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RESEARCH ARTICLE

Biodiversity maintains soil multifunctionality and soil organic carbon in novel urban ecosystems

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Abstract

1. Biodiversity in urban ecosystems has the potential to increase ecosystem functions and support a suite of services valued by society, including services provided by soils. Specifically, the sequestration of carbon in soils has often been advocated as a solution to mitigate the steady increase in CO_2 concentration in the atmosphere as a key driver of climate change. However, urban ecosystems are also characterized by an often high level of ecological novelty due to profound human-mediated changes, such as the presence of high numbers of non-native species, impervious surfaces or other disturbances. Yet it is poorly understood whether and how biodiversity affects ecosystem functioning and services of urban soils under these novel conditions.
2. In this study, we assessed the influence of above- and below-ground diversity, as well as urbanization and plant invasions, on multifunctionality and organic carbon stocks of soils in non-manipulated grasslands along an urbanization gradient in Berlin, Germany. We focused on plant diversity (measured as species richness and functional trait diversity) and, in addition, on soil organism diversity as a potential mediator for the relationship of plant species diversity and ecosystem functioning.
3. Our results showed positive effects of plant diversity on soil multifunctionality and soil organic carbon stocks along the entire gradient. Structural equation models revealed that plant diversity enhanced soil multifunctionality and soil organic carbon by increasing the diversity of below-ground organisms. These positive effects of plant diversity on soil multifunctionality and soil fauna were

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not restricted to native plant species only, but were also exerted by non-native species, although to a lesser degree.

4. *Synthesis*. We conclude that enhancing diversity in plants and soil fauna of urban grasslands can increase the multifunctionality of urban soils and also add to their often underestimated but very valuable role in mitigating effects of climate change.

KEYWORDS
Anthropocene, biological invasions, ecosystem function and services, functional diversity, global change, non-native species, novel ecosystems, urbanization

1 | INTRODUCTION

In the Anthropocene, urbanization is increasing across the globe and challenges the future of ecosystems, their functioning and the services they provide for human well-being (Ellis, 2015; Haase et al., 2014; Schebella et al., 2019). Urban areas are expanding faster than any other land-use type (Hansen et al., 2005). The majority of people already live in cities (53% in 2018), with an expected growth reaching 68% within the next three decades (United Nations, 2018). This increasing urbanization has profound impacts across ecosystem compartments. For example, the urban heat-island effect (Imhoff et al., 2010; Oke, 2015) is not only detectable for air temperatures, but also for soil temperatures (Shi et al., 2012). Similarly, habitat fragmentation and isolation (Scolozzi & Geneletti, 2012) affect both above-ground and below-ground biota. Despite the various anthropogenic impacts, cities can harbour a high biological diversity (Aronson et al., 2014; Hall et al., 2017; McKinney, 2002) including endangered species (Ives et al., 2016; Planchuelo et al., 2019; Soanes & Lentini, 2019). Thus, developing biodiversity-friendly cities is required to tackle the global biodiversity crisis and has consequently attracted recent scientific and public attention (Bonthoux et al., 2014; Fischer et al., 2020; Nilon et al., 2017; Parris et al., 2018). Furthermore, positive relationships between biodiversity and ecosystem functions have been demonstrated (Engemann et al., 2019; Haase et al., 2014; Onandia, Schittko, et al., 2019; Schwarz et al., 2017), which makes biodiverse urban systems also a requirement of urban sustainability due to the values of associated ecosystem services (Luederitz et al., 2015; Tzoulas et al., 2007).

Soils provide many ecosystem functions that are essential for the biosphere, including resources that support plant biomass production, nutrient cycling or water maintenance (Amundson et al., 2015; Wall et al., 2015). They also deliver an often overlooked variety of relevant ecosystem services benefitting human well-being, such as the supply of clean water and food, control of air pollution (e.g. capture of particle matter by plant foliage), moderation of urban climate (e.g. control of urban temperature, local thermal insulation), storage of soil organic carbon (SOC) or forming an archaeological archive (Blanchart et al., 2018; Edmondson et al., 2012; Morel et al., 2015). Particularly SOC storage received broad attention in the last decades due to its mitigating effect in climate change by acting as a natural carbon sink and thereby lowering the concentration of CO_2 from the atmosphere (e.g. Lal, 2004, 2008). This process is also known as terrestrial carbon sequestration and is primarily mediated by plants (through carbon fixation and biomass production) and soil organisms (as biomass decomposers). Indeed, soils constitute the largest terrestrial organic carbon pool world-wide (Batjes, 2014), which is three times the amount of CO_2 currently in the atmosphere and 240 times the current annual fossil fuel emissions (Ciais et al., 2013). Thus, increasing net soil carbon storage by even a few per cent represents a substantial carbon sink potential (Paustian et al., 2016).

Yet the potential of urban soils to store carbon is often overlooked (Edmondson et al., 2012), and SOC stocks in urban areas have rarely been quantified (but see Canedoli et al., 2020; Edmondson et al., 2012; Raciti et al., 2012). A few manipulative experimental studies at small spatial scales (i.e. biodiversity–ecosystem functioning experiments) have shown that high plant diversity (both as species and functional group richness) increases SOC stocks by elevating carbon inputs (particularly below-ground carbon inputs) and by increasing microbial activity (Fornara & Tilman, 2008; Lange et al., 2015). For example, in a 12-year-long grassland biodiversity experiment, high-diversity mixtures of perennial grassland plant species stored on average 500% more soil carbon than monoculture plots of the same species (Fornara & Tilman, 2008). This positive relationship has also been detected in natural forest, shrubland and grassland sites across China (Chen et al., 2018), but evidence from soils in urban environments is largely missing.

Ecosystem multifunctionality can be defined as the ability of an ecosystem to provide multiple functions and services simultaneously; accordingly, measures of multifunctionality have become increasingly common in recent years in ecosystem science (Manning et al., 2018). These measures have been used to analyse a wide range of relationships, such as land-use intensification altering multifunctionality of ecosystem services (Allan et al., 2015), habitat diversity affecting multifunctionality of biogeochemical processes (Alsterberg et al., 2017) or the interaction between microplastics and drought affecting soil multifunctionality (Lozano et al., 2021). In the urban context, a recent study suggested that high plant diversity in urban gardens has positive effects on soil fauna and soil multifunctionality, but also that increasing garden management intensity decreases plant diversity (Tresch et al., 2019). However, still very little is known

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about the links between above- and below-ground diversity and soil multifunctionality, especially for urban soils.

Urbanization also alters the species composition of communities. For example, urban areas are highly susceptible to invasion by non-native plant species, as cities are important points of entry for their introduction (both intentional and unintentional) and their further establishment and spread (Gaertner et al., 2016; Kowarik, 2008; Pyšek, 1998). Consequently, plant communities in cities are often dissimilar to surrounding communities as urban species may become reshuffled into novel communities (Angold et al., 2006; Lurgi et al., 2012), which is a characteristic feature of novel urban ecosystems (Kowarik, 2011; Kowarik & von der Lippe, 2018). Notably, these novel species assemblages are formed by organisms that have not evolved together historically, but now interact with each other and their urban environment. Novel communities are thus characterized by low levels of eco-evolutionary experience (sensu Saul et al., 2013; Saul & Jeschke, 2015) of the interacting species. Whether they form functional units is largely unknown in many respects, and addressing this gap is a frontier challenge in ecosystem science in a rapidly urbanizing world (Groffman et al., 2017). Within the umbrella concept of 'ecological novelty' (Heger et al., 2019; Radeloff et al., 2015), the term 'biotic novelty' describes these human-mediated compositional and structural changes of ecological communities.

Biotic novelty of urban communities is pervasive but can be considered occurring along a continuum (Heger et al., 2019; Radeloff et al., 2015; Schittko et al., 2020), with some communities being more novel than others, which leads to the capability of quantifying degrees of novelty. Several approaches—mainly focusing on community dynamics and species turnover over time—have been proposed to capture the biotic novelty of ecological communities (Baselga, 2010; Harris et al., 2013; Shimadzu et al., 2015). Here, we quantify novelty with the recently proposed Biotic Novelty Index (BNI, Schittko et al., 2020), which incorporates this aforementioned eco-evolutionary perspective of novelty by using species' residence times in the focal area. A recent study showed that an increasing BNI of urban plant communities was not negatively related to the intensity of several above-ground functions related to above-ground plant productivity and water and nitrogen cycling (Onandia, Schittko, et al., 2019). This indicates that more novel plant communities function comparably to their more natural counterparts.

