 1979). Second, we hypothesize that differences in soil parameters across vegetation types and climatic zones would be greater in old parks compared to young parks, since older vegetation in old parks has modified soils for decades compared to younger parks with recently planted trees and lawn.

1.2 | Parks versus reference forests

Third, we hypothesize that concentrations of OM, carbon and nitrogen in the soil will be lower in urban parks compared to reference forests (Setälä et al., 2016). This is, for example, because

management practices characteristic of urban parks, such as the raking of leaves, reduce OM inputs into these disturbed ecosystems. Furthermore, the difference in these parameters between these habitat types (parks vs. reference forests) will be climate dependent so that the difference is large in the boreal zone, less so in the temperate zone, and low or non-existent in the tropics (Figure 1a: native reference forest vs. urban parks, the slope and narrowing gap between the dotted and solid lines). Ecological theory suggests that plant-trait structure should guide the outcomes of processes resulting from plant–soil interactions independently of the biome (Grime, 2001; Wardle et al., 2004). However, the favourable abiotic conditions for decomposition in the tropics unlikely limit biological activity in the soil, thus minimizing the role of habitat and vegetation type in affecting soil properties and processes, compared to the boreal zone where decomposition is hindered by adverse abiotic conditions while habitat and vegetation type play a larger role (Setälä et al., 2016, 2017). Fourth, relative to natural/semi-natural native forest, we hypothesize a convergence of soil physicochemical properties in parks across these three climatic zones where anthropogenic drivers dominate natural ones (Groffman et al., 2017; Pouyat et al., 2015, 2017). Essentially, we expect that soils under lawns and trees in young urban parks are more similar (i.e. converge) across biomes than soils under these cover types in old parks. This is because age and local climate will gradually become more important in the development of plants, soils and plant–soil interactions in parks that are not irrigated or fertilized.

2 | MATERIALS AND METHODS

This study was performed in three cities in three climatic zones: boreal (Lahti, Finland), temperate (Baltimore, USA) and tropical (Singapore), with a similar field design implemented in each city (see Table 1 for details). Throughout the manuscript, we used the terms boreal, temperate and tropical zones or cities with the understanding that the cities investigated are situated in these climatic zones, but are not necessarily representations of the entire zone. Ideally, 10 similarly managed public parks, five young (10–20 years) and five old (>60 years, up to 200 years), were selected per zone, each park with representatives of three distinct vegetation types that are typical to that area and that differ in their functional types and traits. The three vegetation types—selected based on decomposability of the litter produced by the plants (Grime, 2001)—included (1) lawns dominated by highly labile grasses and forbs; (2) tree species producing labile litter and (3) tree species producing recalcitrant litter. In the boreal city, the labile tree was linden (*Tilia × vulgaris*, C/N ratio = 31.6) and the recalcitrant tree was Norway spruce (*Picea abies*, C/N ratio = 72). In the temperate city, the labile tree was the tulip tree (*Liriodendron tulipifera*, C/N ratio = 43) and the recalcitrant tree was oak (*Quercus* spp., C/N ratio = 75.9). In the tropical city, the labile tree was tembusu (*Cyrtophyllum fragrans*, C/N ratio = 69.4) and the recalcitrant tree was the rain tree (*Samanea saman*, C/N ratio = 20). The C/N ratio of senescent leaves was used to classify

TABLE 1 The locations (from Google Earth), climate, primary parent material, soil order and human population size (in 2020) of the three cities investigated in the three climatic zones

Climatic zone	City	Location	Climate	Parent material	Soil order	Population
Boreal	Lahti, Finland	60°58'57.74"N 25°39'40.29"E	Boreal-hemiboreal	Granite/till	Spodosol	120,000
Temperate	Baltimore, USA	39°17'24.73"N 76°36'43.89"W	Humid-subtropical	Igneous/metamorphic/ unconsolidated material	Alfisols and Ultisol	593,490
Tropical	Singapore	1°21'7.47"N 103°49'11.40"E	Humid-tropical	Igneous/sedimentary	Ultisol and oxisol ^a	5,703,600

^aLeitgeb E, Ghosh S, Dobbs M, Englisch M, Michel K 2019. Distribution of nutrients and trace elements in forest soils of Singapore. *Chemosphere* 222, 62–70.

trees as either labile or recalcitrant (Taylor et al., 1989), and in the case of the rain tree in Singapore, also the exceptionally high polyphenolic content, which makes the leaves decompose slowly (Rita et al., 2018). All park plots were covered with lawn (C/N ratio of grasses and herbs ~12–40, with the highest ratio in Singapore), including plots sampled underneath the tree canopies. As a result, our experimental design was, in essence, lawn with and without trees, which either produce recalcitrant or labile litter. The parks selected had little to no fertilization or irrigation, with leaves raked and removed, and grass clippings left on site. Although C and N input to the soil from leaves is minimal in these managed parks, there is ample evidence that tree fine roots are large contributors to stable soil OM formation (Cotrufo et al., 2013; Persson, 2012), especially at shallow soil depths (Jackson et al., 2017; Jobbágy & Jackson, 2000). Our design also included five reference sites (semi-natural to natural native forest) for each climatic zone, with no or minimal management and, except in the tropics, with a well-developed leaf-litter layer. These reference sites included the same mature labile and recalcitrant tree species as in the parks with significant annual litter input, but without lawn, and were either within the city limits or adjacent to the city. Reference forests in the boreal city are protected with no disturbance other than, in some cases, forest logging and/or thinning more than ca. 100 years ago. Reference forests in the temperate city have not been managed for at least 100 years. Reference forests in the tropical city were between 60 and 150 years old, and developed via natural processes after the cessation of various anthropogenic activities, including dairy farming, tree crops or were part of botanical gardens.

In 2019, we established 40 study plots per city (10 public parks × 3 vegetation types + 5 reference sites × 2 vegetation types), totalling 120 plots across the three climatic zones (see <https://www.google.com/maps/d/u/0/viewer?mid=1XLYE2s4-PTbWzW8IAsqdqxxH6cb9UUzV&ll=34.831620442620356%2C13.62469550000003&z=2>, and Table S1). In some cities, more than 10 public parks were sampled because all vegetation types were not present in each park. The plots were established between 2 and 8 March in the tropical zone (Singapore), between 7 and 13 May in the boreal zone (Lahti) and between 6 and 16 June in the temperate zone (Baltimore). In parks, plots were established at the outer edge of the canopy projection of the trees so that distance

to the nearest tree trunk ranged from 1 m (young park trees) to several meters (old park trees and reference trees), whereas lawn plots were placed in open lawn areas away from any tree, at a distance greater than the height of the nearest tree. The canopy was closed in all reference sites.

