



Ecosystem properties in urban areas vary with habitat type and settlement age

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Abstract

Aims Urban ecosystems comprise a range of habitats that support key ecosystem processes that are fundamental for the functioning of their soils. Relatively little is known about how different types of urban greenspaces and settlement ages influence the functioning of these important environments.

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Methods We evaluated how four types of urban greenspaces (habitat types: natural areas, parks, gardens, roadside verges) and three settlement ages (5 to 150 years) influence multiple plant and soil ecosystem properties at 60 sites in two seasons in urban areas in eastern Australia.

Results The type of urban greenspace and the age of the settlement influenced their ecosystem properties. In particular, habitat type had a greater effect on nutrient pools and plant biomass than settlement age, with greater nutrient pools in household gardens, but lower plant cover and plant height on roadside verges. Natural areas supported richer plant communities. We found that soil pH and soil moisture (particularly in summer) explained the contrasting effects of urban environments and settlement age on fundamental ecosystem properties. Older settlements tended to have lower soil pH, which was generally associated with greater enzyme concentrations. Soil pH effects varied depending on functions and season.

Conclusions Our work highlights the importance of considering settlement age and urban greenspace type for understanding the complexity of urban ecosystems, and the functions that they provide to humanity. Understanding the links between urban habitats, settlement age and ecological functions is a first step to promoting practices that sustain healthy and productive urban environments.

Keywords Peri-urban · Urban ecology · Soil function · Suburbs · Cityscapes · Soil nutrients · Microbes

Introduction

More than half of the global human population now live in large cities, and this figure is expected to rise to more than 66 % within the next half century (UN 2007). Over the past century, there has been increasing migration of human populations towards large cities due to better employment opportunities and access to health and educational facilities, and a general desire for a more city-based lifestyle (UN 2018). Increases in the human population will result in an expansion in the number and size of urban settlements globally, placing increasing pressure on the stock of urban greenspaces, which are increasingly important for human wellbeing (Dunnett and Qasim 2000) and urban biodiversity (Padullés Cubino et al. 2019). Natural and semi-natural habitats within urban greenspaces also support a wide range of important ecosystem services such as plant production, pollination, and waste decomposition. Understanding how urbanization affects these ecosystem services is important if we are to effectively manage urban greenspaces to support healthy human populations.

Urban greenspaces are far from homogeneous. Undeveloped areas within an urban matrix comprise a complex mosaic of patches of semi-natural (remnant) vegetation, generally on the peri-urban outskirts, highly modified habitats dominated by perennial grasses (city parks, roadside verges), or private gardens, that support a wide variety of perennial and annual plants (Goddard et al. 2009). The planting of exotic species in parks and gardens often leads to their invasion into remnant vegetation surrounding the city, potentially altering ecosystem processes such as pollination, hydrology, and microbial-mediated functions that result from a change in plant species traits (Gaertner et al. 2016). Pollution from automobiles, and chemicals from roadways, would be expected to lead to marked changes in plant and soil functions along roadsides. Finally, the application of mulches, amendments and fertilisers would be expected to alter soil function in gardens (Lorenz and Lal 2009). Differences in soil function between these different urban greenspaces (semi-natural areas, parks, roadside verges, household gardens) have been little explored. Further, consistent with ecosystem development and soil formation theories (Jenny 1941; Wardle et al. 2004; Pickett and Cadenaso 2009), urban soils are likely to change over time, either naturally, or as a result of human activity such as soil amendment. This means that older settlements might have higher quality

(healthier) soils and greater plant diversity than younger settlements due to a longer period of recovery after disturbance (Jenny 1941). Although there has been considerable research on the differences in soils in urban environments (e.g., Goddard et al. 2010; Edmondson et al. 2014; Tresch et al. 2018), the extent to which different habitats in settlements of different ages control key ecosystem properties related to soil and plant function remains less well understood.

We conducted topsoil and vegetation surveys across four urban greenspaces (remnant natural areas, parks, roadside verges, household gardens) in two contrasting seasons (summer and autumn) in three settlements of different ages (5, 50 and 150 years old) from eastern Australia to test the notion that ecosystem properties such as diversity, and microbially-driven processes such as decomposition and mineralisation of organic matter, might increase as soil develops, and that these would vary with ecosystem property and habitat type. A total of 60 sites was investigated in this study. We hypothesized that plant biomass and nutrient pools would likely develop independently of settlement age because homeowners and park managers intensively manage these ecosystems on a regular basis by fertilising and mowing. Furthermore, specific habitats might display different ecosystem properties simply because they are more intensively managed, or in closer proximity to major disturbing agents such as roads and pollution from motor vehicles. Our study area in eastern Australia provides an ideal opportunity to test the effects of habitat (greenspace type) and age on functions for two reasons. First, although the first settlement by Europeans in Australia occurred in the 1820s, multiple waves of development have occurred over the past 50 years, providing three markedly different settlement age classes. Second, we know the exact time of settlement and age of multiple settlements and their features (e.g., parks) in Australia, allowing us to address our research question. These three settlements are also ideal because they are relatively close, on similar substrates, and subject to similar climatic conditions.