In this study, we investigated the relationship between different biodiversity components and soil functioning and services of urban grasslands in the context of increasing urbanization and plant invasions (as a potential cause of biotic novelty). We focused on plant diversity (measured as species richness and functional trait diversity) and, in addition, on soil organism diversity as a potential mediator for the relationship of plant species diversity and ecosystem functioning. We investigated earthworms (Oligochaeta: Lumbricidae), representing soil macrofauna species, as well as microarthropods, predominantly springtails (Hexapoda: Collembola), and mites (Arachnida: Acari), representing soil mesofauna species. Earthworms are generally regarded as ecosystem engineers (Darwin, 1881; Jones et al., 1994) due to their impact on nutrient cycling, soil aggregate stability, water infiltration, plant growth and soil carbon storage (Coleman et al., 2018). Microarthropods are mostly soil or litter dwellers and transform plant litter physically and chemically into substances amenable to further degradation and mineralization (Roy et al., 2018). For calculating soil multifunctionality, we used independent estimates of below-ground plant productivity, decomposition and nutrient supply. In addition to soil multifunctionality, we focused on SOC storage as an ecosystem service that plays an important role in mitigating anthropogenic increase in atmospheric CO_2 concentrations (Lorenz & Lal, 2014; Sommer & Bossio, 2014).

Specifically, the overall objective of our study was to investigate the effects of plant biodiversity, an increased biotic novelty of the plant community and urbanization (as a driver of abiotic novelty) on soil multifunctionality and SOC stocks in urban grasslands. In a second step, we used structural equation modelling (SEM) to identify potential mediating factors and improve mechanistic understanding of the complex above- and below-ground interactions described in the preceding objective. In particular, we intended with the SEM approach to disentangle direct and indirect effects of urbanization, associated urban soil characteristics, native and non-native plant diversity, and below-ground diversity on soil multifunctionality and SOC. Since it is pivotal to inform city planners, property owners, landscape architects and other stakeholders on the value of multifunctionality (Giling et al., 2019; Manning et al., 2018), it is our final objective to empirically assess the relationship between soil multifunctionality and SOC. This explicit link between multifunctionality and ecosystem services is missing from many such studies.

2 | MATERIALS AND METHODS

2.1 | Study area and study sites

This study was carried out in Berlin, Germany's largest city with 3.7 million inhabitants within a total area of 891.1 km^2 (Amt für Statistik Berlin-Brandenburg, 2020). Berlin's climate is temperate with an annual average temperature of 9.9 °C and a mean annual precipitation of 576 mm, measured by an inner-city weather station in the observation period of 1981–2010 (Quanz et al., 2018). About 59% of Berlin's surface is dominated by built-up areas and streets (Senate Department for Urban Development and Housing, 2016). However, Berlin's polycentric urban structure is closely interwoven with numerous remnants of natural landscapes (forests, rivers, lakes and wetlands) and the pre-industrial cultural landscape (agricultural fields and grassland, forest plantations), which are located between individual settlement cores. Sandy and loamy soils from the last ice age prevail in the (near-)natural landscapes, while strongly modified, anthropogenic soils are associated with different urban land-use types (von der Lippe et al., 2020). Dry grasslands are a vegetation type that spans a range of near-natural to strongly human-influenced sites throughout the city. For this reason, urban dry grasslands have been selected as a model ecosystem within the CityScapeLab Berlin, an experimental research platform with a network of 56 permanent

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plots, established for the evaluation of biodiversity in urban environments (von der Lippe et al., 2020). The investigated dry grasslands are extensively managed by mowing up to two times per year, without additional fertilization or irrigation. All plots belong to the same biotope type in the classification scheme of the Berlin biotope mapping (biotope code 05120, i.e. dry grasslands; Senate Department for Urban Development and Housing, 2014) and can be assigned to the same vegetation type following the phytosociological classification (i.e. Sedo-Scleranthetea). The dry grassland plots clearly differ from traditional short-cut lawns in parks that are subject to much higher levels of management intensity and recreational activities.

We selected a subset of 20 dry grassland plots of 16 m^2 each that were relatively evenly distributed across the city (Figure 1) and whose surroundings were subject to different levels of urbanization, indicated by, for example, human population density or percentage of impervious surface. The same subset of 20 plots has been used by a complementary study exploring the effects of urbanization on the relationship of biodiversity and above-ground plant productivity and functions related to water and nutrient cycling (Onandia, Schittko, et al., 2019).

2.2 | Above-ground diversity

Vascular plant diversity was characterized both by taxonomic and functional diversity, estimated as species richness and Rao's quadratic entropy (Rao's Q, Rao, 1982; Botta-Dukát, 2005). From April to May and June to July 2017, two vegetation surveys were carried out following the Braun-Blanquet approach within each of the 20 grasslands, recording the per cent cover of 145 vascular plant species (Table S9). Based on expert knowledge and region-specific literature, plant species were classified according to their biogeographic origin into native or non-native species. Note that the class 'non-native' encompasses species introduced by human agency before the year 1492 (archaeophytes) and after 1492 (neophytes). Rao's Q was calculated using Gower distances between species pairs based on 12 plant functional traits: plant height, specific leaf area, life-form, flower colour, flower class, clonal growth organs, length of dispersal unit, seed mass, leaf area, leaf nitrogen content, nitrogen fixation and mycorrhizal infection (Table S10). Trait data were extracted from the databases TRY (Kattge et al., 2011) and BiolFlor (Klotz et al., 2002).

2.3 | Below-ground diversity

Microarthropods were sampled in late summer 2017 by taking three soil cores of 10 cm depth with a 5 cm diameter (Wurzelbohrer V2A, Umwelt-Geräte-Technik GmbH) at three corners of every plot. The animals were extracted using a modified MacFadyen funnel for 20 days and were preserved in 70% ethanol. Arthropods were identified at the level of order or family based on the identification of easily classifiable descriptor taxa with known functional roles (e.g. trophic guilds, Rota et al., 2015, Table S11). Abundances of taxa were recorded for each replicate. It should be noted that a classification of microarthropods at the order or family level is rather coarse, limiting comparisons to a species-level classification. Earthworms were collected in five smaller subplots of 20 cm × 20 cm to a soil depth of 20 cm by hand sorting in November 2017. Earthworms were stored in 70% ethanol to be

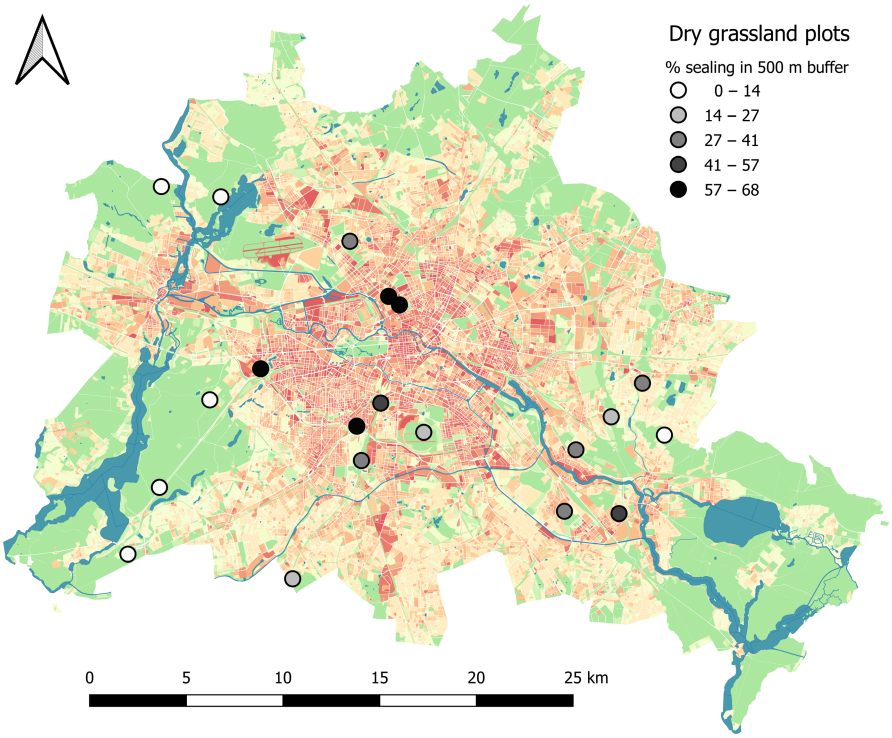


FIGURE 1 Selected study plots (n = 20) in Berlin (Germany) with degree of impervious surfaces in a 500 m buffer around each plot (black dots). The colours on the map represent the degree of impervious surfaces for the whole area of the city; ranging from green (low percentage per block area) to red (high percentage per block area)

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later identified to the species level and counted to record abundances (Table S12).