Physicochemical parameters were analysed from a mixture of organic and mineral soils (the A-horizon with earthworms present across all zones) collected from each of the 120 plots using a metal soil corer (diameter = 2.54 cm) to a depth of 10 cm. The uppermost organic layer (the O-horizon composing mainly of grass litter mixed with grass roots) was removed. We only sampled the top soil layer since we were not interested in the legacy effect of vegetation on soil properties, typical in deeper soil layers as a decoupling between current vegetation and organic carbon pools, including root biomass (Conant et al., 2001; Jackson et al., 2017; Jobbágy & Jackson, 2000; Yaling et al., 2010). Additionally, by focusing on the top 10 cm, we minimized the influence of parent soil texture on these parameters (Fry et al., 2018). Our previous work in Finland (Setälä et al., 2016) concluded that the uppermost soil layer in urban parks and reference forests has the greatest concentration of OM, carbon and nitrogen, and is often the most responsive layer to vegetation type (see Jobbágy & Jackson, 2000). The top 2 cm of turf and soil was carefully removed from the corer and used as a cap to cover the hole made once the soil sample was placed into a plastic bag. Three subsamples were collected per plot and mixed thoroughly in one plastic bag, resulting in a homogenized sample of ca. 100 g per plot. All soils were analysed at the University of Helsinki in Lahti. After passing the soil through a 2 mm sieve to remove larger mineral particles, roots and other organic debris, the following variables were measured; pH (1:5 v/v, fresh soil/distilled water), bulk density (bulk density sampling kit [Part # 400.80; AMS, Inc.] according to the manufacturer's instructions), percentage OM (% OM; loss on ignition, 5 h at 550°C in a muffle furnace), total carbon (C), total nitrogen (N) and the C/N-ratio. Total carbon and nitrogen were analysed by dry combustion at 1350°C using a LECO CNS-2000 Elemental Analyzer (0.07% C and 0.09% N detection limits).

All statistical analyses were performed in R ver. 3.6.3 (R Core Team, 2020). Three analyses were performed, the first to compare vegetation type in parks of different ages across climatic zones (*Parks*), and the second and third to compare soils under

park trees with soils under trees in reference sites (no lawn samples included; *Parks vs. reference*). First, a linear mixed model was used to evaluate how soil variables under vegetation producing very labile litter (lawn), labile litter (labile tree) or recalcitrant litter (recalcitrant tree) change as parks age (young vs. old parks), and whether this relationship is influenced by climatic zone. The *lmer* function in the *lme4* library (Bates et al., 2015) in R was used to construct the following model: response (the soil variable measured)~climatic zone*park age*vegetation type. Climatic zone is a three-level factor including boreal, temperate and tropical; park age is a two-level factor including young and old parks; vegetation type is a three-level factor including labile lawn, labile tree and recalcitrant tree. Park identity was included as a random effect to account for multiple vegetation types per park. Models were simplified by removing the three-way interaction from all models since none were statistically significant ($p < 0.05$). Second, a linear mixed model was used to evaluate the hypothesis that the relationship between soil variables under trees producing labile or recalcitrant litter is either mediated by the biotic or abiotic environment (*Parks vs. Reference*). The following *lmer* model was constructed: response (the soil variable measured)~climatic zone*habitat type+climatic zone*vegetation type. Habitat type is a two-level factor including reference sites and old parks (young parks were excluded due to their recent management legacy, which presumably overrides vegetation effects); vegetation type is a two-level factor including labile tree, recalcitrant tree. Again, park identity was included as a random term. The two two-way interactions were included since we were primarily interested in the effects of the climatic zone on habitat type and on vegetation type, and not on the general effect of habitat type on vegetation type. Third, we determined whether soil physicochemical parameters of park trees producing labile and recalcitrant litter converged across climatic zones using the coefficient of variation (CV). This statistical metric is normalized by the mean allowing direct comparisons between soil parameters. A lower CV indicates higher similarity in parameters across climatic zones, thus permitting inferences about divergence/convergence among treatment. Soil parameters under different litter types (trees producing labile litter, trees producing recalcitrant litter) were compared between reference and park sites.

3 | RESULTS

3.1 | Vegetation type and park age affect soil physicochemical properties inconsistently in parks across climatic zones

Soil C and N concentrations decreased from the boreal to the temperate city (by ca. 20% for C, 20% for N) and from the boreal to the tropical city (by 55% for C, 46% for N; Figure 2; Table 2), with values generally higher in soil under trees than under lawns, and older parks having higher values than younger parks (by ca. 6% for C, 18%

for N) except for the tropical city where older parks displayed lower values (by ca. 21% for C, 27% for N). Our results do not support the hypothesis that the difference in soil parameters under recalcitrant versus labile vegetation would be greatest in urban parks in the boreal zone and non-existent in the tropics (bars associated with the solid line in Figure 1a). Results only partly supported our hypotheses that vegetation type has a universal effect on the levels of C, N and OM in park soils, and that differences in these parameters would consistently be greater in old relative to young parks. We found high OM in the boreal city (ca. 9.6%), and lowest values in old parks under both labile and recalcitrant trees in the tropical city (5.9%). The soil C/N-ratio showed an inconsistent pattern but was higher in park soils under labile trees in the tropical and particularly the temperate city.

Variation in soil pH increased from boreal to temperate to tropical, with particularly high means under lawns in the tropics (Table 2; Figure 2). Soil pH was consistently low under old trees producing recalcitrant litter. Overall, older parks appeared to have lower soil pH than younger parks, but this depended on vegetation type. Soil bulk density (BD) was lower under trees and higher under lawns, particularly in the boreal and temperate cities. Furthermore, BD was generally higher in the tropics, especially in old parks.

