



Woody Plant–Soil Relationships in Interstitial Spaces Have Implications for Future Forests Within and Beyond Urban Areas

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ABSTRACT

Relatively unmanaged interstitial areas at the residential–wildland interface can support the development of novel woody plant communities. Community assembly processes in urban areas involve interactions between spontaneous and cultivated species pools that include native, introduced (exotic/non-native) and invasive species. The potential of these communities to spread under changing climate conditions has implications for the future trajectories of forests within and beyond urban areas. We quantified woody vegetation (including trees and shrubs) in relatively unmanaged

“interstitial” areas at the residential–wildland interface and in exurban reference natural areas in six metropolitan regions across the continental USA. In addition, we analyzed soil N and C cycling processes to ensure that there were no major anthropogenic differences between reference and interstitial sites such as compaction, profile disturbance or fertilization, and to explore effects of novel plant communities on soil processes. We observed marked differences in woody plant community composition between interstitial and reference sites in most metropolitan regions. These differences appeared to be driven by the expanded species pool in urban areas. There were no obvious anthropogenic effects on soils, enabling us to determine that compositional differences between interstitial and reference areas were associated with variation in soil N availability. Our observations of the formation of novel communities in interstitial spaces in six cities across a very broad range of climates, suggest that our results have relevance for how forests within and beyond urban areas are assessed and managed to provide ecosystem services and resilience that rely on native biodiversity.

Key words: nitrogen cycling; carbon cycling; woody plant community; urban land-use change; urban–residential interface; novel ecosystems.

HIGHLIGHTS

- There are marked differences in woody plant composition between interstitial areas—at residential-wildland interface—and natural reference areas across cities.
- Differences in woody plant composition were related to variations in soil Nitrogen (N) availability.
- Novel communities in interstitial areas have implications for management of ecosystem services that rely on native biodiversity in forests within and beyond urban areas.

INTRODUCTION

Urban expansion in the continental USA has created large areas of urban, suburban and exurban land-use intermixed with remnant native ecosystems and agricultural land (Pouyat and others 2007). These land-use patterns are similar across different climate regimes and biomes, creating

ecological homogenization at regional and continental scales (Groffman and others 2017). For example, plant communities and functional diversity in residential yards converge across the continental USA due to similarities in human preferences and management (Polsky and others 2014; Locke and others 2019; Padullés Cubino and others 2019b). Beyond residential yards, interactions between human decisions and natural processes of community assembly have the potential to affect less populated areas surrounding the dense urban core (Groffman and others 2014). In relatively unmanaged interstitial spaces (that is, remnant or spontaneously forested areas surrounded by residential development), native and introduced (exotic/non-native) vegetation (introduced to an area outside its native ecosystem and reproduced spontaneously; USDA, NRCS 2023) have the potential to mix and assemble into new or novel communities (Hobbs and others 2009; Andrade and others 2021). These areas are common throughout metropolitan areas but are especially common in large and expanding suburban and exurban land uses at the residential–wildland interface (Brown and others 2005).

In this study, we addressed the question of whether analysis of forests that have spontaneously assembled in in urban interstitial spaces provides insight into how global environmental change will affect the forests of the future. We ask whether the complex mix of anthropogenic factors affecting these spaces (altered climate and atmospheric chemistry, altered disturbance regimes, altered species pool) is analogous to factors playing out across the globe at lower intensity (McDonnell and Pickett 1990). If so, the novel communities that assemble in these spaces may provide a glimpse of the forests that may become widespread across the world.

Understanding processes of community assembly in interstitial spaces requires an understanding of the factors sorting for cultivated and spontaneous species pools in urban ecosystems (Knapp and others 2012; Pearse and others 2018; Lopez and others 2018; Blouin and others 2019; Padullés Cubino and others 2019a, b, 2020; Cavender-Bares and others 2020). Native vegetation originates from the pool of continental flora interacting with regional climatic drivers, resulting in assemblages adapted to the regional biome. These native species interact with spontaneous (that is, self-propagated) and cultivated species pools introduced by humans (Pearse and others 2018; Avolio and others 2021). The former results from the natural dispersal of regional flora that adapt to or persist in the urban

environment, and the latter include pools introduced from the horticultural industry—primarily determined by human preferences and policies. Cultivated and horticultural species—including both native and introduced (exotic/non-native) species—that escape and establish on their own can also become part of the urban spontaneous pool, dispersing and mixing with regional and continental native flora to create novel communities (Aronson and others 2016; Pearse and others 2018; Blouin and others 2019; Cavender-Bares and others 2020; Avolio and others 2021). The potential for these novel communities to spread under changing climatic conditions has implications (for example, for ecosystem services, social benefits and potential for biodiversity conservation) for the future trajectories of forests within and beyond urban areas (Hobbs and others 2006, 2009; Johnson and Handel 2016).

Novel ecosystems can differ in diversity, composition, age and structure from native ecosystems and, therefore, potentially exhibit different ecosystem functions (Hobbs and others 2009). In urban areas, novel ecosystems can consist primarily of species that are adapted to or persist under urban-associated stresses (for example, urban heat, air, soil, light and noise pollution). Introduced (for example, exotic/non-native)—including invasive species—are disproportionately represented in urban species pools (Avolio and others 2015; Pregitzer and others 2019). Invasive species tend to thrive in nutrient-rich soils, often escape natural enemies and are frequently quick to establish in unmanaged lands (Ehrenfeld 2003; Carreiro and Tripler 2005; Heneghan and others 2004; Johnson and Handel 2016). The presence of these species has implications for the ecosystem functions and services that rely on native biodiversity to support food webs (Narango and others 2018; Tallamy and others 2021), water resources (Richardson and van Wilgen 2004; van Wilgen and others 2008; Le Maitre and others 2000) and soil conservation (Scott and others 1998).