2.4 | Urbanization

To estimate the level of urbanization (as a driver of abiotic novelty), we applied a commonly used indicator of urbanization: the percentage of impervious surfaces in the surroundings of an area (Lu & Weng, 2006; Schwarz, 2010). We calculated the mean percentage of impervious surfaces in a 500 m buffer area around each of the 20 dry grassland areas containing the study plots using publicly available urban habitat maps from the Berlin Senate Department for Urban Development and Housing and QGIS 2.18.0 (QGIS Development Team, 2016). Furthermore, we performed independent analyses with CityScapeLab data (i.e. principal component analyses and correlations, results not shown) revealing that the percentage of impervious surfaces is the best performing urban indicator (and better performing than human population density) for the data. It correlates well with many climatic (e.g. urban heat island), environmental (e.g. soil pollution, soil pH), and urban matrix related (e.g. population density, road density) variables.

2.5 | Biotic novelty

For each of the 20 plots, the degree of biotic novelty of the plant communities was assessed with the Biotic Novelty Index (BNI; Schittko et al., 2020). The BNI incorporates the eco-evolutionary perspective of novelty and may lead to deeper insights compared to counting a simple number of non-native species. The index captures the functional diversity contributed by novel species recently arrived in the community, weighted by their relative abundance. It is based on two components: the pairwise functional distance between species (i.e. Rao's *Q*; Rao, 1982) and a temporal coexistence component that weighs the functional differences between pairs of species based on how long both species have been present in the region. For example, if a given species pair consists of one native and one recently arrived non-native species, the trait distance between both will receive a higher weight than the distance between a pair consisting of one native and one earlier arrived non-native species. This idea is based on the finding that non-native species will gradually become familiar with their interaction partner(s) over time (i.e. their eco-evolutionary experience will increase), which may lead to a decrease in novelty in the community. The temporal coexistence component of the index was calculated from species' residence times in the Berlin area (see Schittko et al., 2020 for a detailed description on how residence times were calculated). For the calculation of the functional diversity component after Rao, we used the same method and traits as described above.

2.6 | Soil characteristics

Soil characteristics were assessed with a combination of two chemical measurements (pH and cation-exchange capacity) and four physical measurements (bulk density, field capacity, clay content and silt content, Table S1). Chemical measurements were conducted in June 2017, and exact specifications of the methodology can be found in the description of the CityScapeLab Berlin (von der Lippe et al., 2020). Data for the physical parameters were extracted from the Berlin Environmental Atlas provided by the Berlin Senate Department for Urban Development and Housing (2018).

2.7 | Soil functions and multifunctionality

For the calculation of soil multifunctionality, we used in total five measurements (Table S2) which are related to three key soil functions: (a) below-ground plant productivity, (b) decomposition rate and (c) soil nutrient supply. To assess below-ground plant productivity, we measured root biomass, since equivalent to the measurements above-ground, the standing biomass of roots can be used as a proxy for below-ground net primary productivity (Deng et al., 2020; Meyer et al., 2015; Ni, 2004). For measuring root biomass, three soil cores of 30 cm depth were extracted with a 5 cm diameter soil core sampler (see description above) at every plot in late summer in 2017. Roots were washed with a 1 mm sieve, oven-dried at 70 °C and weighed. To assess decomposition rates of standardized plant litter, we used the tea-bag index method (Keuskamp et al., 2013) and buried Lipton green tea and Lipton rooibos non-woven polypropylene tea bags in each plot. Tea bags were prepared according to Keuskamp et al. (2013), and four pairs of tea bags were buried from November 2017 to April 2018 at the four corners of each plot. To assess soil nutrient supply, we used data for the concentrations of soil macronutrients N, P and K available from the CityScapeLab Berlin research platform. Nutrient measurements were conducted in June 2017, and exact specifications of the methodology can be found in the publication on the CityScapeLab Berlin (von der Lippe et al., 2020). Using concentrations of nutrients as a proxy of soil nutrient supply and potential nutrient cycling is comparable to other soil multifunctionality studies (Wang et al., 2019; Wang et al., 2020). Next, we used the averaging approach (Byrnes et al., 2014) to calculate soil multifunctionality in a comparable manner to previous soil studies (Tresch et al., 2019; Wagg et al., 2014). The averaging approach provides an intuitive way to assess changes in several ecosystem functions simultaneously and is commonly used in studies assessing diversity effects on functions (Byrnes et al., 2014). Averaging consisted in calculating a mean value across different standardized values of the abovementioned soil measurements (Table S2) for each sampling site. We are aware of the advantages and disadvantages of presenting an aggregate measure of ecosystem multifunctionality (see Manning et al., 2018 for a review), which is why we present and discuss also results based on the individual soil measurements.

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2.8 | Soil organic carbon

Stratified soil sampling was performed in late summer 2017: three soil cores of 30 cm depth were extracted with a 5 cm diameter soil core sampler (see description above) at every plot. The soil core was segmented to a depth resolution of 5 cm, yielding six subsamples per 30 cm core. Total carbon concentration was analysed on ball-milled subsamples (RETSCH MM 200, RETSCH GmbH) by an elemental analyser at 1,150 °C (Euro EA 3000, HEKAtech GmbH). To determine the organic carbon concentration, either the inorganic or the organic carbon compounds need to be removed (Bisutti et al., 2004; Steinbeiss et al., 2008). Comparable to previous SOC studies (e.g. Lange et al., 2015; Steinbeiss et al., 2008), we measured inorganic carbon concentration by elemental analysis at 1,150 °C after removal of organic carbon for 16 h at 450 °C in a muffle furnace (RETSCH SV 1, RETSCH GmbH) of all samples. Organic carbon concentration was then calculated as the difference between both measurements and by accounting for bulk density estimates for the plots.

2.9 | Statistical analysis

We used linear models to investigate the role of plant biodiversity, biotic novelty and urbanization on soil multifunctionality and SOC (first aim of this study) and the relationship between soil multifunctionality and SOC (third aim of this study). Model assumptions of linear models were evaluated with diagnostic plots in R and in cases where the assumptions were not met, we applied generalized linear models (GLMs) with an appropriate error distribution family and link function.

We fitted piecewise SEMs, using the piecewiseSEM package (Lefcheck, 2016), to evaluate the relative importance of direct and indirect effects of native and non-native plant species richness, respective plant cover, urbanization, and soil characteristics on soil fauna, soil multifunctionality and SOC (second aim of this study, Figure 2). For this analysis, we intentionally used the number and cover of non-native plants in the SEMs instead of the BNI as a measure of biotic novelty. This was done to compare the direct and indirect effects of native and non-native vegetation, since it was shown before that both groups respond differently to parameters associated with urbanization (Onandia, Schittko, et al., 2019). To account for multicollinearity and reduce the dimensionality of our dataset, we applied a PCA for the soil characteristics and used the first three PCA axes explaining 73.5% (Figure S1) of the variation (the number of axes was determined by performing a parallel analysis in R with the package multicon). Due to the different resolutions of diversity estimations for microarthropods (taxon richness) and earthworms (species richness), and differences in the sampling methods, we tested both in two different set of models. Thus, we constructed in total four SEMs with either soil multifunctionality or SOC as response variable, and microarthropod diversity or earthworm diversity as potential mediators. To avoid multicollinearity of soil organism abundance and species (or taxon) richness, we calculated Shannon's diversity index (Shannon, 1948) for microarthropods and earthworms (although individual effects of abundance and species richness are reported in Table S7). The four a priori SEMs with hypothesized links between factors are represented in Figure 2. We reduced the number of variables in the full models using Bayesian information criteria and Fisher's C statistic, as suggested by Hertzog (2019). The full and reduced final models differed in at least ΔBIC = 46.39 units and ΔFisher's C = 6.96 units (Table S4), indicating improved model fitness. Model assumptions of individual component models within an SEM were evaluated with diagnostic plots in R and in cases where the assumptions were not met, we applied GLMs with an appropriate error distribution family and link function. We present the standardized coefficient β for each path from each model and estimated indirect effects through coefficient multiplication and total effects