Specifically, we explored how the age of urban settlement controls multiple ecosystem properties directly, and indirectly, *via* changes in topsoil physical attributes (pH, moisture). These ecosystem properties are important surrogates of biodiversity, plant production, soil fertility, gaseous exchange and the breakdown of waste material. Ecosystem properties included multiple plant (richness, height and cover), microbial (abundance and

activity via decomposition and mineralisation of organic matter, lignin and glucose) and soil (activity of enzymes including glucosidase, glucosaminidase, cellobiosidase and phosphatase associated with the breakdown of carbon (C), nitrogen (N) and phosphorus (P) (N and P soil pools) functional attributes. We considered two contrasting seasons, summer and autumn, because it is important to understand how urban ecosystems might respond in dry environments in Australia. For example, we expected that effects would be stronger in autumn than summer because of lower levels of evaporation in autumn, and therefore greater soil moisture and biological activity. Moreover, we included four independent urban habitats in our investigations including city parks, roadsides, gardens and natural areas. Cities often provide a wide range of ecosystem types with different degrees of management from natural areas that are not cultivated, fertilised or irrigated. For example, household gardens are often fertilised, watered and mown, and weeds treated with herbicide. Roadsides are, however, less intensively managed, but are directly affected by pollutants from motor vehicle exhaust fumes (Spencer et al. 1988). Despite this, roadsides often provide habitat for rare and endangered plants (Bolund and Hunhammar 1999). Considering multiple urban habitats is therefore fundamental to understanding global cities because they provide a range of resource-rich niches or refugia for plants and animals as well as recreation opportunities for millions of people.

Methods

Study area

The study was conducted at three cities (hereafter ‘settlements’) of varying age on the Cumberland Plain, which is centred on the City of Hawkesbury, about 70 km west of Sydney, Australia (-33.6° , 150.75° ; Fig. 1). The area lies at the foothills of the Great Dividing Range and average temperatures range from about 11°C in winter to about 24°C in summer. The topography is undulating and soils poorly drained and characterised by Tertiary alluvial deposits of sandy clay or loams (Keith 2007). The soils of remnant natural areas were characterised as Chromosols and Sodosols (Australian Soil Classification Order, Isbell, 1996), derived from shale or alluvial material, with sandy loam surface textures, and surface pH values of about 6.0 (see

Table S1 and Supporting Information Appendix S1). All three soil profiles exhibited typical duplex development with a clear change in soil texture from loams and sandy loams at the surface to clay or clay loams at about 50 cm depth. The native vegetation is categorised as eucalypt woodland, and dominated by *Eucalyptus sclerophylla* (Blakely) L.A.S. Johnson & Blaxell, *Eucalyptus parramattensis* E.C. Hall and *Angophora bakeri* E.C. Hall (Benson 1992). Substantial areas of the Cumberland Plain have been cleared for urban development or mixed farming, but small areas of native vegetation now occur within a matrix of residential use, parks, gardens and playing fields.

Our three urban settlements of increasing age were Jordan Springs, South Penrith and Richmond, respectively. Jordan Springs is the newest and smallest (10 km^2) and was designated a suburb in 2011 after the construction of 4,800 houses in 2004 (<https://penrithhistory.com/home>). Its population in 2016 was about 5,000 people. South Penrith was established as an urban area in the 1970s. Its current population is about 11,000 people. Richmond was established in 1810 and proclaimed a municipality in 1872, later becoming a suburb of Sydney. Its population in 2018 was just over 5,000. We acknowledge that, in terms of settlement age, our study is pseudoreplicated because we have only one replicate of each settlement age. Other than the youngest settlement, it would have been impossible to replicate the two older settlements (Richmond, Penrith) in a similar environment without having sites in a different region with different environmental conditions. However, such a design as ours can provide important information on soil function within different habitats, and an indication of the effects of settlement age. Nonetheless, any conclusions relating to settlement age are applicable only within our specific study system (*sensu* Davies and Gray 2015).

Within each of the three urban centres we selected five replicate plots of each of four habitat types (semi-natural vegetation, parks and parkland, roadsides, private gardens). Replicates of the four habitat types were separated by distances of at least 1 km, ensuring that they were statistically independent (Fig. 1). Areas of semi-natural vegetation included remnants of Cumberland Plain woodland dominated by *Eucalyptus* species and a groundstorey of mixed shrubs and grasses such as *Aristida ramosa* R.Br. and *Rytidosperma caespitosum* (Gaudich.) Connor & Edgar, with a variable cover of soil mosses and lichens. These remnants were found