Evaluation of community and ecosystem processes in interstitial areas must consider soil properties. Urban soils are very heterogeneous (Pouyat and others 2007). For example, while many urban soil profiles have been markedly altered by physical, chemical and biological disturbance such as compaction, atmospheric deposition and invasion by exotic earthworms (Pouyat and others 2010; Herrmann and others 2020), others are relatively undisturbed (Raciti and others 2011; Trammell and others 2020a; Ryan and others 2022). These alterations, as well as natural variation in the properties

of relatively unaltered soil profiles, have marked implications for plant community development and ecosystem function (Frelich and others 2019). Soil properties are thus potentially important drivers of novel plant community structure and function in interstitial areas and must be considered when evaluating the potential of these novel communities to spread within and beyond urban areas. More practically, if soils in interstitial areas have been disturbed by site-specific activities such as tillage, fertilization, compaction or pollution, the value of these areas as locations for analysis of how forests that have spontaneously assembled in in urban interstitial spaces provide insight into how global environmental change will affect the forests of the future is reduced.

This study evaluated woody plant community composition and soil microbial carbon (C) and nitrogen (N) cycle processes in interstitial (relatively unmanaged) and natural reference ecosystems (representative of regional biomes) in six metropolitan areas across the USA (Baltimore, MD; Boston, MA; Los Angeles, CA; Miami, FL; Minneapolis-St. Paul, MN; Phoenix, AZ). We tested whether woody plant community composition in interstitial sites differed from that in natural reference sites and whether soil properties were related to those differences. Woody community composition was measured to identify whether plant assemblages included combinations of introduced (for example, non-native/exotic) and native species that differed from assemblages in natural reference sites. We measured basic soil properties (moisture, bulk density), soil microbial biomass C and N content, basal respiration, inorganic N pools, potential net N mineralization and nitrification, and denitrification potential and visually inspected soil profiles to ensure that there were no major anthropogenic differences between reference and interstitial sites such as compaction, profile disturbance or fertilization, and to explore effects of novel plant communities on soil processes. We aimed to answer two questions: (1) How does woody plant community composition differ between interstitial and natural reference sites? (2) Are these differences in vegetation associated with variation in soil C and N cycling processes? We hypothesized that: (1) Woody plant community composition in interstitial sites would differ from that in reference sites, with higher proportion of introduced species and (2) soil N cycling would be altered in interstitial sites, with higher N pools and rates of N cycling processes in the sites with plant communities most distinct from those in reference sites. Results were evaluated in terms of implica-

tions for how forests within and beyond urban areas are assessed and managed to provide ecosystem services and resilience that rely on native biodiversity.

METHODS

Site Selection

We sampled interstitial and reference sites in six major US Metropolitan Statistical Areas (cities): Boston, MA (BOS), Baltimore, MD (BAL), Los Angeles, CA (LAX), Miami, FL (MIA), Minneapolis-St. Paul, MN (MSP) and Phoenix, AZ (PHX) that represent different ecological biomes and/or major climatic regions across the USA (Trammell and others 2016). Within each region, between four and six natural areas that represented the dominant ecological biome(s) were selected as reference sites. The natural areas were located in protected areas with native vegetation (including trees, shrubs and cacti) and were located 1 km or more from other sites. Reference ecosystems include mature (over 75-year-old) oak and tulip poplar forests (BAL); mature (roughly 100-year-old) northern oak-dominated hardwood forests (BOS); remnant southern California chaparral (LAX); coastal upland pine rockland, subtropical hardwood hammock, coastal hammock and pine flatwoods (MIA); oak savanna on sandy outwash, tallgrass prairie and bluff prairie on moraine, and maple-basswood forest on moraine (MSP); and native Sonoran Desert (PHX).

Interstitial sites were sampled ($n = 4$ to 6) on public lands within each metropolitan area. These sites were located in relatively unmanaged areas (generally absent of intensive human intervention such as plowing, mowing, irrigation, fertilization) with vegetation that had developed spontaneously. In addition, the selection criteria included sites with natural soil profiles similar in texture and landscape position to those in the reference areas, without signs of anthropogenic soil disturbance. In some cities, for example, Minneapolis-St. Paul this required distributing sites across different soil parent materials. Unmanaged patches that fit these criteria were located within the same region as the reference sites, either on the edge of the city, at the interface with suburban residential land in public parklands or woodlands (for more detailed description, see Padullés Cubino and others 2020; Lerman and others 2021a). Soil taxonomy was identified using USDA Natural Resource Conservation Service (NRCS) maps for each native reference and interstitial site in each city (Table S1).

Woody Vegetation Sampling

Within each interstitial and native reference site, we established three 8-m radius plots to assess tree (including shrubs and cacti in Phoenix) density, basal area, height and condition (for example, live/dead). Plot locations were randomly selected with a Geographic Information System (GIS) mapping tool before field sampling. We sampled all individuals above 1 m height with a stem greater than 2.54 cm diameter at breast height (DBH) in each plot. We used the USDA Forest Service i-Tree Eco v6.0 manual (<https://www.itreetools.org/>) as a reference for recording species in the field. Woody plant stems were split into understory (< 10 cm DBH) and overstory (> 10 cm DBH). Species identifications were cross-checked with World Flora Online (formerly The Plant List), a comprehensive open-access database containing 400,000 recorded plant species contributed by various institutions (<http://www.worldfloraonline.org/>), the online tools for standardizing taxonomic names Taxonomic Name Resolution Service version 5.0 (Boyle and others 2013; <https://tnrs.biendata.org/>) and Integrated Taxonomic Information System (ITIS) online database (<https://itis.gov/citation.html>). Species were also classified according to origin (native or introduced) based on whether the species was considered native or introduced to the state it was sampled in according to the USDA PLANTS database (<https://plants.usda.gov>). Introduced species are defined as reproducing spontaneously in the wild without human help and tend to persist, and invasives are defined as (1) non-native (or alien) to the ecosystem under consideration and (2) a species whose introduction causes or is likely to cause economic harm, environmental harm or harm to human health (USDA, NRCS, 2023). One reference site in Minneapolis-St. Paul (Cedar Creek Ecosystem Science Reserve BU 103) did not have woody plant species present (Table S1).