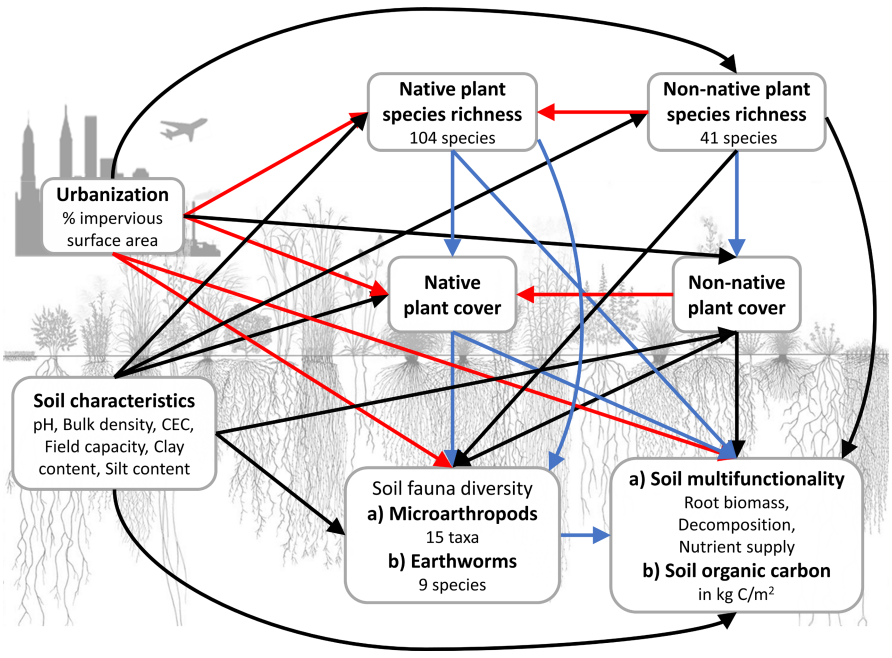


FIGURE 2 A priori SEM models with hypothesized direct and indirect effects of native and non-native plant species richness, respective plant cover and soil fauna diversity on soil multifunctionality and SOC. In total, we constructed four SEMs differing in soil organism group (earthworms or microarthropods) and functional response (soil multifunctionality or SOC). Expected positive relationships are given in blue and negative ones in red, black arrows represent rather unclear outcomes (see also Figure S2 and Table S3 for detailed a priori hypotheses for each relationship). 'CEC' = cation-exchange capacity

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through summing direct and indirect effects. To calculate the standardized coefficients, we used the observational–empirical approach after Menard (2011; see also Lefcheck, 2016; Grace et al., 2018), which was done to address the use of GLMs with nonlinear responses. In this method, error variance is based on the differences between predicted scores and observed data. The standard deviation used for standardization is computed as the square root of the variance of the predictions (on the linear scale) plus the correlation between the observed and predicted values of the response (on the original scale). As a goodness-of-fit measure for GLMs, we used the adjusted pseudo-R^2 after Cameron and Windmeijer (1997) from the package RSQ (Zhang, 2020). All calculations were carried out using R version 3.4.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Urban plant biodiversity, soil multifunctionality and soil organic carbon

The 20 dry grassland plots studied in Berlin varied considerably in terms of plant species richness, plant functional diversity and biotic novelty. Plant species richness varied more than threefold among grasslands (on average 27.8 species per plot ± 7.6 *SD*, range 13–48), and functional diversity calculated with Rao's *Q* showed a twofold variation (on average 0.073 ± 0.017 *SD*, range 0.050–0.107). Native species richness was higher (on average 20.9 species ± 5.9 *SD*) than non-native species richness (on average 7.0 species ± 2.8 *SD*). The biotic novelty of the plant communities estimated with the BNI showed a 10-fold variation (on average 0.021 ± 0.024 *SD*, range 0.002–0.092).

Statistical analyses of the soil multifunctionality across the 20 plots indicated that multifunctionality was positively related to plant species richness. Nineteen per cent of the variation in soil multifunctionality was explained by plant species richness ($p = 0.024$, Figure 3a). Among the individual soil measurements used to calculate multifunctionality, only root biomass was significantly correlated with plant species richness ($R^2 = 0.36$, $p = 0.005$, Table S5). However, soil multifunctionality was not related to plant functional diversity ($R^2 = 0.01$, $p = 0.63$, Figure 3b). Neither of the two indicators of urbanization (percentage of impervious surface area, $R^2 = 0.00$, $p = 0.99$, Figure 3c) and biotic novelty (BNI of the plant communities, $R^2 = 0.02$, $p = 0.59$, Figure 3d) had an effect on soil multifunctionality.

On average, 8.35 kg/m^2 (± 2.64 kg/m^2 *SD*) carbon was stored in the top 30 cm of the soils of the 20 dry grassland plots. Soil organic carbon was positively related to the total plant species richness in the plots ($R^2 = 0.19$, $p = 0.025$, Figure 4a). Plant functional diversity calculated with Rao's *Q* based on 12 functional traits showed a similar positive relationship with soil carbon ($R^2 = 0.20$, $p = 0.046$, Figure 4b). Consistent with soil multifunctionality, neither the percentage of impervious surface area ($R^2 = 0.00$, $p = 0.93$, Figure 4c) nor the biotic novelty of the plant communities ($R^2 = 0.10$, $p = 0.22$, Figure 4d) had significant effects on SOC.

3.2 | Direct and indirect effects of above- and below-ground diversity on soil multifunctionality and soil organic carbon

Overall, microarthropod diversity (Figure 5a) and earthworm diversity (Figure 5b) had strong positive effects on soil multifunctionality ($\beta = 0.57$, $p = 0.016$ and $\beta = 0.47$, $p = 0.025$ respectively, Table S6). Other strong predictors with positive direct effects on multifunctionality were native plant cover ($\beta = 0.58$, $p = 0.018$) and soil characteristics (PC2, $\beta = 0.57$, $p = 0.013$) in the SEM including earthworms (Figure 5b), and soil PC3 in the SEM including microarthropods ($\beta = 0.38$, $p = 0.049$, Figure 5a). Soil PC2 was represented by a higher cation-exchange capacity and a lower clay content (Figure S1), indicating that soils with either a higher cation-exchange capacity or a lower clay content covaried with multifunctionality. Soil PC3 was associated with high scores of bulk density and low field capacity scores (Figure S1). Urbanization had a strongly negative effect on earthworm diversity ($\beta = -0.67$, $p < 0.001$) and consequently a negative indirect effect on multifunctionality ($\beta = -0.31$, Figure 5b).

Soil microarthropod diversity was strongly positively affected by native and non-native plant cover ($\beta = 0.87$, $p < 0.001$ and $\beta = 1.09$, $p < 0.001$ respectively), less strongly by soil PC2 ($\beta = 0.47$, $p < 0.001$) and native plant species richness ($\beta = 0.26$, $p = 0.013$, Figure 5a). Non-native plant species richness and soil PC3 had negative effects on microarthropod diversity ($\beta = -0.82$, $p < 0.001$ and $\beta = -0.46$, $p < 0.001$ respectively, Figure 5a). The relationship between microarthropod diversity and soil PC3 is indicative for positive and negative effects of soil field capacity and bulk density, respectively, on microarthropod diversity (Figure S1). Both native and non-native plant species richness had positive indirect (and separate) effects on microarthropod diversity ($\beta = 0.44$ and $\beta = 0.84$ respectively) mediated by an increase in plant cover. Consequently, both native and non-native plant species richness also exhibited positive indirect effects on soil multifunctionality—through a positive cascading effect leading from the respective plant species richness to plant cover to soil fauna diversity and ultimately affecting multifunctionality. However, the positive indirect effect of non-native plant species richness on microarthropod diversity was almost balanced by the respective negative direct effect ($\Delta\beta = 0.02$).

Consistent with the results on multifunctionality, SOC was positively affected by increasing microarthropod diversity ($\beta = 0.67$, $p = 0.004$, Figure 6a) and also by increasing earthworm diversity ($\beta = 0.49$, $p = 0.022$, Figure 6b). Both effects were slightly more pronounced compared to the effects on multifunctionality. In contrast, no other factor was directly related to SOC in the two SEMs. However, urbanization had a negative indirect effect on SOC ($\beta = -0.33$, Figure 6b) due to the decrease in earthworm diversity. Both native and non-native plant species richness indirectly (and separately) increased SOC; again, through a positive cascading effect leading from the respective plant species richness to plant cover to soil fauna diversity and ultimately affecting SOC. However, analogously to the results on multifunctionality, a direct negative relationship between non-native plant species richness and microarthropod diversity was observed ($\beta = -0.82$, $P < 0.001$, Figure 6a).