3.2 | Soil physicochemical property differences between reference forests and old parks

Our hypothesis that the effects of habitat type on soils are greatest in the city in the boreal zone compared to the temperate and tropical cities (decreasing abiotic constraints) is supported, especially for % OM, C and N (Table 3; Figure 3, see the slope and gap between the dotted and solid lines in Figure 1a). In the boreal city, values for these three parameters were significantly higher in the reference sites compared to the old parks (by ca. 39% for OM, 46% for C, 32% for N). The same pattern was observed in the temperate (by ca. 12% for OM, 17% for C, 4% for N) and tropical cities (by ca. 33% for OM, 44% for C, 29% for N), with differences between reference and old park soils smallest in the temperate city. The influence of vegetation type (recalcitrant vs. labile) on % OM, C and N was more pronounced in the boreal city, less so in the temperate city and practically non-existent in the tropical city.

Soil pH, BD and the C/N-ratio did not follow the pattern we detected for % OM, C and N (Table 3; Figure 3). In both the boreal and temperate cities, pH was lower in soils under recalcitrant trees, but was higher under recalcitrant trees in tropical soils. BD increased from boreal to temperate to tropical soils (except for high values in boreal urban parks), with values lower for soils under recalcitrant trees compared to labile trees, but again, this pattern was reversed for tropical soils. The soil C/N-ratio showed no consistent pattern across zones: it was higher in soils under recalcitrant trees in the boreal city, but higher in soils under labile trees in both the temperate and tropical cities. The C/N-ratio was lower in park soils compared to reference soils.

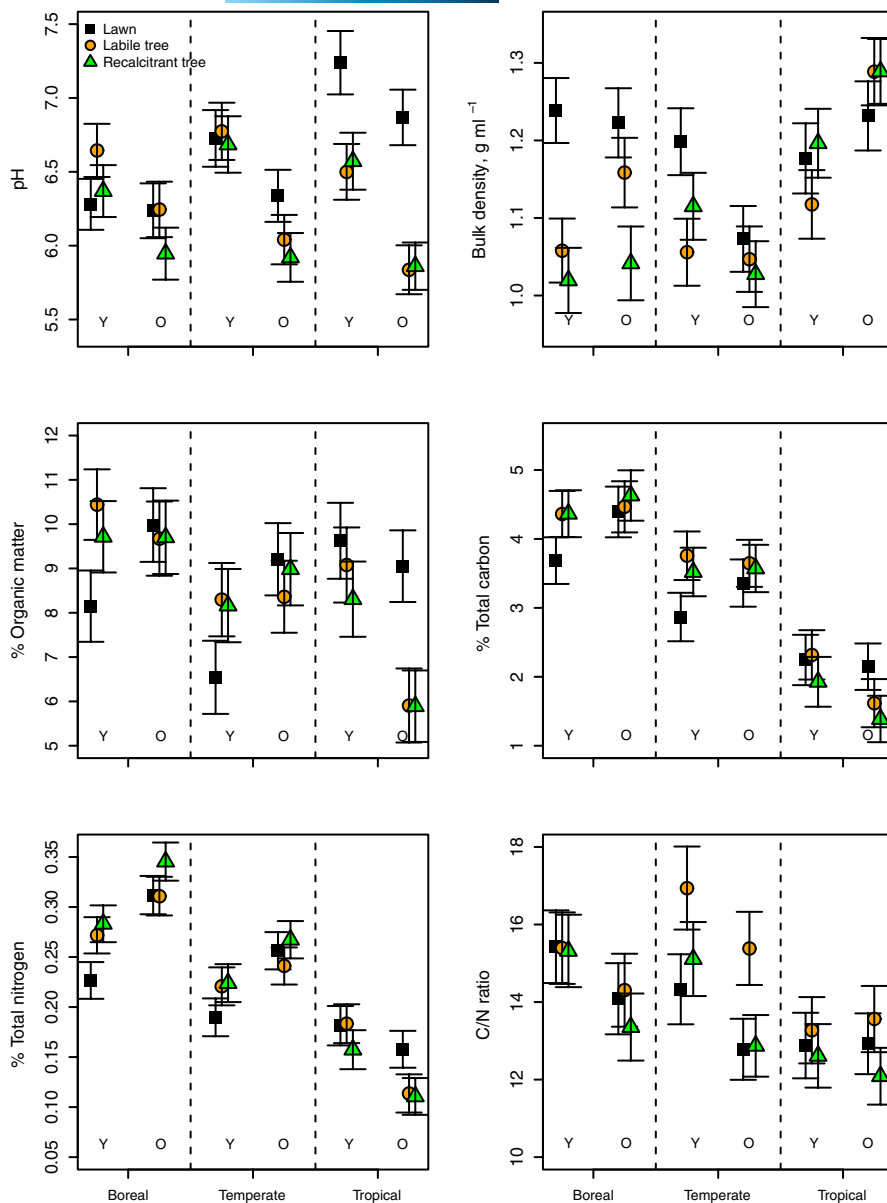


FIGURE 2 The effects of vegetation type and park age on soil pH, bulk density, percentage organic matter, total carbon, total nitrogen and the C/N-ratio across three biomes (boreal, temperate and tropical). Predicted means \pm SE values ($n = 5$) are presented, see Table 2. O, old parks; Y, young parks

3.3 | Soil properties convergence across climatic zones

Most of the soil properties measured (% OM, C, N, pH, BD), independent of vegetation type, converged across climatic zones as depicted by their CV (Figure 4), that is, variation was lower in urban parks than in the reference sites. Convergence was also evident for the C/N-ratio in soils under trees producing recalcitrant litter but not under trees with labile litter. In general, convergence was highest (low CV) in soils in young parks and lawns, and for % OM, C and N, while soils in old parks showed low convergence (high CV, thus higher variation) across biomes, similar to variation displayed by these parameters in reference sites.