Soil Sampling and Laboratory Analysis

Two soil cores up to 30 cm depth were collected at random locations along transects at each site using a 3.3-cm-diameter soil corer, enclosed in plastic sleeves with end caps, put into coolers, and shipped on ice to the Cary Institute of Ecosystem Studies, Millbrook, NY, USA, where they were stored at 4 °C (up to 21 days) until they could be processed. In the laboratory, analysis followed procedures described by Raciti and others (2011) and Ryan and others (2022). Soil cores were first visually in-

spected for evidence of obvious anthropogenic alteration of the soil profile and then divided into 0–10 cm and 10–30 cm sections. Coarse roots and rocks (> 2 mm) were removed by hand. The separated roots and rocks were dried at 105 °C, and rock volumes were estimated using an assumed density of 2.7 g/cm³. Water content was measured via gravimetric analysis, where soil samples were dried for 48 h at 105 °C. Dried samples were used to calculate bulk density (BD) as (total dry mass – rock mass)/(total volume – rock volume). Soil organic matter content was measured by loss on ignition at 450 °C. Cores were not available for one reference site in Los Angeles (Zuma Canyon) and one reference site in Miami (Pine Ridge Sanctuary; Table S1).

Soil exchangeable nitrate (NO₃⁻) and ammonium (NH₄⁺) were extracted in 2 M KCl and analyzed colorimetrically using a Lachat Flow Injection Analyzer. Potential net N mineralization and nitrification, and basal respiration were measured in a 10-day laboratory incubation of soils at room temperature and field moisture. Soils were placed in glass jars fitted with rubber septa to allow for sampling of headspace gas. After incubation, the headspace of the jars was sampled and analyzed for carbon dioxide (CO₂) by gas chromatography with a thermal conductivity detector, and soils were extracted for NO₃⁻ and NH₄⁺. Potential net N mineralization was calculated as the total accumulation of inorganic N, nitrification was calculated as the accumulation of NO₃⁻, and respiration was calculated as the accumulation of the CO₂ during the incubation (Robertson and others 1999).

Microbial biomass C and N content were measured using the chloroform fumigation–incubation method (Jenkinson and Powlson 1976). Soil samples were fumigated with chloroform for up to 24 h to lyse microbial cells, inoculated with 0.1 g fresh soil and incubated for 10 days in mason jars with fitted rubber septa. Microbial biomass C was calculated from the production of CO₂ in the fumigated samples using a proportionality constant (0.41). Microbial biomass N was not corrected with a proportionality constant, and values are just the inorganic produced over the 10-day incubation of fumigated samples.

Rates of potential denitrification were measured using the denitrification enzyme assay (Smith and Tiedje 1979; Groffman and others 1999). Soil subsamples were amended with NO₃⁻, glucose, chloramphenicol and acetylene and incubated anaerobically for 90 min. Gas samples were removed after 30 and 90 min and analyzed for ni-

trous oxide (N₂O) by gas chromatography with an electron capture detector.

Data Analysis

All analyses were performed in R (version 3.3.3; R Core Team 2019). To prepare the species data for site- and city-level comparison, we first characterized woody plant structure in each plot in terms of species' relative abundance, frequency, dominance and importance, and in terms of species diversity (richness, evenness) to examine biodiversity patterns. Relative abundance (RA) for each woody plant species, that is, the proportion of individuals of a particular species to the total number of individuals in a plot, was determined per plot. At each site, frequency was recorded as the percentage of plots in which a species was found, and relative frequency (RF) was calculated as the proportion of total frequency of all species to the total frequency per plot. Relative dominance (RD) was calculated as the proportion of basal area per species to the total basal area per plot. Basal area was calculated as ($\pi \times (\text{DBH}/2)^2$), and values were converted from cm² to m². The importance value index (IVI), which presents the ecological importance and dominance of a species, was calculated as the sum of RA, RF and RD (Curtis and McIntosh 1951). Woody plant species diversity (richness and evenness) was calculated using the *codyn* package in R (Hallett and others 2016) for each site. Species richness was calculated as the overall number of species, and community evenness was calculated as the inverse of Simpson's D. The relative proportion of introduced species was calculated as the percent abundance for canopy (DBH > 10 cm) and sapling (DBH < 10 cm) layers. All plot-level values were averaged for each interstitial and reference site.

To evaluate differences in species composition (that is, the identity of species present in a community) among interstitial and reference areas, we used non-metric multidimensional scaling (NMDS) from the *vegan* package (Oksanen and others 2020). NMDS is an unconstrained method that uses the pairwise dissimilarity of species composition and reduces dimensional space to better assess compositional differences between sites (Legendre and Legendre 2012). We used Bray–Curtis dissimilarity, which is a semi-metric index of distance between species vectors and quantifies the compositional dissimilarity between sites based on species abundance data (Legendre and Legendre 2012). Species contributions to vegetation patterns were determined using Pearson correlation coefficients between species abundance and NMDS dimensions

with the ‘scores’ function included in the *vegan* package in R (Brown 2019; Oksanen and others 2020). The ‘betadisper’ function was used to calculate the homogeneity of group variances (distance between centroids and group means for interstitial and reference sites). Finally, the ‘adonis’ function—a permutational analysis of variance—was applied using 999 permutations to test compositional differences (differences in centroid locations) between reference and interstitial sites.

To characterize and compare soil characteristics between interstitial and reference sites, we averaged whole-core (0–30 cm) estimates of microbial biomass C and N, basal respiration, NO_3^- NH_4^+ , potential net N mineralization and nitrification, denitrification potential, soil organic matter content and bulk density per site. We used bulk density values to convert all soil parameters to an areal basis (g/m^2). For each soil parameter, departures from normality were determined using Levene’s test and to determine variances within land-use type in each city. We compared whole-core differences between interstitial and reference sites between sites using the nonparametric Wilcoxon rank sum test for each soil parameter.

To determine multivariate patterns in soil parameters across interstitial and reference sites in each city, we conducted principal component analysis (PCA) using the ‘prcomp’ function in R. The data were standardized (divided by their standard deviation) prior to performing the PCA. Loadings were extracted for all soil parameters in relation to each principal component to explain soil patterns in ordination space. The soil parameters used in the analyses were coded as microbial biomass C (BiomassC), microbial biomass N (BiomassN), basal respiration (Respiration), NO_3^- (NO_3), NH_4^+ (NH_4), total inorganic nitrogen (TIN), potential net N mineralization (Mineralization), potential net nitrification (Nitrification), denitrification potential (DEA), organic matter content (OM) and bulk density (BD).