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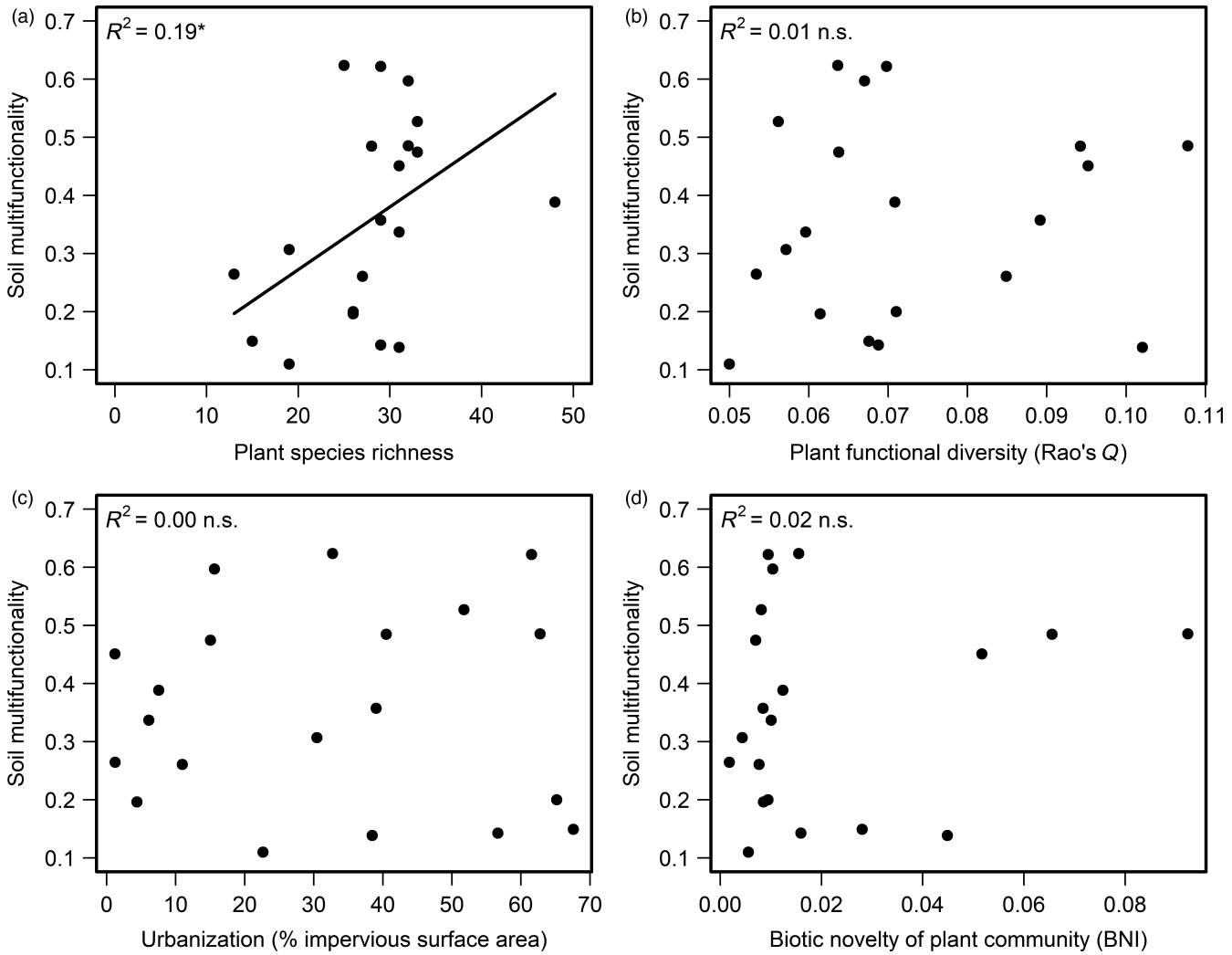


FIGURE 3 Relationships between soil multifunctionality and (a) plant species richness, (b) plant functional diversity (calculated with Rao's Q), (c) the percentage of impervious surface area in a 500 m buffer zone around the 20 urban grassland plots and (d) the biotic novelty of the 20 plant communities (calculated with the Biotic Novelty Index, BNI). Soil multifunctionality was calculated as an averaged value across five measurements that are indicative for three soil functions (i.e. below-ground plant productivity, decomposition of standardized litter and nutrient supply). See also Figure S3 for individual effects of native and non-native plant species richness on soil multifunctionality. Asterisks indicate statistical significance using generalized linear models ('*' = $p < 0.05$, 'n.s.' = $p \geq 0.05$)

Standardized total effects (i.e. the sum of direct and indirect effects) from the four SEMs revealed that native and non-native plant species richness had different effect sizes on multifunctionality and SOC. In both multifunctionality SEMs, the total positive effect of native plant species richness on soil functioning ($\beta = 0.40$ and $\beta = 0.37$) was higher compared to the total effect of non-native plants ($\beta = 0.03$ and $\beta = 0.13$, Figure S4). However, in the two SEMs explaining SOC, only the model containing microarthropod diversity showed a similar relation of total effects (natives $\beta = 0.47$, non-natives $\beta = 0.03$), whereas in the model with earthworm diversity, non-native plant species richness had a stronger total effect on SOC ($\beta = 0.19$) compared to native plants ($\beta = 0.08$, Figure S4). These differences in total effects can be explained by the direct effects of non-native vegetation on native plant species richness and cover (which were observable in each of the four models).

3.3 | Relationship between soil multifunctionality and soil organic carbon

Soil multifunctionality had a strong positive effect on SOC ($R^2 = 0.52$, $p < 0.001$, Figure 7). All five individual measurements used to calculate multifunctionality showed positive relationships with SOC (although three of five had only marginally significant effects, Table S8). The highest correlations of the soil functions were found between plant root biomass and SOC ($R^2 = 0.25$, $p = 0.026$, Table S8), and soil nitrogen content and SOC ($R^2 = 0.41$, $p = 0.003$, Table S8).

4 | DISCUSSION

The provisioning of ecosystem services by urban grasslands has important consequences, as urban areas are, for example, major

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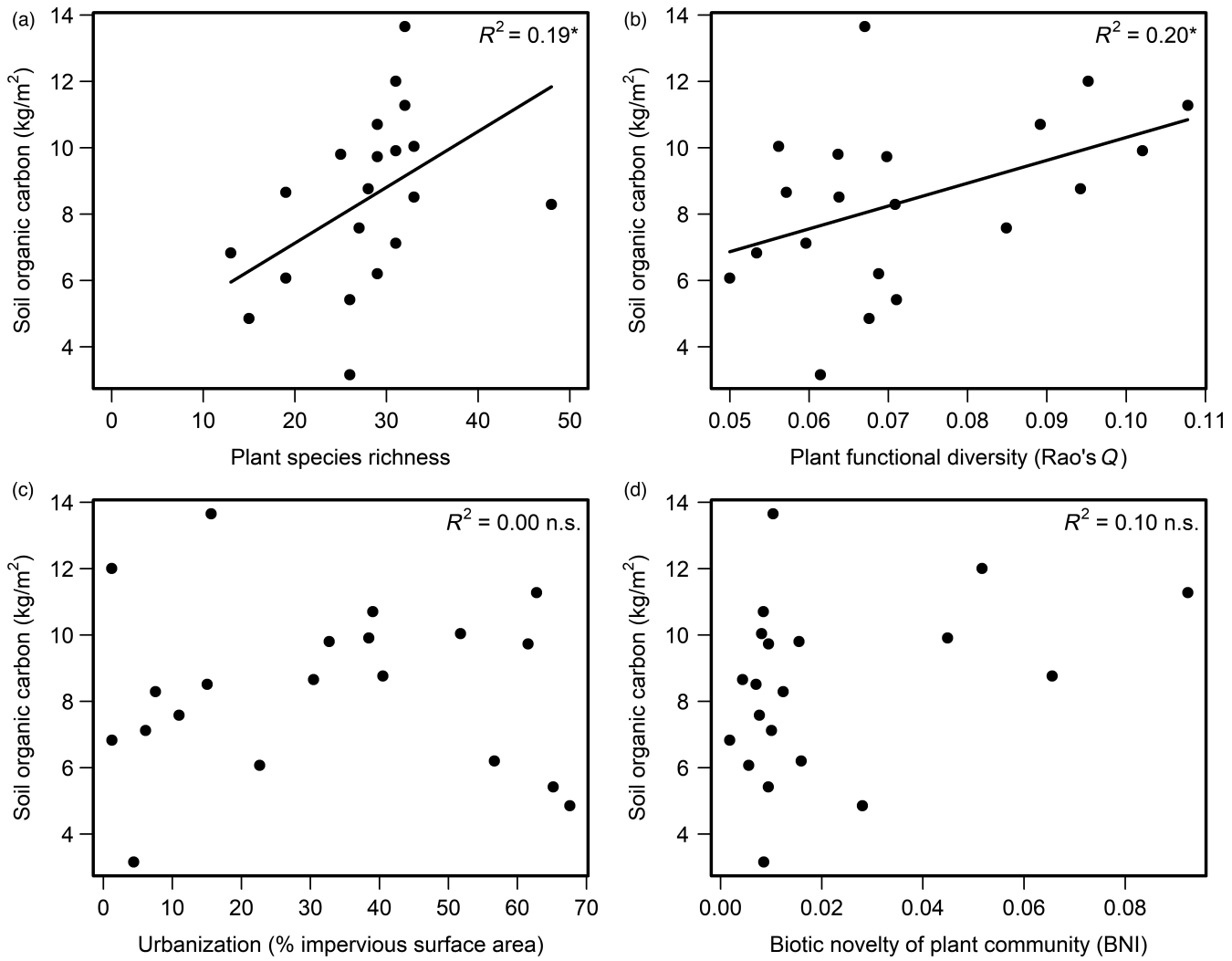