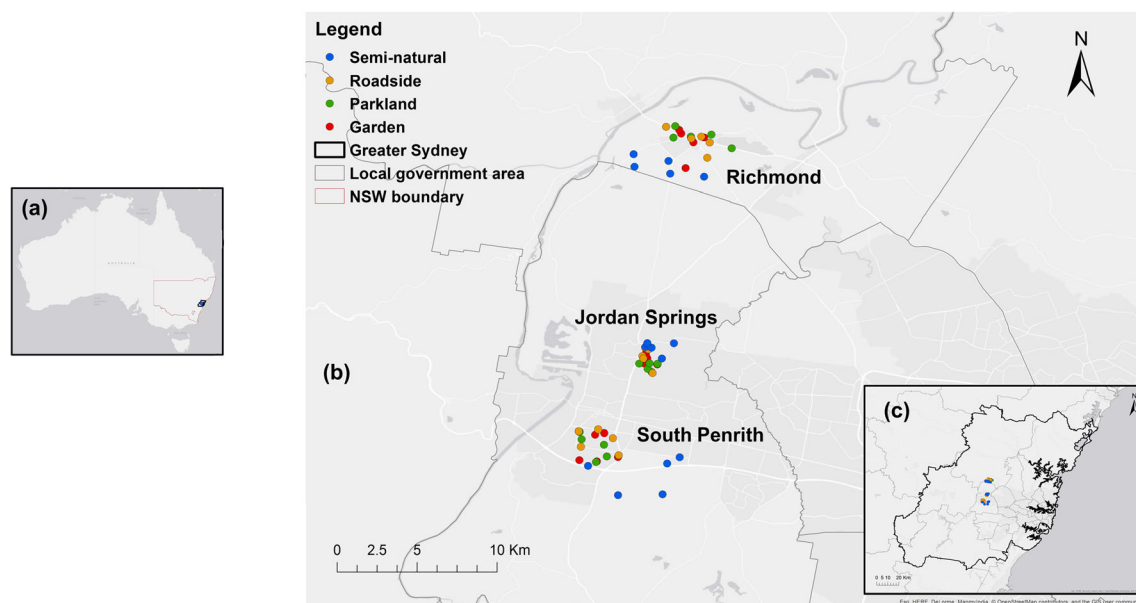


Fig. 1 Location of the three settlements in eastern Australia

close to the other plots, but on the edge of the settled areas. Parks were dominated by extensive areas of exotic lawn grasses such as *Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone and *Cynodon dactylon* (L.) Pers. var. *dactylon*. These areas were mown regularly, received additional nitrogen and phosphorus fertiliser, and were irrigated frequently. Roadside verges were linear structures along footpaths (pavements) between the roadside and adjacent houses. These were typically dominated by exotic lawn grasses such as *Cynodon dactylon* and *Stenotaphrum secundatum* (Walter) Kuntze, as well as exotic biennial herbs such as *Taraxacum officinale* Weber, *Cyperus* spp., *Soliva anthemifolia* (Juss.) R.Br. ex Less., and are generally unfertilised, though they may receive irregular irrigation. The condition of lawns on the footpaths often varied between new and old urban settlements. Finally, gardens varied substantially with settlements age. For example, older established gardens in Richmond and Penrith contained perennial shrubs such as *Camelia japonica* L., *Spirea cantoniensis* Lour. and *Rondeletia*, and assorted annual forbs, whereas those in younger settlements were less developed and dominated by more biannual forbs.

Within each of the plots we placed four small 1×1 m quadrats within which we sampled the soil to 7 cm deep, using a coring device. The four samples were then bulked, and a subsample collected for determination of

soil physical and chemical properties. Within each of the small quadrats we measured average height of five random plants, assessed total plant cover, and counted the number of different species. Sampling was conducted in two seasons; austral summer and austral autumn. Because of the nature of the disturbance associated with plant and soil sampling, measurements within the small replicate quadrats were sampled at different locations in each of the four habitat types in summer and autumn. Average annual rainfall is about 760 mm, 60 % of which falls in the six warmer months (Spring-Summer).

We focused on this depth for three main logistic and biological reasons: (1) First, this depth is commonly used to sample soils in comparable studies. (2) We consider this an appropriate depth to sample because this is the layer of maximum productivity and microbial activity, and most routine gardening activities occur in the surface 10 cm. (3) Finally, because some urban ecosystems have very shallow soils (e.g., roadsides and gardens), sampling more deeply was not possible, and therefore, would not allow us to compare soils at the same depth across all urban habitats. Topsoils are very sensitive to disturbance in urban environments. Consequently, we posit that any settlement effects on ecosystem functions reported in our study are likely underestimated, but never overestimated. This results in a robust, but also conservative approach to assessing settlement age effects on functions.

Soil variables

Soil pH was measured using a pH meter in a 1:2.5 soil water suspension. Available (Olsen) P was determined from bicarbonate extracts using colorimetric analyses (Colwell 1963) as described in Olsen and Sommers (1982), and inorganic nitrogen determined from K_2SO_4 extracts, as described in Delgado-Baquerizo et al. (2016). Gravimetric soil moisture was calculated for the top 7 cm of the soil by recording the mass of soil before and after drying at 160°C for 48 hours.

Soil decomposition, respiration and microbial abundance

We measured: (1) the activities of four soil enzymes: α -glucosidase (AG: starch degradation), N-acetyl- β -glucosaminidase (NAG: chitin degradation), β -D-cellobiosidase (CB: cellulose degradation) and phosphatase (PHOS: organic phosphorus mineralization) as described in Bell et al. (2013) as an index of decomposition. By decomposition, we refer to the breakdown or mineralisation of phosphorus, carbon and nitrogen to inorganic forms that can be used by plants, and which are good indicators of the nutrient demand by soil microorganisms (Bell et al. 2013). For BG activity, 1 g of air-dried soil and 33 ml of sodium acetate buffer (pH < 7.5) was shaken at 200 rpm for 30 minutes and 800 μ l soil slurry was sampled and 200 μ l substrate of 4-methylumbelliferyl β -D glucopyranoside solution were added to the slurry. The 1000 μ l (1 ml) of solution was incubated at 25 °C for 3 hours and the activity (nmol activity g^{-1} dry soil h^{-1}) measured at 365 nm excitation wavelength and 450 nm of emission wavelength in a microplate reader. The same procedure was used, but with different substrate solutions, for an additional three enzymes. We used 4-methylumbelliferyl β -D-cellobioside for CB, 4-methylumbelliferyl N β -D-glucosaminide for NAG, and 4-methylumbelliferyl phosphatase for PHOS activity (Bell et al., 2013). Substrate-induced respiration rates were assessed for lignin (lignin degradation) and glucose (glucose degradation) using the Microresp procedure (Campbell et al. 2003). Soils with and without lignin (or glucose) were incubated for 6 h and read at 570 nm to assess respiration. Lignin and glucose degradation was calculated as respiration in lignin minus basal respiration.