To investigate relationships between woody plant species composition and soil parameters, we also ran a canonical correspondence analysis (CCA), a constrained ordination method to analyze associations between environmental variables and community composition data, for each city. We computed the variance inflation factor (VIF) using the ‘vif.cca’ function to check for redundancy among predictor variables (soil parameters). Conventionally, $\text{VIF} > 10$ indicates high levels of redundancy among the predictor variables that affect model fit (Zuur and others 2009). The variables which contributed to $\text{VIF} > 10$ were removed, and

the model was run again. Analysis of variance (ANOVA) was conducted to test significance effects of individual predictors (soil parameters) and of the full model using 999 permutations.

RESULTS

Question#1: Does Woody Plant Community Composition Differ Between Reference and Interstitial Areas?

Across cities, there was no consistent difference in mean woody plant species richness between reference and interstitial sites (Table 1). Baltimore had the highest woody plant species richness in the interstitial sites, in the sapling layer (9.4 ± 2.54). Boston had the highest woody species richness in the reference sites, also in the sapling layer (6.6 ± 1.12). Woody plant communities were most even (measured on a scale from 0 to 1, where 1 is the most even) in interstitial sites in Boston and Baltimore and in reference sites in Miami, Minneapolis-St. Paul, Los Angeles and Phoenix (Table 1). Evenness was higher in the sapling layer of interstitial sites for most cities, except for Baltimore (0.88 vs. 0.56), but was higher in reference site canopy layers for most cities (Table 1).

Overall, there was a higher proportion of introduced species in interstitial sites than in natural reference sites, except in Boston (30% vs. 50%, respectively; Table 1). Overall, the sapling layer ($\text{DBH} < 10$ cm) contained a greater proportion of introduced species than the canopy layer ($\text{DBH} > 10$ cm), except in Minneapolis-St. Paul and Miami reference sites (7.14% and 9.60%, respectively). Introduced species were not found in any sites in Los Angeles and Phoenix (Table 1).

Across cities, species abundance and dominance differed between interstitial and reference sites, but some species were present in both site types in most cities (average of 37%; Table 2; Figure S1; Figure S2). The exceptions were Los Angeles and Phoenix, which had fewer total species (Table 1), and less compositional overlap (in Phoenix) between interstitial and reference sites (Table 2; Figures S1; Figures S2). In the majority of cities, native species were the most abundant and dominant in both interstitial and reference sites, with the exception of Miami and Minneapolis-St. Paul, where introduced species were more dominant in interstitial sites (Table 2; Figures S1). Several native species were common in temperate cities, for example, *Fraxinus pennsylvanica*, *Quercus velutina* and *Quercus alba* (Table 2; Figure S1; Figure S2).

Non-metric multidimensional scaling (NMDS) showed differences in woody plant community composition between reference and interstitial sites in most cities, as shown by the lack or minimal overlap of group centroids among interstitial and reference sites (Figure 1). However, there were strong, but not statistically significant compositional differences between interstitial and reference sites in Los Angeles ($r^2 = 0.47$, $p = 0.10$, respectively; Table S2). Moreover, dispersion from group centroids (homogeneity among group variances) among interstitial and reference sites was significant for Los Angeles and Phoenix ($F_{1,3} = 35.66$, $p = 0.008$ and $F_{1,6} = 8.20$, $p = 0.03$, respectively; Table S2). Native species were most important in determining variation in composition along both dimensions in the NMDS analysis (Table S3), except for Baltimore, Boston and Minneapolis-St. Paul (Figures 1b, 1f). In Baltimore, the introduced species *Prunus avium* was significant ($p = 0.013$) at explaining variation in species composition in sites along MDS2. In Boston, species that were important at explaining variations in species composition in sites along MDS1 included *Acer ginnala* ($p = 0.011$), *Ailanthus altissima* ($p = 0.011$), *Lonicera tatarica* ($p = 0.011$), *Malus floribunda* ($p = 0.034$) and *Rhamnus cathartica* ($p = 0.011$), while the cultivated hybrid *Tilia x europaea* was significant ($p = 0.01$) at explaining variation in community composition in sites along MDS2 (Figure 1b; Table S3). In Minneapolis-St. Paul, the introduced species *Rhamnus cathartica* and *Ulmus pumila* were significant ($p = 0.03$ and $p = 0.003$, respectively) at explaining variation in community composition in sites along MDS1 and MDS2, respectively (Figure 1f; Table S3).

Figure 1. Interstitial and reference areas have distinct woody species compositions. Non-metric multidimensional scaling (NMDS) of woody community composition in interstitial and reference sites in **a** Baltimore, **b** Boston, **c** Los Angeles, **d** Miami, **e** Minneapolis-St. Paul, **f** Phoenix. Plot points are based on Bray–Curtis distances of relative abundance data. Distance between points represents compositional similarity, with closer points being more similar than points further apart. Stress values for **a** 0.091, **b** 0.076, **c** 0, **d** 0.064, **e** 0.048, **f** 0.