4 | DISCUSSION

We explored whether the effects of urbanization on C and N dynamics in urban greenspace soils are similar in cities located in

three climatic zones. More specifically, we studied the degree to which plant functional types modify the soils beneath them in public urban parks, and whether these changes take place independently of climatic region. We demonstrated that—as with natural ecosystems—vegetation trait (trees producing recalcitrant or labile litter, and lawn) plays a significant, yet variable role in influencing soil physicochemical characteristics in urban parks (Bardgett & Wardle, 2010; Pouyat et al., 2007; Setälä et al., 2016), and that the strength of this effect is modulated by climate and urbanization. Indeed, urbanization per se affected soil properties more than vegetation type, as demonstrated by the greater differences in soil characteristics observed between reference forests versus urban parks than between soils under the plant functional types (Figures 1b and 3). In essence, our results support the notion that anthropogenic drivers, including park management, dominate natural constraints, such as plant–soil interactions, which is supported by differences observed in soil parameters between

TABLE 2 Linear mixed-effects model results, testing the effects of biome (boreal, temperate and tropical), vegetation type (lawns, labile trees and recalcitrant trees) park age (young and old) and their two-way interactions on six soil physicochemical properties

	Interc	Temp	Trop	Labile	Recalc	Old	Temp × Labile	Trop × Labile	Temp × Recalc	Trop × Recalc	Temp × Old	Trop × Old	Labile × Old	Recalc × Old
pH	1.837 (0.036) <0.001	0.069 (0.050) 0.169	0.142 (0.051) 0.005	0.057 (0.036) 0.115	0.014 (0.033) 0.669	-0.007 (0.049) 0.887	-0.049 (0.041) 0.231	-0.164 (0.041) < 0.001	-0.020 (0.040) 0.610	-0.111 (0.041) 0.007	-0.053 (0.058) 0.366	-0.046 (0.058) 0.433	-0.055 (0.034) 0.101	-0.062 (0.033) 0.059
Bulk density	1.239 (0.055) <0.001	-0.040 (0.075) 0.591	-0.062 (0.077) 0.425	-0.181 (0.062) 0.004	-0.219 (0.060) < 0.001	-0.016 (0.073) 0.826	0.038 (0.073) 0.601	0.121 (0.075) 0.104	0.136 (0.072) 0.060	0.239 (0.075) 0.001	-0.109 (0.086) 0.202	0.071 (0.086) 0.414	0.116 (0.060) 0.053	0.038 (0.060) 0.526
Organic matter	8.150 (1.056) <0.001	-1.606 (1.428) 0.261	1.475 (1.460) 0.312	2.292 (1.240) 0.065	1.566 (1.196) 0.190	1.831 (1.342) 0.173	-0.539 (1.471) 0.714	-2.838 (1.478) 0.055	0.053 (1.448) 0.971	-2.883 (1.466) 0.049	0.834 (1.580) 0.598	-2.403 (1.595) 0.132	-2.598 (1.199) 0.030	-1.843 (1.187) 0.121
Carbon	3.685 (0.444) <0.001	-0.818 (0.617) 0.185	-1.441 (0.629) 0.022	0.677 (0.440) 0.123	0.680 (0.407) 0.094	0.706 (0.607) 0.245	0.212 (0.505) 0.675	-0.603 (0.507) 0.234	-0.027 (0.487) 0.956	-0.997 (0.499) 0.046	-0.213 (0.719) 0.767	-0.804 (0.718) 0.263	-0.603 (0.410) 0.142	-0.442 (0.401) 0.270
Nitrogen	0.227 (0.024) <0.001	-0.037 (0.033) 0.261	-0.045 (0.034) 0.178	0.045 (0.027) 0.099	0.057 (0.026) 0.030	0.085 (0.031) 0.006	-0.014 (0.032) 0.660	-0.043 (0.032) 0.183	-0.022 (0.032) 0.477	-0.081 (0.032) 0.012	-0.019 (0.037) 0.611	-0.109 (0.037) 0.003	-0.046 (0.026) 0.079	-0.023 (0.026) 0.371
C/N-ratio	2.736 (0.079) <0.001	-0.074 (0.110) 0.501	-0.181 (0.112) 0.107	-0.002 (0.082) 0.976	-0.007 (0.077) 0.927	-0.091 (0.107) 0.393	0.170 (0.095) 0.075	0.033 (0.096) 0.734	0.060 (0.093) 0.516	-0.014 (0.094) 0.884	-0.023 (0.127) 0.854	0.095 (0.127) 0.456	0.018 (0.078) 0.817	-0.046 (0.076) 0.544

Note: Values presented include the coefficient, the standard error (in parenthesis) and p value. Statistically significant effects ($p < 0.1$) are highlighted in bold. Young lawns in the boreal biome is in the intercept.

Abbreviations: Interc, model intercept; Recalc, recalcitrant; Temp, temperate; Trop, tropical.

TABLE 3 Linear mixed-effects model results, testing the effects of biome (boreal, temperate and tropical), habitat age (old, reference), vegetation type (labile trees and recalcitrant trees) and their two-way interactions on six soil physicochemical properties

	Intercept	Temperate	Tropical	Reference	Recalcitrant	Temp × Reference	Trop × Reference	Temp × Recalc	Trop × Recalc
pH	6.269 (0.308) < 0.001	-0.208 (0.433) 0.630	-0.722 (0.455) 0.113	-0.806 (0.362) 0.026	-0.187 (0.259) 0.470	0.824 (0.484) 0.089	0.740 (0.488) 0.129	0.058 (0.366) 0.874	0.374 (0.405) 0.356
Bulk density	1.116 (0.048) < 0.001	-0.059 (0.068) 0.385	0.165 (0.070) 0.018	-0.304 (0.058) < 0.001	-0.025 (0.049) 0.619	0.253 (0.079) 0.001	0.186 (0.079) 0.018	-0.026 (0.069) 0.703	0.084 (0.073) 0.245
Organic matter	2.236 (0.119) < 0.001	-0.138 (0.169) 0.414	-0.630 (0.173) < 0.001	0.501 (0.140) < 0.001	0.088 (0.126) 0.486	-0.372 (0.195) 0.057	-0.102 (0.196) 0.601	0.016 (0.179) 0.931	-0.050 (0.185) 0.785
Carbon	1.432 (0.129) < 0.001	-0.260 (0.183) 0.155	-1.109 (0.190) < 0.001	0.617 (0.153) < 0.001	0.129 (0.126) 0.305	-0.437 (0.210) 0.038	-0.032 (0.211) 0.881	-0.025 (0.178) 0.887	-0.268 (0.190) 0.159
Nitrogen	-1.165 (0.121) < 0.001	-0.347 (0.171) 0.042	-1.100 (0.177) < 0.001	0.378 (0.143) 0.008	0.071 (0.124) 0.567	-0.334 (0.198) 0.092	-0.031 (0.199) 0.877	0.080 (0.176) 0.648	-0.093 (0.185) 0.615
C/N-ratio	2.611 (0.080) < 0.001	0.089 (0.112) 0.428	-0.084 (0.118) 0.476	0.200 (0.093) 0.032	0.067 (0.065) 0.304	-0.103 (0.124) 0.406	0.097 (0.125) 0.438	-0.111 (0.092) 0.225	-0.140 (0.102) 0.170

Note: Values presented include the coefficient, the standard error (in parenthesis) and the *p* value. Statistically significant effects (*p* < 0.1) are highlighted in bold. Old labile tree plots in the boreal biome is in the intercept.