Soil DNA was extracted from 0.5 g of thawed soil samples with the Powersoil DNA Isolation Kit (Mo Bio

Laboratories) to provide a measure of microbial biomass. We performed qPCR reactions with 96-well plates, in triplicate, on an ABI 7300 Real-Time PCR (Applied Biosystems). Fungal ITS and bacterial 16S-rRNA genes were amplified with the ITS 1-5.8S and Eub 338-Eub 518 primer sets (Evans and Wallenstein 2011).

Statistical analyses

All data were standardised from 0 to 1 before calculating four indices of function. The nutrient pool index was calculated as the average standardised values of available nitrogen and phosphorus for each site, and respiration index as the average standardised values for substrate-induced respiration of lignin and glucose, respectively. The decomposition index was calculated as the average standardised values for the four enzymes (BG, CB, NAG, PHOS), and the plant biomass index as the average standardised values for plant cover and plant height. All analyses were separated between the two seasons (summer and autumn). For the microbial data, we calculated average standardised values for microbial biomass as our microbial abundance index.

We used three approaches to examine the relationships between settlement age, habitat type and variables of interest. First, we examined differences in plant cover, soil moisture, pH and plant height among different aged settlements and different habitat types, and their interactions using a mixed-models (split-plot) ANOVA approach. The first stratum of our model examined differences among ages, and the second stratum differences among habitats and interactions with age. We tested our data for homogeneity of the residuals using Levene's Test prior to analyses. Separate analyses were conducted for the two seasons. Second, we used Structural Equation Modelling (SEM) to build a system-level understanding of the effects of settlement age and habitat on function. Structural Equation Modelling was used because it partitions direct and indirect effects of one variable upon another and estimates the strengths of these multiple effects. Unlike regression or ANOVA, SEM offers the ability to separate multiple pathways of influence and view them as parts of a system. It is useful therefore for examining complex relationships among predictors commonly found in natural ecosystems (Newman and Girvan 2004).

We developed an *a priori* model of how we expected our system to behave in relation to settlement age and

habitat (Fig. S2 in Appendix S2). In the *a priori model* we expected that settlement age and habitat would have direct effects on functions, and indirect effects, moderated by changes in soils or microbes. We also expected that these relationships might differ between summer and autumn given differences in rainfall and temperature between the two seasons. Each model included Age (coded as -1, 0, +1), Habitat (Park, Roadside, Garden), Soils (moisture, pH), microbial biomass and function, with separate models for the four functions. Native vegetation was our model control, with the effects of park, roadside and garden compared against this control, which was not explicitly considered in the models.

Hypothesized pathways in our *a priori model* were compared with the variance-covariance matrix of our data in order to calculate an overall goodness-of-fit using the χ^2 statistic. The goodness of fit test estimates the likelihood of the observed data given the *a priori* model structure. Thus, high probability values indicate that models are highly plausible causal structures underlying the observed correlations. Before fitting empirical data to our *a priori* models, we examined the univariate correlations among all variables and standardized (z-transformed) the data. Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software. For each of our models, those with low χ^2 and high Goodness of Fit Index [GFI] were considered appropriate models. Finally, we plotted significant relationships among a range of variables of interest using linear models.

Results

Our analyses show that settlement age and urban greenspace habitats are major drivers of important ecosystem services such as nutrient cycling and microbial activity, and further highlighted the importance of seasonal variability in these urban environments. For example, settlement age was a major driver of microbial activity (respiration rates and enzymatic activities) and plant richness but had a much lesser role in controlling nutrient pools and plant biomass, which varied more in relation to different city habitats (Fig. 2). Plant richness declined markedly, however, in all habitats in summer (Fig. 2a), but only in parks in autumn (Fig. 3b). Settlement age also influenced important soil properties such as moisture and pH. For example, in older settlements, the positive effect of moisture on all four functions

tended to be lower, particularly in summer (Fig. 2). Older settlements also tended to have greater enzymatic activity, particularly in autumn when soil moisture levels were higher (Fig. S3). Finally, older settlements tended to have lower microbial abundance, but only in summer (Fig. 3e).