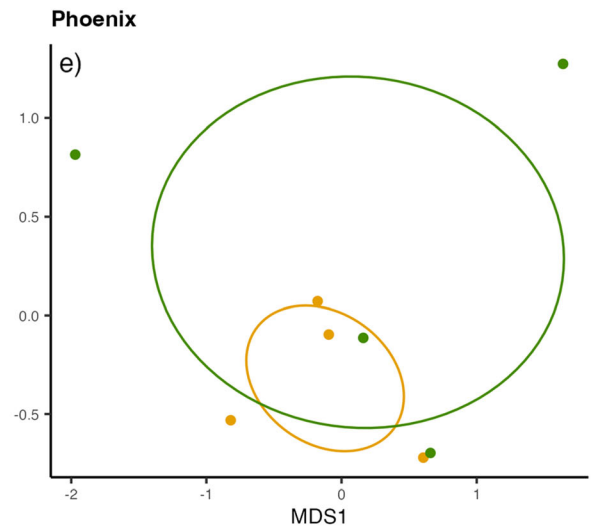
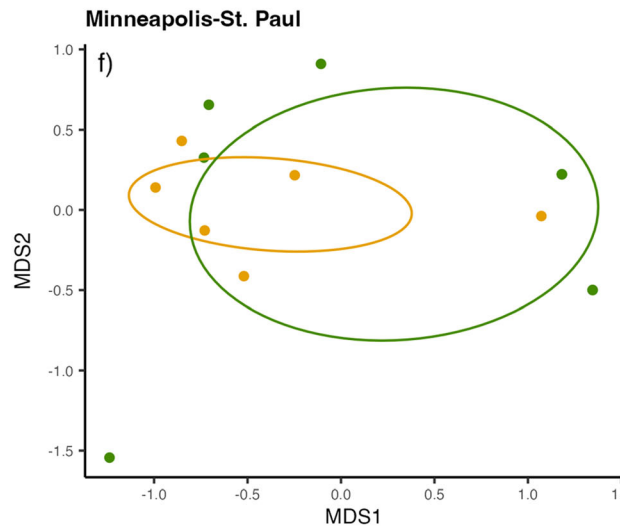
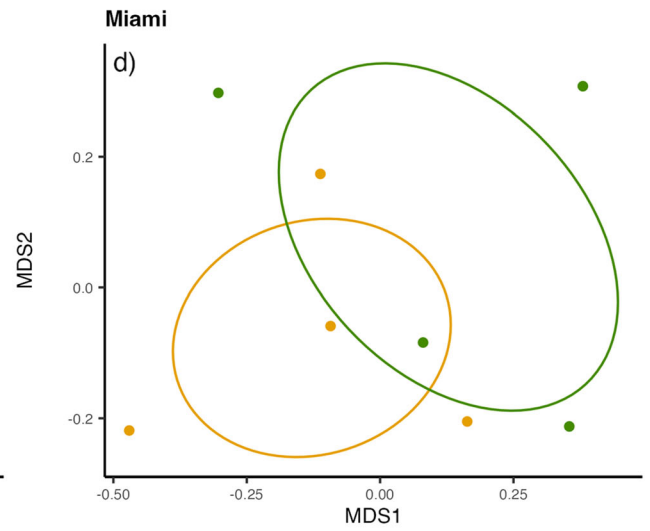
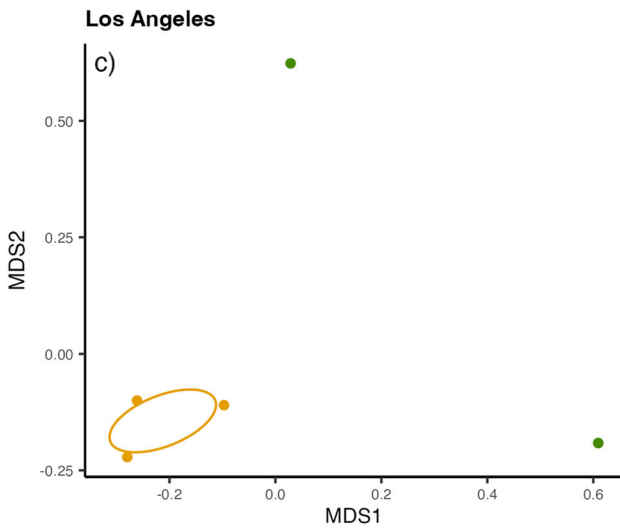
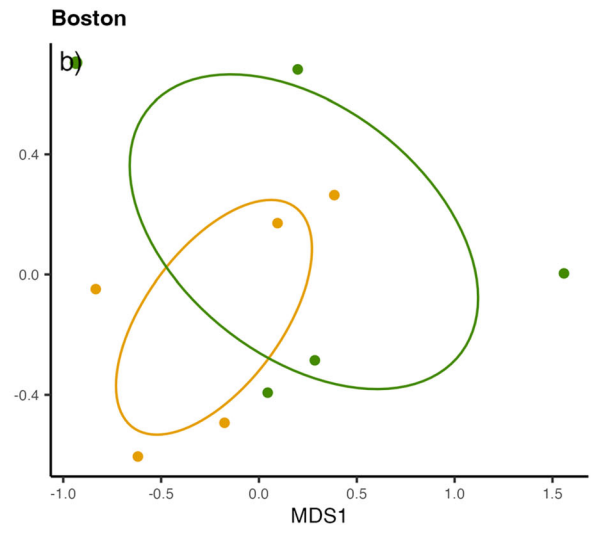
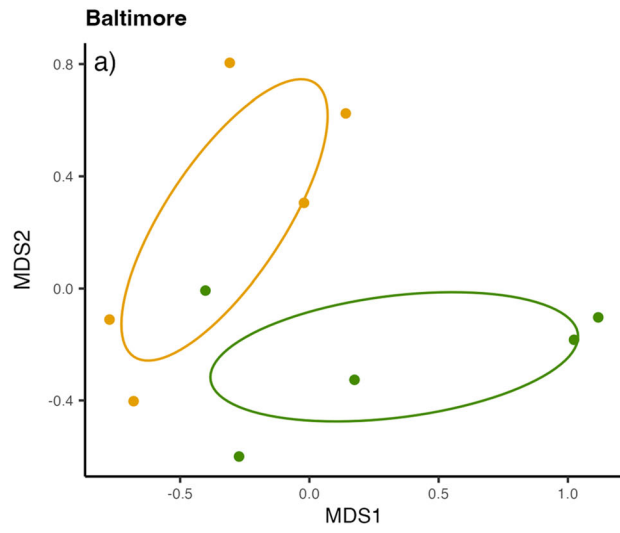
Question #2: Is Woody Plant Community Composition in Reference and Interstitial Areas Related to Variation in Soil C and N Cycling Processes?

Across all cities (Figure 2), N cycling variables (inorganic N pools, microbial biomass N, potential net N mineralization and nitrification) and carbon cycling variables (organic matter content, microbial biomass C, respiration) did not differ between reference and interstitial sites (Figure 2). On a city-by-city basis, microbial biomass C was significantly higher in reference sites in Boston ($p < 0.05$; Figure S4). There was marked variation in C and N cycle variables among sites in each city (Figures S3–S8). There was no visual or taxonomic evidence of extensive human alteration of interstitial site soil profiles (Table S1), and there were no consistent differences in soil moisture or bulk density between interstitial and reference sites (data not presented).