FIGURE 4 Relationships between soil organic carbon and (a) plant species richness, (b) plant functional diversity (calculated with Rao's Q), (c) the percentage of impervious surface area in a 500 m buffer zone around the 20 urban grassland plots and (d) the biotic novelty of the 20 plant communities (calculated with the Biotic Novelty Index). See also Figure S3 for individual effects of native and non-native plant species richness on SOC. Asterisks indicate statistical significance using generalized linear models ('*' = $p < 0.05$, 'n.s.' = $p \geq 0.05$)

producers of atmospheric CO_2 emissions, but can also offset some of the associated carbon losses by retaining stable organic carbon in their soils. However, while the maintenance of biodiversity in cities received growing attention in the last decades (Bonthoux et al., 2014; Fischer et al., 2020; Nilon et al., 2017; Parris et al., 2018), its direct and indirect effects on ecosystem functioning and services are still rather poorly studied and understood.

4.1 | Urban plant biodiversity, soil multifunctionality and soil organic carbon

As one of the main results of this study, we found that soil multifunctionality and SOC were both positively related with plant diversity. Contrary to our expectations, however, the proportion of impervious surfaces surrounding these urban grasslands (which we used as an indicator for urbanization) had no detectable effect on soil multifunctionality or SOC in the GLMs. Similarly, the BNI of the plant communities, which tells us how novel (high BNI) or natural (low BNI) these communities are, showed no significant relationship with either of the two factors in the GLMs. Therefore, these models provide empirical evidence that significant plant diversity effects on multiple soil functions and the provision of an associated service (SOC) may be considered robust to human-mediated changes in abiotic and biotic conditions associated with ecological novelty in urban systems. However, it should be noted that our study has a relatively small scale and that only one urban ecosystem type was investigated, which calls for further research to support this finding.

Positive effects of plant species richness on ecosystem functioning are well documented, with above-ground plant productivity supposedly being the most investigated function (e.g. Hector et al., 1999; Hooper & Vitousek, 1997; Jochum et al., 2020; Marquard et al., 2009). In our study, a strong significant correlation between individual soil functions and plant species richness was found for root

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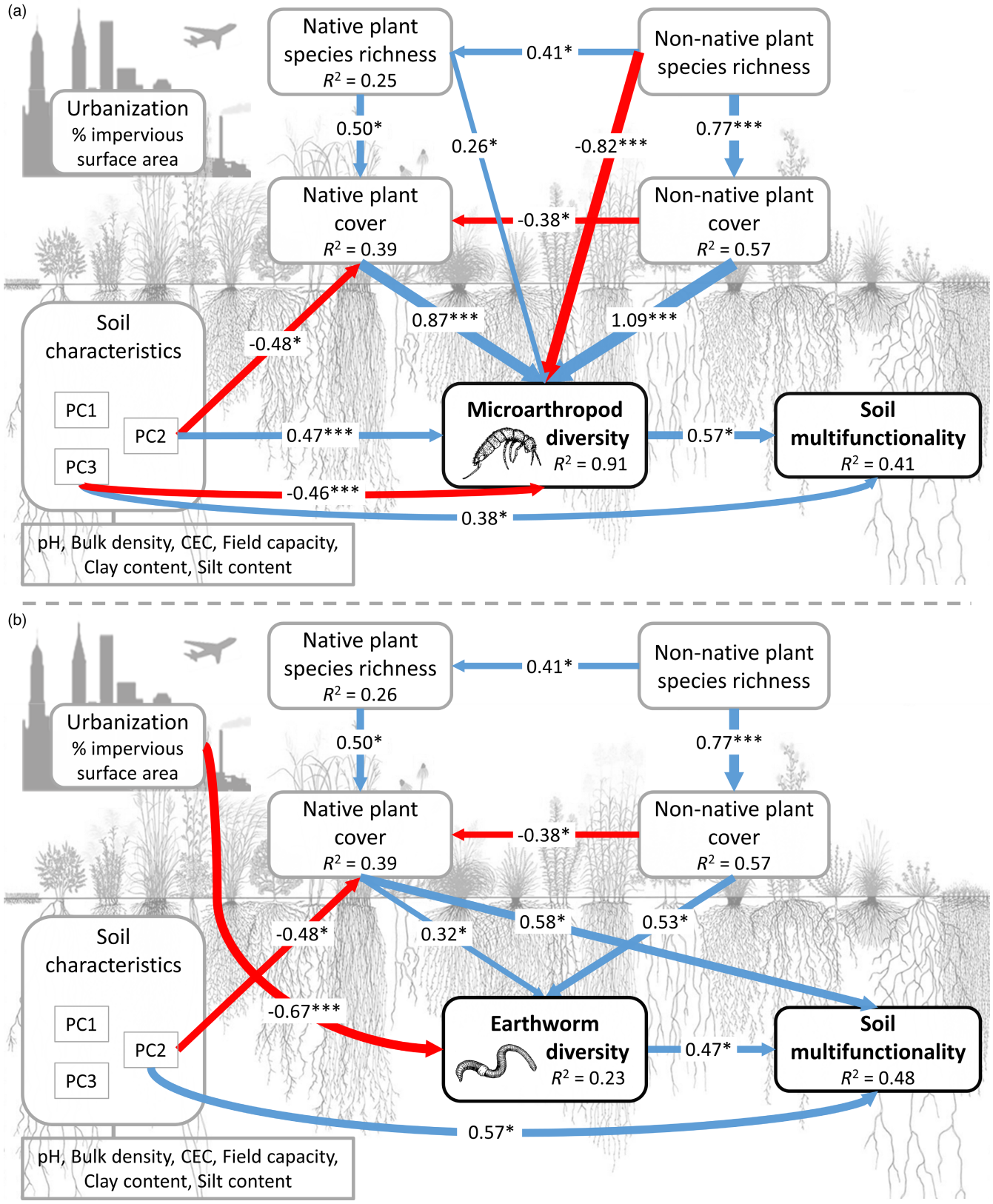


FIGURE 5 Final two most parsimonious SEMs connecting native plant species richness and cover, non-native plant species richness and cover, urbanization and soil characteristics with soil multifunctionality, and including (a) soil microarthropod diversity and (b) earthworm diversity (both calculated with Shannon's diversity index). Blue arrows represent significantly ($p < 0.05$) positive and red arrows significantly negative relationships. The thickness of the significant paths represents the magnitude of the standardized regression coefficient or effect sizes, given on the arrows. Pseudo-R^2s for component models are given in the boxes of the response variables. 'PC1-3' = first three PCA axes explaining 73.5% of the variation of soil characteristics; 'CEC' = cation-exchange capacity