Nutrient pools (Fig. 2e and f) and plant biomass (Fig. 2a and b) were driven more by urban habitat type than settlement age. In summer, our index of decomposition declined with increasing plant richness (Fig. S4a), nutrient pools declined with increasing plant height (Fig. S4c), and soil pH declined with increasing settlement age (Fig. S4e). In autumn, there was a weak increase in the index of decomposition with increasing settlement age (Fig. S4b), and increases in nutrient pools (Fig. S4d) and respiration rates (Fig. S4f) with increasing soil moisture. Increasing soil pH was associated with greater concentrations of cellobiosidase, β -glucosidase and N-acetyl- β -glucosaminidase in autumn (Figs. S3b, S3d, S3f and S3h), but only β -glucosidase in summer (Fig. S3a).

Overall, nutrient pools were greatest in gardens, and plant cover and height least on roadside verges (Table S5.1 and S5.2). Habitat effects on nutrient pools were positive (Fig. 2e and f) while those on plant biomass were negative (Fig. 2a and b). Semi-natural areas generally had the tallest plants (summer only: $F_{3,36} = 21.02$, $P < 0.001$; Table S5.1) and greatest plant richness (S5.1 and S5.2).

Direct and indirect associations among settlement age and ecosystem properties

The standardised total effects (STE) derived from the SEM represent the overall effects of our variables of interest on the four measures of function, after accounting for both positive and negative, and direct and indirect, effects of soils, settlement age and habitat. Our standardised total effects revealed four main trends (Fig. 4). First, compared with semi-natural areas, gardens, roadsides and parks had strong positive effects on nutrient pools in both seasons whereas their effects on the decomposition index differed between seasons. Second, plant biomass was substantially lower in gardens, roadside verges and parks than in semi-natural remnant areas in both seasons. Third, soil moisture had strong positive effects on all functions, particularly in autumn, while the effects of pH changed from positive to negative depending on the season and particular function. Finally, increasing settlement age was generally associated

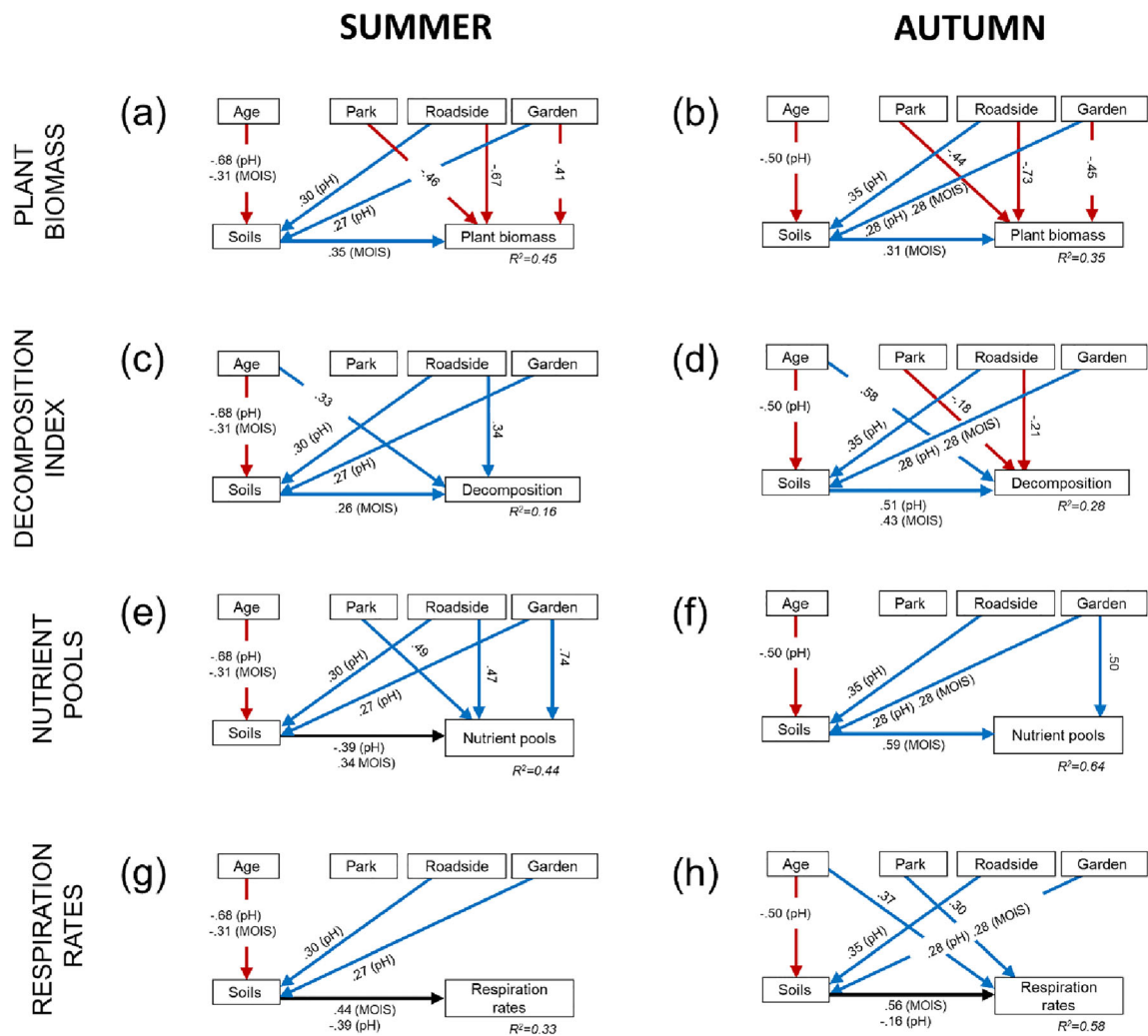


Fig. 2 Structural equation models describing the effects of multiple drivers, Settlement age (new, recent, old settlements), Habitat (park, roadside, garden), and Soils (pH, soil moisture) on four soil functional measures (plant biomass, decomposition index, nutrient pools) in summer and autumn. Numbers adjacent to arrows are path coefficients, which are analogous to partial correlation

with increases in functions, particularly respiration rates and the index of decomposition.