Across cities, at least 61% of the total variance in soil parameters was explained by the first two components (Dim1 and Dim2) in a principal components analysis (Figure 3; Table S4). On average, the first principal component (Dim1) explained 44.6% and the second principal component (Dim2) explained 26.3% of the variation in interstitial and reference soils. Nitrogen cycle variables were the most strongly loaded on the two principal compo-

Table 2. Percent of the Number of Species in Interstitial Sites, Reference Sites and Shared Between Interstitial and Reference Sites in Each City ($n = 6$)

Cities	Interstitial (%)	Reference (%)	Interstitial and reference (%)
Baltimore	54	46	32
Boston	64	36	26
Los Angeles	57	43	64
Miami	51	49	18
Minneapolis-St. Paul	50	50	20
Phoenix	40	60	20



Sites — Interstitial — Reference

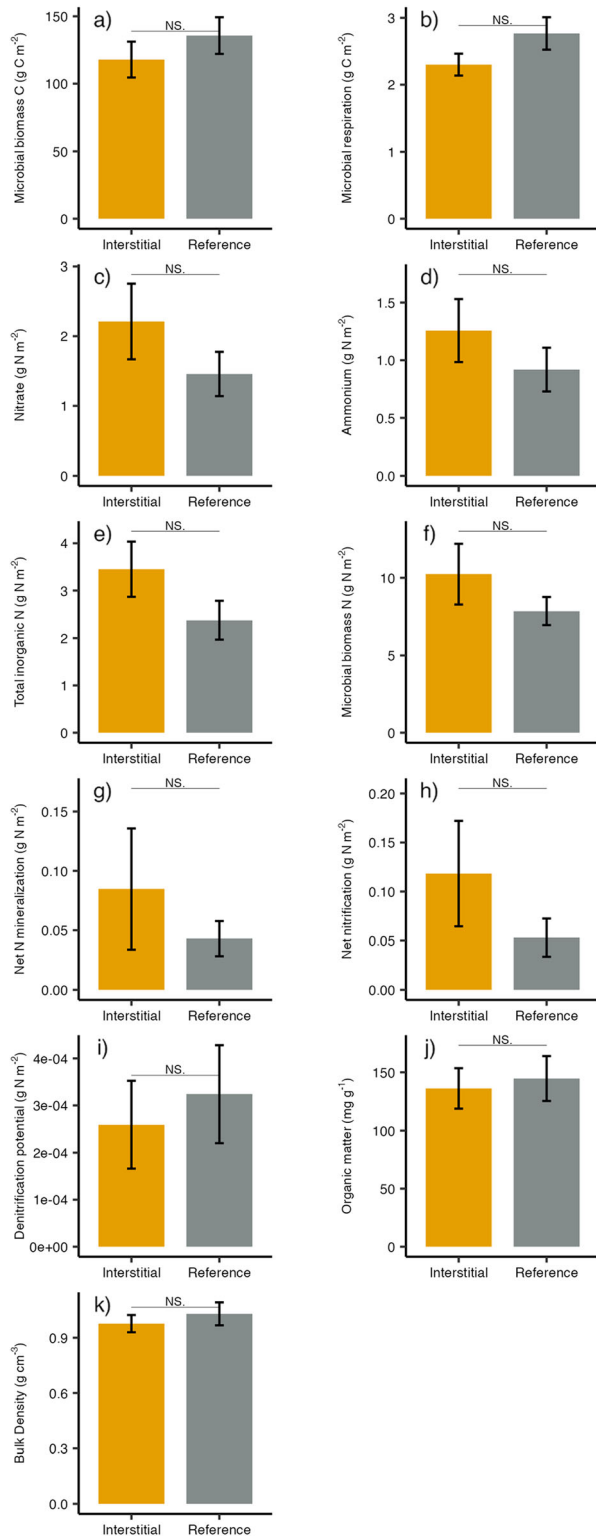
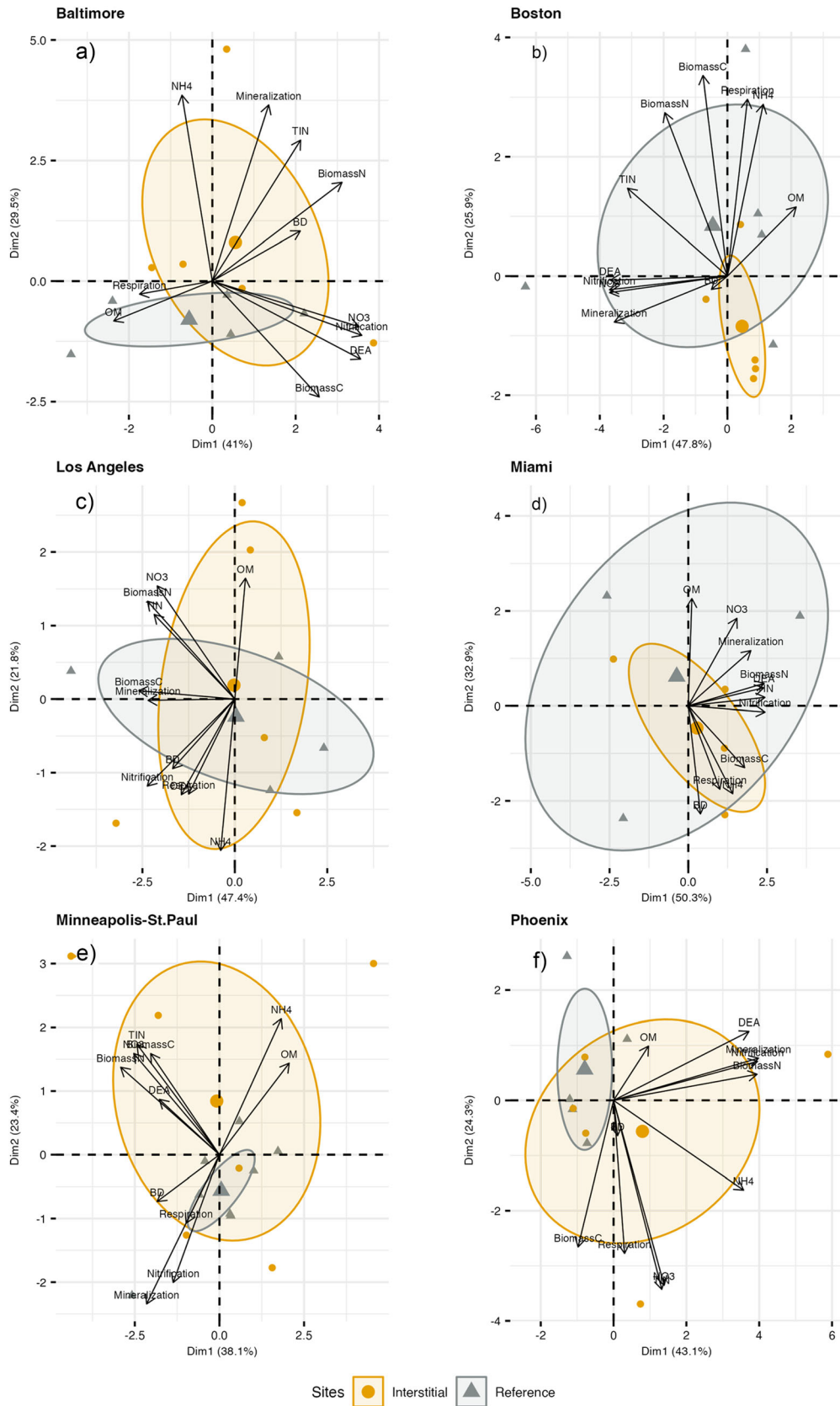