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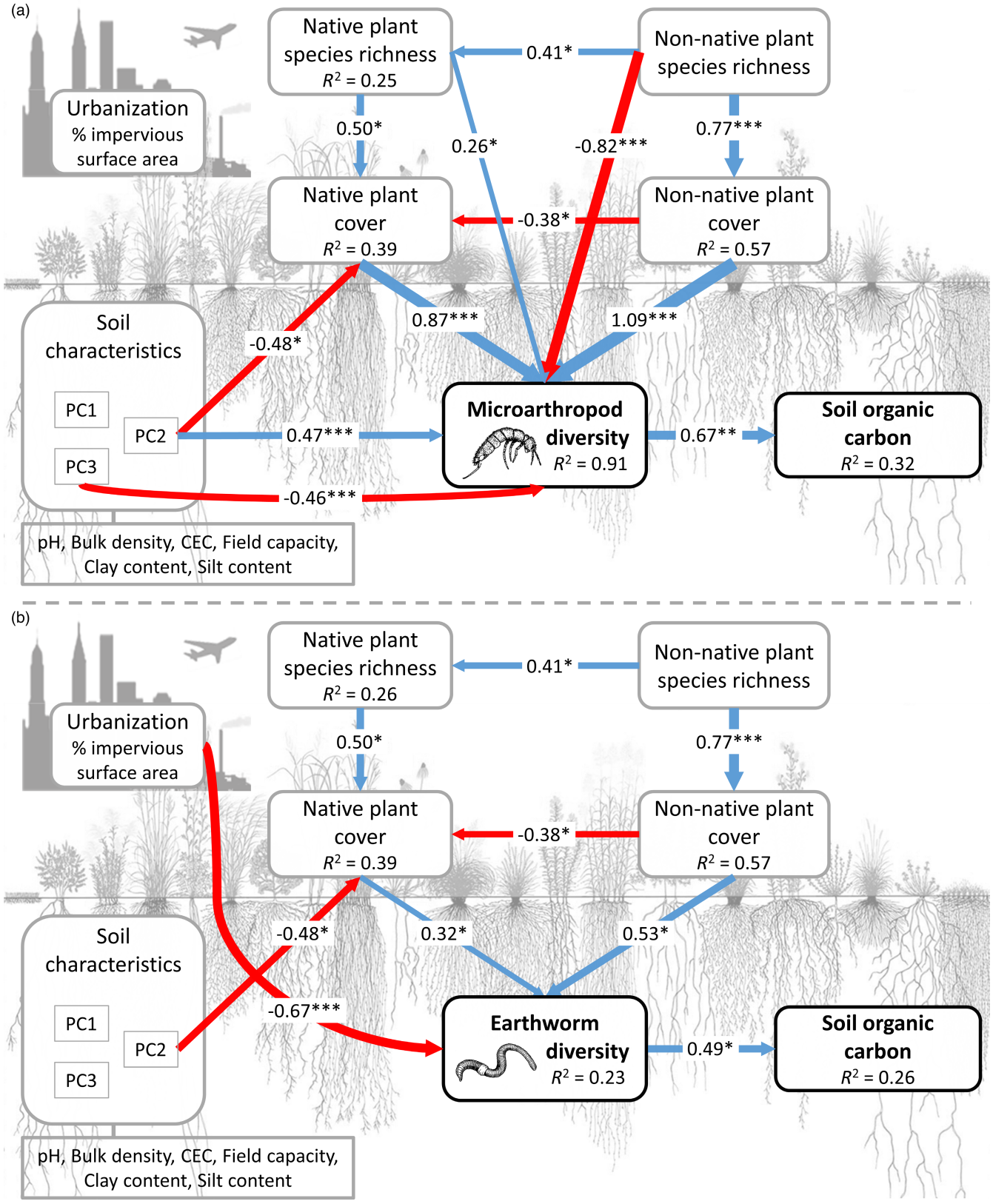


FIGURE 6 Final two most parsimonious SEMs connecting native plant species richness and cover, non-native plant species richness and cover, urbanization and soil characteristics with soil organic carbon, and including (a) soil microarthropod diversity and (b) earthworm diversity (both calculated with Shannon's diversity index). Blue arrows represent significantly ($p < 0.05$) positive and red arrows significantly negative relationships. The thickness of the significant paths represents the magnitude of the standardized regression coefficient or effect sizes, given on the arrows. Pseudo-R^2s for component models are given in the boxes of the response variables. 'PC1-3' = first three PCA axes explaining 73.5% of the variation of soil characteristics; 'CEC' = cation-exchange capacity

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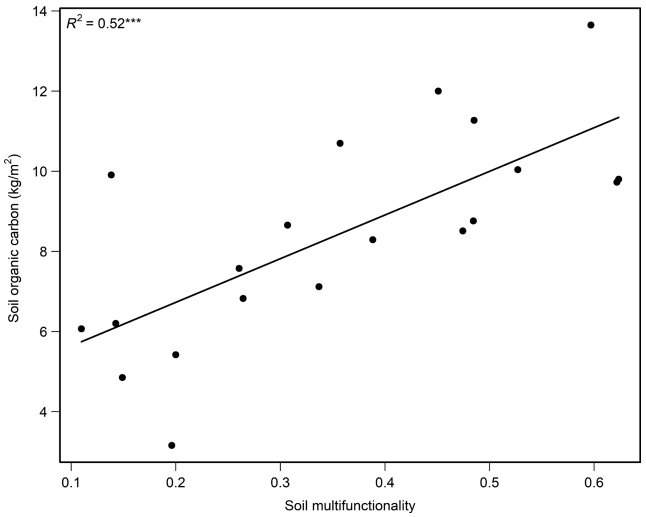


FIGURE 7 Relationship between soil multifunctionality and soil organic carbon stocks of the 20 urban grassland soils. Soil multifunctionality was calculated as an averaged value across five measurements that are indicative for three soil functions (i.e. below-ground plant productivity, decomposition of standardized litter and nutrient supply). Asterisks indicate statistical significance using a linear model ('***' = $p < 0.001$)

biomass, which is in line with studies that manipulated plant species richness in experimental grassland plots (e.g. Gastine et al., 2003; Lange et al., 2015). However, evidence for this positive relationship in non-manipulated grasslands is scarce, and the present study provides empirical evidence that this relationship is also maintained in an urban context. Interestingly, Onandia, Schittko et al. (2019) reported an analogous positive relationship between above-ground plant productivity and plant species richness for the same 20 plots within the CityScapeLab Berlin.

Similarly, ecosystem services, such as SOC storage, are known to be driven by plant diversity (Cong et al., 2014; Lange et al., 2015), and the results reported in this study indicated that this beneficial effect of biodiversity is also persistent in urban areas. We found that, on average, 8.35 kg/m^2 carbon was traceable in the 20 urban grassland soils. It is remarkable that this value is almost twice as high as that given by the Berlin city administration based on a city-wide SOC inventory conducted in 2015. The Berlin Senate Department for Urban Development and Housing (2018) used a GIS-modelling approach to estimate SOC stocks for Berlin's soils and had values available for all of our 20 plots (mean value for the estimated SOC stock = 4.4 kg/m^2). This difference reflects the limitations in the relatively low spatial resolution of GIS-based methods used in national studies when applied to urban areas which have many small patches of greenspaces. It also highlights that city-wide carbon budget calculations can be partially inaccurate. For example, Berlin's total CO_2 emissions amounted to approximately 16.5 million tons in 2015 (Amt für Statistik Berlin-Brandenburg, 2018). Based on the estimated values from the Berlin Senate Department, a total of 4.8 million tons of carbon are stored in Berlin's soils, which equals 17.6 million tons of CO_2. Consequently, the Senate Department reports that Berlin's soils stored more CO_2 than was emitted by primary energy consumption in 2015. Our findings support these budget estimations but also suggest that unsealed soils have an even greater potential to mitigate climate change than previously estimated.

4.2 | Direct and indirect effects of above- and below-ground diversity on soil multifunctionality and soil organic carbon

The SEM approach provided a more complex picture, revealing that the positive effects of plant species richness on soil multifunctionality and SOC were mediated by increasing soil organism diversity. The SEMs also showed that in our urban grassland systems, both native and non-native plant species richness indirectly affected multifunctionality and SOC, suggesting that both groups contributed to the overall positive effect of plant species richness shown with the regression models. However, in contrast to these positive effects on ecosystem functioning, native and non-native plant species differed in their direct influence on microarthropods. Native plant species richness was positively related to microarthropod diversity, whereas non-native plant species richness showed a negative relationship. Consequently, non-native plant species richness also exerted a negative indirect effect on soil multifunctionality and SOC in these two models, whereas no such effect was detected for native plants. These opposing positive and negative indirect effects from non-native plants thus led to lower positive total effects of non-native plant species richness on multifunctionality and SOC compared to native plant species richness, which was observed in three of four SEMs.