We also found a number of indirect age-related effects. For example, plant richness increased with settlement age due to reductions in both soil pH (in both season; Fig. 3a and b), and soil moisture (in autumn; Fig. 3b). In summer, older settlements tended to have less plant cover due to less soil moisture (Fig. 3c). Older settlements also tended to be associated with more acidic soils (Fig. 3), which were associated with a lower decomposition index in autumn (Fig. 2d), and greater nutrient pools (Fig. 2e) and respiration rates (Fig. 2g) in

summer. We also detected some indirect effects of habitat, mediated by changes in soil pH and moisture. For example, both gardens and roadside habitats increased the suppressive effect of soil pH on respiration rates in both summer and autumn (Fig. 2g, h) and nutrient pools in summer (Fig. 2e).

Discussion

Our study shows that settlement age and urban greenspace type were important drivers of multiple

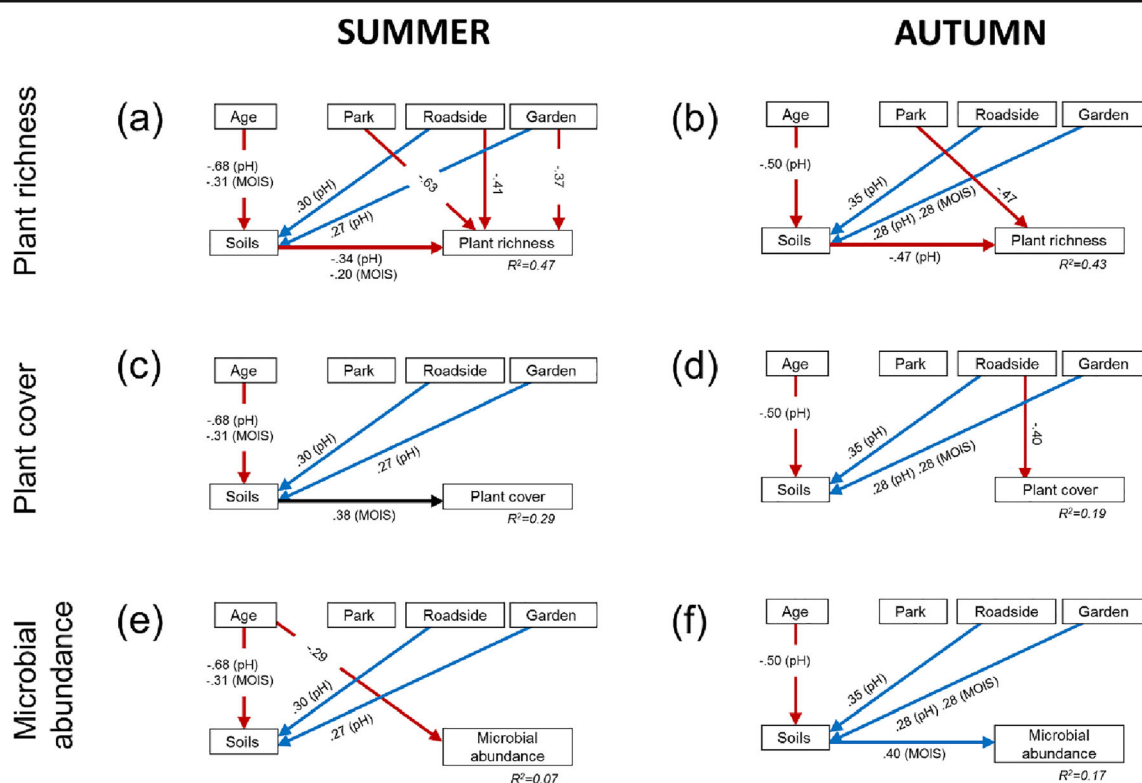


Fig. 3 Structural equation models describing the effects of multiple drivers, Settlement age (new, recent, old settlements), Habitat (park, roadside, garden), and Soils (pH, soil moisture) on plant richness, plant cover and microbial abundance in summer and autumn. Numbers adjacent to arrows are path coefficients, which are analogous to partial correlation coefficients and indicative of

the effect size of the relationship and may be positive (blue), negative (red) or mixed (black). Only significant ($P < 0.05$) pathways are shown. R^2 represents the total variance in soil function explained by the model. $\chi^2 = 0.1$, $df = 3$, $P = 1.0$, RMSEA = 0, Bootstrapped $P = 1.0$

key ecosystem properties in urban environments. In particular, older settlements were associated with greater microbially-driven breakdown of organic matter (decomposition index), and greater plant richness in road-sides, private gardens and parks in urban areas of all ages. We also found some season- and habitat-dependent effects. For example, topsoil function and microbial biomass were greater in autumn, corresponding with periods of lower evaporation, and soil pH and moisture were major drivers of the indirect effects of settlement age on ecosystem properties. Topsoil pH generally declined with age across all habitats, and had a suppressive effect on plant richness. Changes in soil moisture in both seasons led to an overall increase in all soil functions. Finally, we also found some ecosystem properties, independent of settlement age, such as nutrient pools and plant biomass, which were driven by different habitats such as roadside verges and gardens. Our results illustrate the types of

changes in ecosystem structure that occur across different urban habitats of different age, providing important insights into how we might manage soil functions as settlements get older.