Abbreviations: Recalc, recalcitrant; Temp, temperate; Trop, tropical.

reference forests and parks and the clear convergence of these parameters in young parks and lawns. As C is the 'common currency' controlling virtually all ecosystem processes (Reekie & Bazzaz, 1987), our discussion focuses primarily on soil OM and C, and also N because of its close association with C in biogeochemical cycles (Vitousek et al., 1997). With a few minor exceptions, these three soil parameters responded similarly to habitat and vegetation type across our study design and for simplicity, we will refer collectively to them as OM^{coll}. We recognize the important role of microbial residues and the formation of organo-mineral complexes to stabilize soil OM (Cotrufo et al., 2013; Dungait et al., 2012); however, we focused on the effects of plant traits on soil properties in this study.

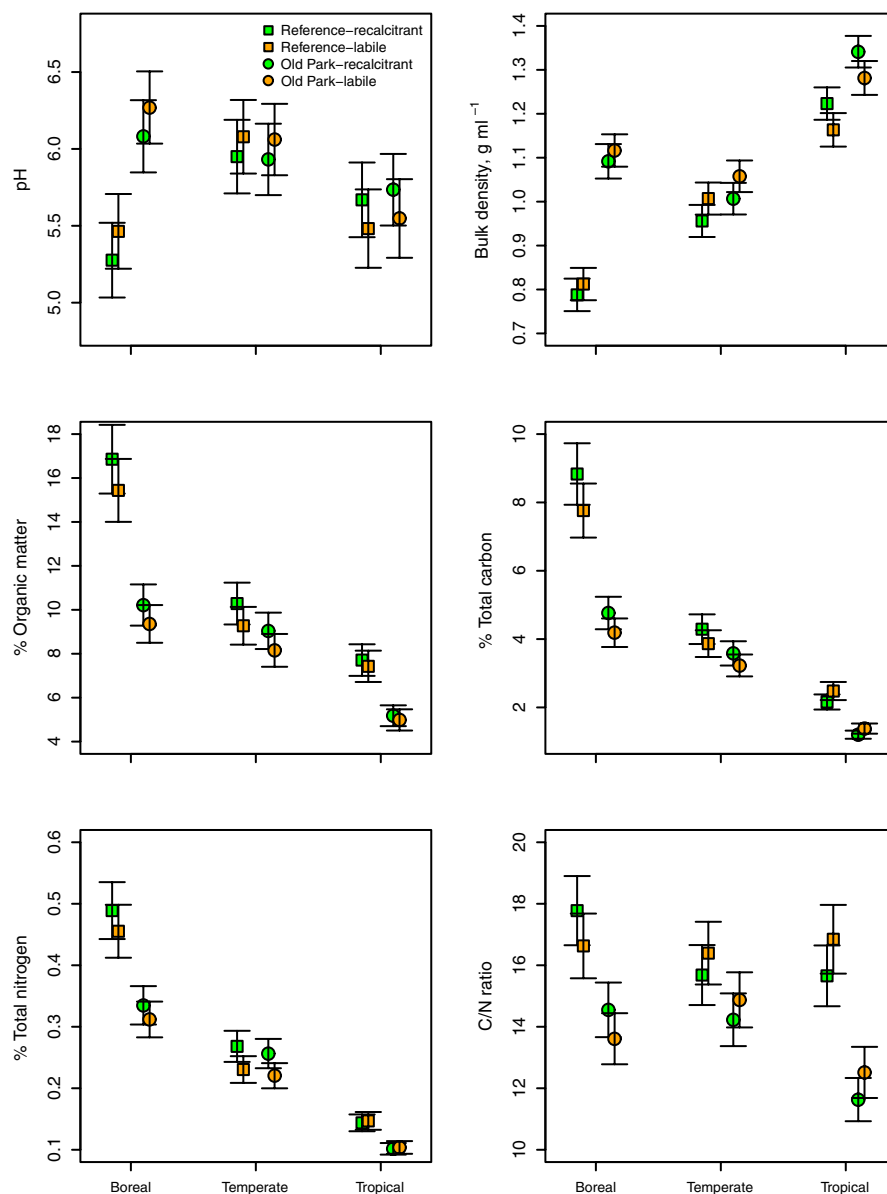
We will first focus our discussion to plant-soil interactions within urban parks. Next, we explore the hypothesis that concentrations of OM^{coll} in the soil will be higher in reference forests compared to old urban parks. Finally, we explore whether the effects of humans in urban parks across biomes, that is, management, lead to convergence of ecosystem functioning in these strongly managed systems.

4.1 | Climatic zone influences the impact of vegetation type and park age on soil properties

Contrary to our two *urban park* hypotheses, soil physicochemical properties were not uniformly affected by vegetation across climatic zones: (i) vegetation producing recalcitrant litter did not have consistently higher concentrations of OM^{coll} than vegetation producing labile litter across climatic zones; and (ii) the difference in soil parameters under vegetation producing labile versus recalcitrant litter did not diminish towards the tropics. Furthermore, these parameters did not systematically become more dissimilar with park age. Our results suggest that, in the absence of aboveground litter input from trees due to continuous maintenance practices such as the removal of litter by raking, the length of time plants have had to modify their soils—that is, park age—is not sufficient to produce differences in soil properties under vegetation of different traits in these highly disturbed systems. In essence, disturbances in young and old urban parks, including trampling, grass mowing and the removal of leaves by raking may prevent plant-soil interactions from reaching a steady state even decades after park construction, resulting in similar soil properties under different vegetation types regardless of park age. Furthermore, urban parks receive an initial input of mulch, unlike most natural systems where OM accumulates with time (Vogt et al., 1995), thus minimizing the effect of park age.