The SEM analyses not only supported the positive effects of plant diversity on ecosystem functioning but also provided a more mechanistic insight due to the integration of plant cover, soil biota, abiotic conditions and different aspects of ecological novelty into the models. In this strictly confirmatory approach (Grace, 2006), all four SEMs revealed that the positive effects of plant species richness on ecosystem functioning were mediated by increasing soil organism diversity. This result agrees with a recent study by Tresch et al. (2019) who identified indirect effects of plant diversity on soil multifunctionality mediated by soil fauna diversity (more specifically, Collembola and earthworms) in urban gardens in Zurich, Switzerland. Moreover, similar to our study, the researchers from Zurich found no effects of increasing urbanization influencing this top-down cascading effect of plant diversity. In contrast to our study, Tresch et al. (2019) reported also a direct positive effect leading from plant diversity to soil multifunctionality. Furthermore, it is also important to note that in our study urbanization had a negative effect on earthworm diversity and thus a negative indirect effect on multifunctionality and SOC. Although this effect was not strong enough to eliminate the indirect and positive plant diversity-functioning relationship, it can be assumed that the latter could happen if earthworm diversity declined any further. The SEM approach further revealed that increasing plant species richness was

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associated with higher plant cover, which led to the positive effect on soil fauna diversity.

The idea of considering non-native species in biodiversity–ecosystem functioning studies is controversial because some of these species may become invasive and can pose serious biodiversity threats (Davis et al., 2011; IPBES, 2019; Pauchard et al., 2018; Schlaepfer, 2018; Simberloff, 2011). However, since non-native plants are a constitutive component of urban floras, there are also arguments to consider related functions in urban conservation policies (Kowarik, 2011; Schlaepfer et al., 2020). In this study, it was deliberately intended to present the effects of total plant species richness (natives and non-natives together) on ecosystem functioning (linear models in Figures 3 and 4), but to disentangle the contributions of native and non-native species in the second set of models (the SEMs in Figures 5 and 6). The SEMs revealed that both native and non-native plants positively affected multifunctionality and SOC, while native plants did so more clearly. Although non-native species can represent large fractions of urban ecosystems and regional species pools, their contributions on ecosystem functioning and services are often underrepresented or overlooked. For example, a meta-analysis focusing on the link between urban ecosystems and the provisioning of ecosystem services reports that only 10 of 133 investigated studies explicitly discussed a relationship between non-native species and the provision of services (Ziter, 2016). This is a disproportionately small amount given that non-native plants can make up 50%, or more, of species in cities (Pyšek, 1998), and up to 60% in all urban vegetation types (Kowarik, 2008). For instance, in our study sites, where non-native species made up on average 15% of the above-ground biomass, the relationship between species richness and above-ground biomass was not affected by the proportion of non-native species (Onandia, Schittko, et al., 2019). This is further evidence of the potential positive contribution of some non-native species to ecosystem functioning.

On the other hand, we also found that an increasing number of non-native plant species detrimentally affected soil microarthropod diversity. One possible explanation for this decline may be provided by the novel weapons hypothesis in invasion ecology (Callaway et al., 2008; Callaway & Ridenour, 2004). It states that some non-native species produce biochemicals that are not produced by natives in the invaded range. These chemicals may potentially exert strong effects on naïve native species that lack a coevolutionary-based tolerance. There are two possible pathways of how a potential novel weapon exerts effects on soil communities: via plant litter inputs (Weidenhamer & Callaway, 2010) and/or via root exudation of allelopathic compounds (Thorpe et al., 2009). In our case, a higher number of non-native plant species may have also increased the probability that one of these species contained a novel compound. This may also explain why non-native species richness had a negative effect on microarthropod diversity, while the effect of non-native plant cover was positive.

The diversity of earthworm and microarthropod communities was directly associated with plant diversity and composition and soil characteristics. Interestingly, microarthropods were more strongly affected by plant cover than earthworms, highlighting the dominant influence of plants on soil mesofauna (Gobat et al., 2004; Tresch et al., 2019). In addition, soil microarthropod diversity was positively affected by the soil field capacity and negatively affected by bulk density. Higher field capacity values are associated with longer retention times of water in the soil increasing soil moisture (Rai et al., 2017). Higher moisture conditions, in turn, influence nitrogen mineralization of microarthropods (in particular Collembola), as shown in a microcosm study (Kaneda & Kaneko, 2011). On the other hand, increased soil bulk density is often associated with soil compaction (Larsen et al., 2004). In urban areas, soil compaction can be induced by the use of heavy machinery on construction sites but also by other human activities such as excessive trampling or bicycle riding (Randrup & Dralle, 1997). In compacted soils, there is reduced volume available for air and water, as the mineral components are pressed more closely together, which is a condition that can remain over several years (Raper, 2005). Due to soil compaction, the soil microbial activity can be reduced (Kissling et al., 2009), and the soil meso- and macrofauna that rely on macropores may decrease in abundance or disappear completely (Capowiez et al., 2009). This demonstrates the complexity of abiotic drivers in urban habitats and that this complexity is not always captured by a single measure of urbanization (such as percentage of impervious surfaces). Our results further show that despite the presence of unfavourable abiotic conditions for soil organisms, the biodiversity effects of plants on multifunctionality and SOC were still prevailing, which highlights the robustness of these effects.

4.3 | Relationship between soil multifunctionality and soil organic carbon

Soil multifunctionality exerted a strong positive effect on the SOC stocks of the urban grassland soils of our study. All five individual measurements showed positive relationships with SOC (although three of five had only marginally significant effects), which is indicative for the validity of the considered measurements assessing soil functions. The highest correlations of the soil functions were found between plant root biomass and SOC, and soil nitrogen content and SOC, which is in line with studies investigating SOC stocks in agricultural croplands. Two major pathways of organic matter input—root tissue and exudates—directly involve plants (Rumpel & Kögel-Knabner, 2011). Roots contribute to SOC pools through rhizodeposition (Wilts et al., 2004) and the longer residence time of carbon from root tissue than shoot tissue (Rasse et al., 2005). On the other hand, a nitrogen dependency of SOC is also known from agricultural soils where long-time N fertilization can lead to increased SOC (Horwath & Kuzyakov, 2018; Ladha et al., 2011). Plants are considered to play a mediating role for this relationship: N fertilization enhances biomass production of crops leading to higher C inputs into the soil. Abiotic factors can also affect root growth and SOC. Soil clay content has been associated with greater SOC in many soils (Leifeld et al., 2005; Sollins et al., 1996). Bulk density can limit root growth and decrease

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SOC (Brye et al., 2004). However, none of these direct effects of soil properties on SOC could be detected by the SEM approach in our study, which could be due to the strong effects of vegetation that may overshadow minor effects of abiotic conditions.

5 | CONCLUSIONS

While there is a growing body of evidence from controlled experiments in non-urban ecosystems demonstrating that biodiversity facilitates soil functioning and ecosystem service delivery, comparatively little research on the topic has been conducted in urban areas. Our study indicated consistent positive effects of plant diversity on various below-ground ecosystem functions related to biomass production, nutrient supply and decomposition, as well as on SOC storage. Urban grasslands can store higher amounts of SOC than previously estimated, pointing to a major role urban grasslands could play in mitigating climate change. These positive effects of plant species diversity were mediated by increased soil organism diversity, delivering another piece of evidence corroborating the importance of above- and below-ground biodiversity for ecosystem functioning and services.

A range of reasons support the development of more biodiverse grassland in cites (Ignatieva & Hedblom, 2018) and already gain some support in the public (Fischer et al., 2020). Our study adds the argument of a positive relationship between biodiversity and multiple soil functions, which can inform urban environmental policies in the conservation realm and beyond (e.g. policies on climate change adaptation). This management implication applies not only to native species, but to a lesser degree also to non-native plant species. Non-native species can be regarded an integral component of urban biodiversity, and their contribution to the maintenance of ecosystem functioning and services in urban areas should be further investigated in future studies.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; C.S. collected the data, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13852.

DATA AVAILABILITY STATEMENT

Data on soil multifunctionality, SOC, below-ground diversity and soil physical properties are available from the 'Open Research Data' platform at Leibniz Centre for Agricultural Landscape Research (ZALF) under https://doi.org/10.4228/zalf.bf9z-6x30 (Schittko, 2022). Data on plant species richness, impervious surface area and soil chemical parameters from the CityScapeLab Berlin are available under https://doi.org/10.4228/ZALF.DK.111 (Onandia, Acame Poveda, et al., 2019) and https://doi.org/10.6084/m9.figshare.16811701.v1 (von der Lippe et al., 2021).

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