Settlement age had a major effect on ecosystem properties, however, as hypothesized, these effects varied with the property examined. For example, settlement age had an effect on microbes and plant richness, but had no effect on plant cover or height, or nutrient pools. Gardening plants are often the first species arriving at settlements, but with increasing development, native plants are expected to colonize city environments, potentially explaining the increase in plant richness over time in our study. The effects of plant functional type may also become more pronounced as plants modify soil and microbial properties over time (Hui et al. 2017; though see Ramirez et al. 2014). Nevertheless, we need to be mindful that our results are based on internal replication, i.e., multiple sites within a given age, rather

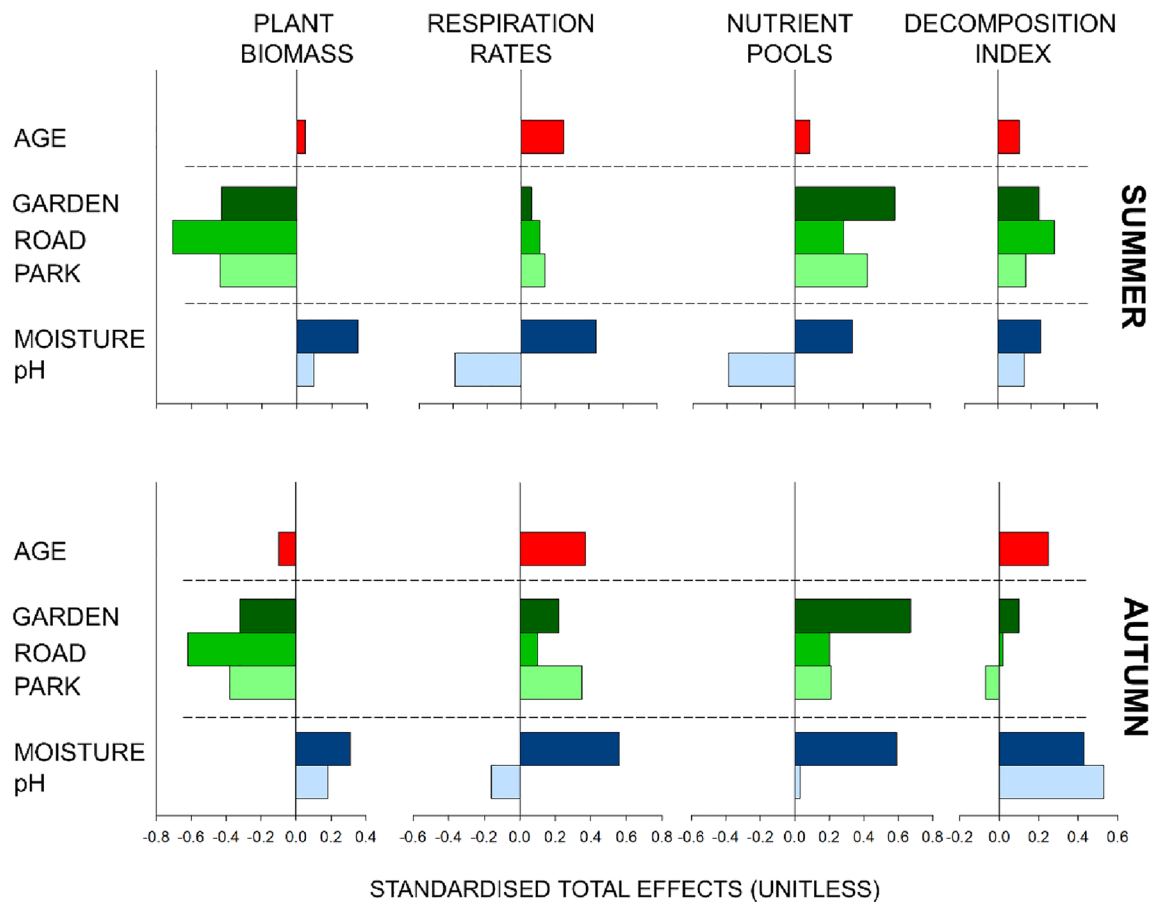


Fig. 4 Standardised total effects (STE: sum of direct plus indirect effects) derived from the structural equation modelling) of Settlement age, Habitat and Soils on the four soil functional measures in summer and autumn

than multiple aged settlements, so future studies would need to include additional settlements to confirm these trends.