The accumulation of OM^{coll} in urban park soils did, however, show three general patterns. First, in old parks, and to some extent also in young parks, soil OM^{coll} decreased from the boreal to temperate to the tropical city, likely due to management practices (Velasco et al., 2021) and favourable climatic conditions in the tropics that lead to high decomposition rates and a loss of C via respiration and leaching (similar to natural ecosystems, see Hättenschwiler et al., 2011; Makkonen et al., 2012). Second, OM and C were generally

FIGURE 3 The effects of vegetation type and habitat type on soil pH, bulk density, percentage organic matter, total carbon, total nitrogen and the C/N-ratio across three biomes (boreal, temperate and tropical). Predicted means \pm SE values are ($n = 5$) presented, see Table 3. The old park data presented here are the same as presented in Figure 2, with slight differences due to model predicted values



unresponsive to tree type and park age in both the boreal and temperate cities investigated, but decreased with park age in the tropical city. This latter result from the tropics contradicts results from parks in Helsinki and Lahti, Finland (Setälä et al., 2016), park-like golf courses in Melbourne (Livesley et al., 2016) and more natural forested ecosystems (Badalamenti et al., 2019; Lewis et al., 2014) where soil C increases with time. As was discussed above, the likely reasons for our result of no difference in soil properties under young versus old trees or those producing labile versus recalcitrant litter are related to management: these public parks receive little to no fertilization or irrigation after establishment and experience continuous and uniform maintenance in terms of mowing and the removal/raking of tree leaf litter (but not grass litter), preventing the accumulation of OM and C in their soils. Total N, however, increased from young to old park soils in the boreal and temperate cities but was only slightly higher under trees producing recalcitrant litter, but an opposite pattern was found in the tropical city. This lack of a clear

litter type effect on N is not surprising given that differences in litter quality have only a small influence on N cycling within ecosystems as most of the N in plant litter is incorporated into soil OM after decomposition so that soil N cycling is primarily determined by OM decomposition (Knops et al., 2002). Additionally, OM^{coll} was generally higher in young than in old park soils in the tropical city. This may be due to favourable climatic conditions in the tropics that result in rapid initial decomposition and C loss, disappearance over time of the OM in the initial soil used to establish the parks, and that the intensive leaf raking of parks limits the input of aboveground OM. These results suggest that, contrary to our hypotheses, surface soils under either young or old trees that produce recalcitrant litter do not accumulate OM or sequester C any better than trees producing labile litter because of management effects (Setälä et al., 2016).

Third, OM^{coll} under lawn was lower than under labile and recalcitrant trees, but only for young parks in the boreal and temperate cities. Essentially, this pattern suggests that with time, OM^{coll}

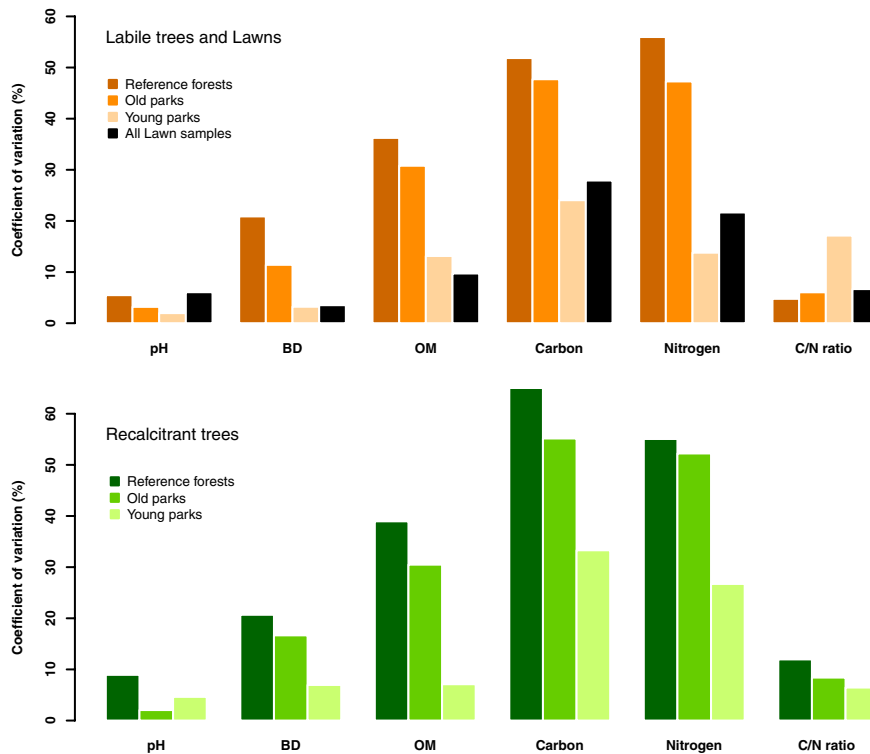


FIGURE 4 Coefficient of variation (presented as a percentage) for the six soil physicochemical properties measured across biomes. Soils under labile trees and all lawns (upper panel), and recalcitrant trees (lower panel) were analysed separately

does accumulate in these higher-latitude unfertilized park lawns, at least in the top 10 cm analysed here. Although lawns produce highly labile grass and herb litter that is rapidly mineralized to CO_2 (Lilly et al., 2015; Lu et al., 2021; Thomson & Kao-Kniffin, 2019), in old parks it may be that the continuous, long-term input of grass clippings (which are not removed) together with dead root input results in the accumulation of OM^{coll} (see also Bae & Ryu, 2015; Golubiewski, 2006; Raciti et al., 2011). Note that these park lawns are not fertilized, yet accumulate OM^{coll} , in a similar manner to residential lawns that do receive considerable fertilization and irrigation (Trammell et al., 2020). Unexpectedly, in the tropical city, soil OM^{coll} was higher under lawns compared to under the two tree types, especially in old parks. Interestingly, in these low-latitude parks, the concentration of OM^{coll} was similar under young and old lawns, whereas OM^{coll} decreased significantly under both labile and recalcitrant trees with park age. The increase in OM^{coll} with time in the upper boreal and temperate lawn soils observed here is similar to that found in Helsinki and Lahti, Finland (Setälä et al., 2016), showing that with time, park lawns can provide an important ecosystem service in terms of C and N sequestration (Bae & Ryu, 2015; Pouyat et al., 2006; Raciti et al., 2011). It is noteworthy, that—besides vegetation type—soil texture is also crucial in affecting soil OM content (Fry et al., 2018), suggesting that the influence of plant functional type on soils and the ecosystem services they provide can be conditional on soil type. However, the role of organo-mineral complexes in controlling decomposition rate is likely much stronger in the deeper soil layers than in the top soil where the input of new litter and fine roots continuously supply free particulate OM (Cotrufo et al., 2013; Jackson et al., 2017; Schmidt et al., 2011).