Figure 2. Mean values of soil (0–30 cm depth) parameters in interstitial and reference sites over all cities. Error bars represent \pm SE. Bars with asterisks are significantly different: $*p < 0.05$. Bars with NS = not significant.

Figure 3. Principal components analysis (PCA) showing soil parameters across interstitial and reference sites in **a** Baltimore, **b** Boston, **c** Los Angeles, **d** Miami, **e** Minneapolis-St. Paul, **f** Phoenix. Soil parameter codes: microbial biomass C (BiomassC), microbial biomass N (BiomassN), basal respiration (Respiration), NO_3^- (NO_3), NH_4^+ (NH_4), total inorganic N (TIN), potential net N mineralization (Mineralization), potential net nitrification (Nitrification), denitrification potential (DEA), organic matter content (OM) and bulk density (BD).

ment axes, especially Dim1. NO_3^- and NH_4^+ strongly loaded on Dim1 and Dim2 in every city, except for Miami (Figure 3; Table S4). Potential net nitrification and denitrification potential were strongly loaded on Dim1 or Dim2 in every city except for Los Angeles (Figure 3; Table S4). Potential net nitrification, microbial biomass N and total inorganic N had strong loadings with both Dim1 and Dim2 in every city. Carbon cycle variables were rarely significantly loaded on either Dim1 or Dim2 although organic matter and bulk density were strongly loaded on Dim2 in Miami (Figure 3; Table S4). Centroids of reference and interstitial sites did not overlap, except in Los Angeles and Miami. Variation among sites was noticeable in many cities, with some interstitial and reference sites having strong association with particular soil variables, while in other cities, site variation was not strongly associated with soil variables (Figure 3).

Across cities, in a canonical correlation analysis (CCA) of woody plant community and soil variables, the proportion of variance explained by the first CCA axis was at least 12%, and the second axis explained at least 10% of the variation across both interstitial and reference sites (Figure 4; Table S5). Variance explained was higher ($> 30\%$) in the driest cities, Los Angeles and Phoenix, that had many fewer species present (Figure 4; Table S5). The proportion of variance in woody plant community composition explained by soil variables was at least 62%, except in Phoenix (22%; Figure 4; Table S5). While the number of soil variables that influenced community composition varied per city, some variables were consistent across cities (Figure 4; Table S5). For example, soil NO_3^- , NH_4^+ and organic matter contents were related to woody plant community composition in both interstitial and reference sites in all cities except Phoenix (Figure 4; Table S5). NO_3^- and community composition were significant in Boston ($p = 0.033$) and Miami ($p = 0.004$), while organic matter content



was statistically significant in Baltimore ($p = 0.019$) and Miami ($p = 0.005$, Figure 4; Table S5). Furthermore, the CCA models were only statistically significant in Baltimore ($p = 0.044$) and Miami ($p = 0.021$) and marginally significant in Boston ($p = 0.064$; Figure 4; Table S5).

DISCUSSION

In this study, we addressed the question if analysis of forests that have spontaneously assembled in urban interstitial spaces provides insight into how global environmental change will affect the forests of the future. We hypothesized that the complex mix of anthropogenic factors affecting these spaces (altered climate atmospheric chemistry, disturbance regimes and species pool) is analogous to factors playing out across the globe at lower intensity (McDonnell and Pickett 1990) and that the novel communities that assemble in these spaces provide a glimpse of the forests that may become widespread beyond urban areas. Our observations of marked differences in woody vegetation composition between interstitial and reference sites in six cities with very different climate across the USA support this idea and provide insight into the novel communities that may become common across the USA over the next 50–100 years. In the sections below, we first discuss these differences in plant communities and then discuss if local human alteration of soils has reduced the value of our sites as analogs for future environmental conditions. Finally, we discuss the effects of altered plant communities on soil processes and ecosystem services.