Although we focused on the immediate topsoil (for logistic and biological reasons, see Methods), which is highly vulnerable to disturbance, we still found substantial effects of urban settlement age and habitat on soil ecosystem functions. This might suggest that settlements might have an even stronger effect than those reported here, and that any legacy effects diminish due to soil disturbance (e.g., Delgado-Baquerizo et al. 2017). Younger settlements tended to have less functional soils, lower microbially-driven functions such as respiration rates and enzyme activities, and supported fewer plant species than older soils, particularly in autumn, a season of greater soil moisture. A feature of young settlements is the extensive physical disturbance that accompanies their establishment. This disturbance includes substantial reorganisation of the soil surface,

including cutting and filling, burial of the original soil material, and is often accompanied by the addition of physical waste materials (Pouyat et al. 2002; Biasioli et al. 2006) and contaminants (Madrid et al. 2002; Imperato et al. 2003). A greater biomass and variety of different plant root types with more varied root exudates (Berg and Smalla 2009; Bezemer et al., 2006) could also help explain the larger amount of microbially-driven enzyme activities found in older soils. Greater plant richness would provide a larger range of resources and microhabitats, as well as recalcitrant carbon products, for microbial communities, resulting in larger enzyme activity (Bardgett et al. 1998; Osanai et al. 2013). Our study suggests that these key soil functions in urban areas tend to increase with increasing time since initial disturbance.

Our work further suggests that changes in important soil properties with age can indirectly explain the effects of soil age on important ecosystem properties. For

example, declines in soil pH with increasing settlement age (Zemunik et al. 2015) could partly account for greater levels of microbial richness in both summer and winter. Ageing soils have higher levels of organic matter and lose cations, reducing soil pH. Irrigation of parks and lawns also results in greater leaching, leading to more acidic soils. Moisture availability also drives function, but only in summer when moisture is limiting, or when transpiration is high. These two drivers operate at different temporal scales; soil pH is slow property that changes over decadal timescales, explaining its consistent effects on ecosystem properties across seasons, whereas soil moisture changes daily or weekly, impacting ecosystem properties when soils are drier. For example, reductions in soil pH over time has been previously associated most strongly with reductions in microbial activity, but also accumulation of organic matter (e.g., phosphorus mineralization and chitin degradation; Sinsabaugh et al. 2008). These results are consistent with our understanding of processes that occur during plant succession, ecosystem development and soil development for natural ecosystems (Stevens and Walker 1970; Chadwick et al. 1999), though this could only be tested by examining more sites of a given age. Increasing ecosystem development is characterised by increased leaching, greater plant cover, and the accumulation of cations in plant biomass or organic matter, leading to reductions in soil pH (Binkley et al. 1989). There are also strong links between soil pH and plant richness. Environmental filtering driven by acidification during soil formation has been previously reported to be positively associated with plant richness in terrestrial ecosystems, supporting this result (Laliberté et al. 2014). Thus, on younger soils, filtering of the regional pool of plants due to higher soil pH may be an important factor driving plant species diversity (Laliberte et al. 2014). Changes in soil pH will also affect soil microbial communities (Fierer et al. 2007). Lower pH levels are likely to constrain some soil fungi (Maestre et al. 2015) and have strong negative effects on some bacteria and their activities, leading to potential changes in enzyme activity and therefore decomposition of organic matter.

We also found some attributes that changed irrespective of age, such as nutrient pools and plant biomass, that were regulated by habitat type. Differences in function among different habitats likely result from the varied management that these areas receive. For example,

nutrient pools in gardens were almost twice that in other habitats (including natural areas) in autumn, though this trend vanished in summer. This is likely associated with nutrient over-fertilization and leaching dynamics in gardens (Horgan et al. 2002). It could also be linked to low uptake by plants and microbes in autumn due to their low growth rates, which could be reversed in spring and summer. Plant attributes differed among habitats, with all city habitats supporting lower plant biomass than natural areas, and plant cover was lower on roadsides and plants taller in natural areas, likely due to the effects of mowing in urban areas. Taken together, our study indicates that the development of soil function with ageing settlements is consistent with expectations under ecosystem development, with increasing soil age accompanied by increases in respiration and the breakdown of organic matter, greater plant richness, and more acidic soils. However, there were less marked effects on nutrient pools and plant biomass, which depended on the specific habitat, peaking in gardens and natural ecosystems, respectively. Reduced soil pH and moisture (in summer) with settlement age indirectly regulated the associations between urbanization and ecosystem functioning.

In summary, our study suggests that settlement age and urban greenspace type are fundamental drivers of ecosystem services such as biodiversity, organic matter decomposition, soil fertility and gas emissions. We further show that seasonal variability can have important impacts on the functioning of these ecosystems impacting plant, soil and microbial attributes. Moreover, we found that, at least part of the impacts of settlement age and urban greenspace type on ecosystem properties are indirectly driven by changes in soil pH and moisture. Our work is important because it reinforces the importance of different urban greenspace habitats for sustaining plant growth and providing habitat, which is important natural infrastructure on which human populations depend. Finally, the results reinforce the importance of retaining semi-natural areas, and their soils close to new settlements in order to provide the full range of functions such as plant diversity and plant biomass, properties that will be more important as urban populations increase.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11104-021-04836-w>.

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Author contributions M.D-B. and M.B. conceived the study and M.B. collected the data. B.K.S. undertook microbial analyses, D.J.E. analysed the data and wrote the first draft and all authors contributed critically to the drafts and gave final approval for publication. Data availability Data will be uploaded to FigShare if the manuscript is accepted for publication.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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