4.2 | Habitat type (old parks versus reference forest) affects OM^{coll} more than vegetation type

As depicted in Figure 1b, climate plays a significant role in influencing OM^{coll} in the soils of both old urban parks and reference forests, with highest values in the boreal city and lowest in the tropical city. This is expected primarily because rates of photosynthesis, and thus net primary production, exceed microbial decomposition at higher latitudes (Averill et al., 2014; Crowther et al., 2019; Schlesinger, 1997).

Furthermore, our finding that OM^{coll} was higher in reference forest soils compared to soils under trees in old urban parks, particularly in the boreal and tropical cities, is consistent with our hypothesis (Figure 1: native reference forest vs. urban parks, the narrowing gap between the green dotted line and the solid red line) and with our previous work in two boreal cities in Finland (Helsinki and Lahti; Setälä et al., 2016). These results suggest that the habitat effect (i.e. reference forests vs. old parks) on soil properties is universally strong and clearly exceeds vegetation type effects (i.e. labile vs. recalcitrant litter). Various non-competing mechanisms may explain this pattern. First, more litter enters the system in natural environments compared to scattered trees in parks due to (i) the higher density of trees and other vegetation in natural environments; and (ii) management, that is, mowing, pruning and the raking of tree leaves in parks. Second, as with aboveground litter, fine root and exudate production, which is another important source of OM (Lin et al., 2020; Persson, 2012; Vesterdal et al., 2008) especially in the upper soil layers (Jobbágy & Jackson, 2000), is higher in reference forests compared to urban parks, at least in the boreal zone (Lu et al., 2021). For example, Clemmensen et al. (2013) estimate that as much as 70%

of stored C in boreal forest soils comes from roots and their associated organisms. Given that root-to-shoot ratios remain equal among biomes (Cairns et al., 1997) or tend to increase with latitude (Qi et al., 2019), it is likely that the contribution of roots in forming OM^{coll} is also of significance in temperate and tropical climates, especially in semi-natural to natural reference forests compared to scattered trees in parks. Finally, as (micro)climate can control both NPP and decomposition rate (Knapp et al., 2014; Liski et al., 2003), its potential influences on differences in OM accumulation within biomes between the two habitat types cannot be ruled out.

We expected differences in soil properties between reference forests and old parks to be greatest in the boreal city where abiotic limitations on NPP and decomposition are the greatest (see Figure 1a), especially for soil properties directly affected by biogenic processes (here OM^{coll} ; Pouyat et al., 2015). These differences were expected to decrease towards the tropics with low or non-existent abiotic limitations on NPP and decomposition rate (Figure 1a). Contrary to expectation, OM^{coll} concentrations in reference forests in the tropical city were double than that in urban park soils, similar to what we observed in the boreal zone (Figure 1b): note however that absolute OM^{coll} differences between reference and park soils were greater in the boreal city compared to the tropical city. Although climate appears to have an overall effect on the reduction in soil OM^{coll} with decreasing latitude, habitat type (reference vs. old parks; essentially urbanization) strongly affected soil properties within climatic zones. We can only speculate on why there was still a significant difference in OM^{coll} between reference forests and old park soils in the tropical city, similar to what we observed in the boreal city, but not in the temperate city. For instance, in all climatic zones investigated, litter does not accumulate in parks due to active management, thus the observed lower OM^{coll} values in old parks compared to reference forests across climatic zones. In boreal zone forests, limitations on NPP and decomposition (due to cold climate and a short growing season) result in the accumulation of OM on the forest floor. In the tropics, aboveground and belowground litter in reference forests enters the system continuously throughout the year, but here the decomposition of generally low-quality leaf litter is relatively slow enough to result in the accumulation of OM in the soil, see the so-called syndrome of poor litter quality (Hättenschwiler et al., 2011; Makkonen et al., 2012). These processes likely result in an elevated OM^{coll} in tropical reference forests compared to old parks where aboveground tree litter is efficiently removed. In essence, both boreal and tropical zones experience resource limitation but via different mechanisms: resources, such as nutrients, are stored in the litter and humus layers in the cool boreal zone, while in the vegetation in the tropical zone, similar to the pattern observed for carbon stocks (see Crowther et al., 2019). In the temperate zone, differences in OM^{coll} between reference forests and old parks were minimal (yet slightly higher in reference forests). That we found little evidence for our hypothesis that differences in soil parameters between reference forests and old parks would be greatest in the boreal city and non-existent in the tropical city (compare the solid and dashed lines in Figure 1), may not be surprising given that meta-analyses

have concluded that resource quality in leaf litter can have stronger effects on litter decomposition than climate parameters (Cornwell et al., 2008; Zhang et al., 2008; see also Makkonen et al., 2012). Furthermore, evidence also suggests that composition of the microbial community can drive carbon storage. Averill et al. (2014) showed that—even after accounting for temperature and moisture effects in their decomposition model—ectomycorrhizal and ericoid mycorrhizal (EEM) fungal systems typical to the boreal zone store 1.7 times more carbon per unit soil than do arbuscular mycorrhizal fungal systems that are prevalent in the tropics. This is in line with our results, both at the habitat type and plant functional type level: the highest soil OM^{coll} concentrations were associated with trees having ectomycorrhizal associations, particularly in the reference forests.

In partial support of our hypothesis, we showed a vegetation type effect, but primarily in reference forests of the boreal and temperate cities where OM^{coll} concentrations were consistently higher under trees producing recalcitrant litter compared to trees producing labile litter. This is in line with our previous findings in the boreal zone (Setälä et al., 2016). Recently, we showed that CO_2 production under conifer trees in the boreal zone is lower than under labile trees (Lu et al., 2021), supporting our findings that OM^{coll} accumulates more readily under trees producing recalcitrant litter. Vegetation type affects C and N accumulation rates in the soil (Edmonson et al., 2014; Livesley et al., 2016; Raciti et al., 2012), but, based on our results, it appears that these effects diminish towards the tropics. The reason for this decline remains open, but is likely because favourable climatic conditions in the tropics neutralizes plant-trait/litter quality effects on soil process rates. In old parks, however, the explanation that plant-trait structure should guide the outcomes of processes resulting from plant–soil interactions independently of the biome is unlikely, as was emphasized by the lack of difference in soil properties under trees producing recalcitrant or labile litter.

4.3 | Convergence of soil properties across climatic zones

We hypothesized that soil physicochemical properties in urban parks should converge, that is, become more similar, across cities in the three climatic zones where anthropogenic drivers dominate natural ones. This hypothesis was supported by our data, primarily in young parks where the soils displayed low variation among climatic zones, that is, convergence in most soil properties (see also Groffman et al., 2014; Herrmann et al., 2020; Pouyat et al., 2015), both for soils under labile and recalcitrant trees. Soils in older parks under old vegetation showed higher variation (or divergence) in soil properties across climatic zones, similar to soils in reference sites. These results support, at least partly, the homogenization concept of a strong, large-scale global human influence on soil formation (Pouyat et al., 2015; Trammell et al., 2020), and add to the consensus that urban greenspaces, and in particular classical urban parks, are managed under similar guidelines globally and produces comparable

soil properties, even if the species planted in these parks, and their traits, differ.

As parks age, however, those soil properties (such as OM, C and N) that are directly influenced by plant resource inputs (see Pouyat et al., 2015) start to diverge across climatic zones, demonstrating the effects of climate and vegetation on the plant–soil process a few decades after establishment. In old parks, even BD diverged, potentially reflecting a difference in use under these large trees between the climatic zones. For instance, the time spent, and thus trampling intensity, by people under large trees in the summer in the boreal zone is arguably less compared to the tropics where such trees provide shade throughout the year.

Our findings also show that convergence (and divergence) was similar in soils under both tree types. This suggests that, even though plant type can control soil properties at a local scale (Lu et al., 2021; Setälä et al., 2016), human activity is an essential driver of soil development in urban parks across the world. This view lends further support from our finding that some soil physicochemical parameters (pH, BD) that are less directly controlled by vegetation showed convergence. However, the question arises whether divergence in soils under old park trees, similarly to the pattern observed for reference plots, can be interpreted as evidence that old park soil properties are gradually escaping anthropogenic control and starting to resemble those of soils in natural environments (reference sites), which can take centuries and millennia to develop (Pouyat et al., 2015). This is, however, not the case (Figure S1): when compared to young parks, soil properties under both labile and recalcitrant trees in old parks were not consistently more similar to those in reference sites, suggesting divergent soil development trajectories across the different climatic zones as parks age. This is likely the result of an increasing influence of natural processes, including vegetation type and climate, on soil development, and suggests that managed urban parks, however old they are, are unlikely to develop soils that share the same structure, function and ecosystem services as the adjacent more natural ecosystems.

5 | CONCLUSIONS

We demonstrated that plant-trait effects on soil properties in urban parks are not universal but influenced by the climatic zone in which park resides. This may be due to the strong influence of frequent human-induced disturbances in urban parks that overshadow the plant functional type effects observed in natural ecosystems (Bardgett & Wardle, 2010; Wardle et al., 2004). Supporting this, soil %OM in reference forests was slightly but constantly higher under trees producing recalcitrant litter than labile litter, and the same holds for C and N in the cities in boreal and temperate climates. In terms of urban parks, it is surprising that, unlike in young parks, there were no differences in OM^{coll} in old park soils under lawns (producing labile litter) compared to soils under either tree type (labile and recalcitrant litter). This suggests that, at least in these boreal and temperate cities, lawns can be as valuable as trees in providing

soil-derived ecosystem services. Furthermore, the strong influence of anthropogenic drivers in controlling plant–soil interactions in urban greenspaces is also reflected in the convergence of soil properties in parks, irrespective of vegetation type. Although soils in old parks across climatic zones showed less convergence when compared to young parks, their soil properties were not comparable to those in (semi)natural reference forests. This suggests that, although old urban parks have the capacity to provide ecosystem services in terms of sequestering C and N—and also in terms of recreational services—their potential to provide services is limited when compared to natural ecosystems, irrespective of climatic region. To develop more sustainable cities, the reintroduction of semi(natural) greenspace—here forests—to the city or their preservation in the urban landscape is recommended as a nature-based solution to improve, for example, the ability of urban greenspace to store C and nutrients in these otherwise strongly disturbed systems.

ACKNOWLEDGEMENTS

This research was made possible by a grant from the Academy of Finland (no. 315987) for the project entitled 'Ecosystem services in urban greenspaces across biomes: the influence of plant functional types and soil biota on soil-derived ecosystem processes (PARKTRAITS)'. We thank numerous people who have helped us in the field, including Yinhong Hu, Elliott Stratham, Mohamed Yusof, John Allen, Janne Auranen, Peter Immonen and Allan Delesantro. Comments from two reviewers have improved the manuscript considerably.

DATA AVAILABILITY STATEMENT

At the moment, data will be made available upon request from the corresponding author. We are currently collecting more data for this project and the plan is to make all data available online once all data have been collected and published.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Kotze, D. J., Ghosh, S., Hui, N., Jumpponen, A., Lee, B. P. Y.-H., Lu, C., Lum, S., Pouyat, R., Szlavecz, K., Wardle, D. A., Yesilonis, I., Zheng, B., & Setälä, H. (2021). Urbanization minimizes the effects of plant traits on soil provisioned ecosystem services across climatic regions. *Global Change Biology*, 27, 4139–4153. <https://doi.org/10.1111/gcb.15717>