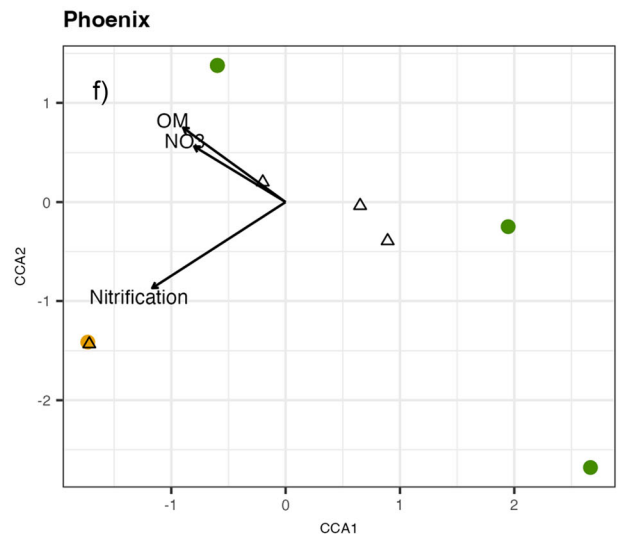
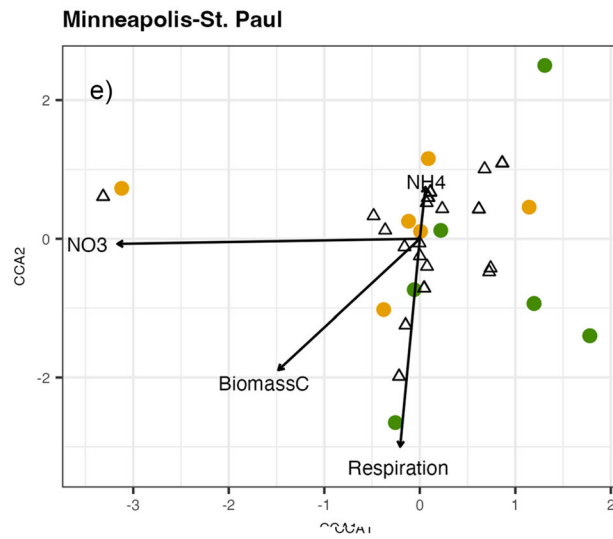
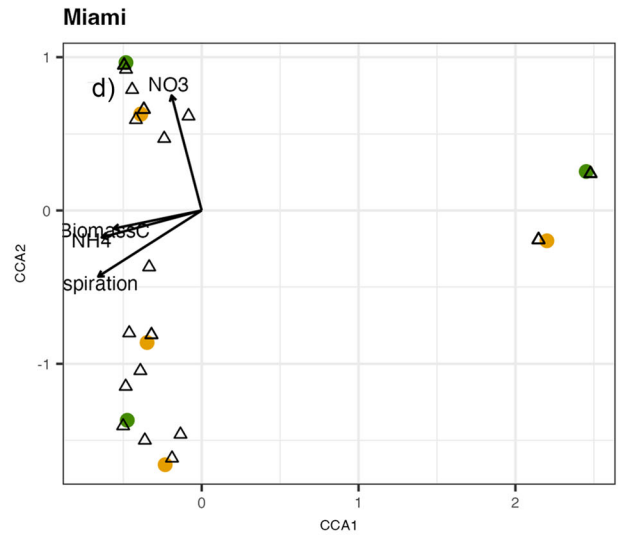
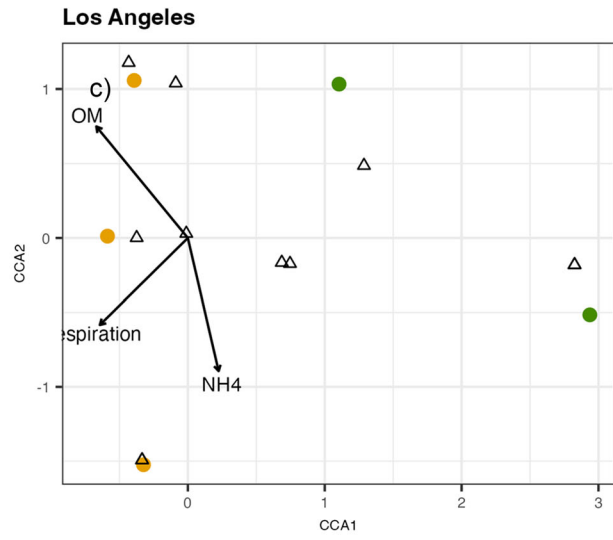
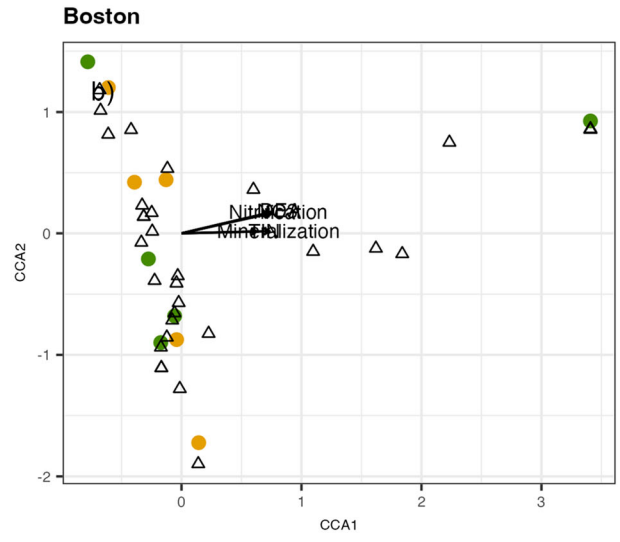
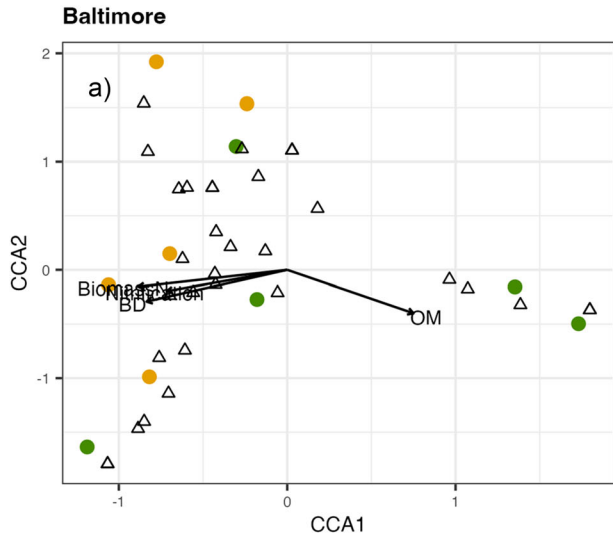
The differences in woody plant communities were most clearly shown by NMDS for Baltimore, Boston, Los Angeles and Phoenix, where interstitial and reference sites separated along NMDS axes (Figure 1; Table S3). Even in cities that did not show clear differences along the NMDS axes (for example, Minneapolis-St. Paul), there was evidence for clustering among the interstitial sites, indicating that interstitial sites were more similar to each other than reference sites. As we discuss below, the differences between reference and interstitial sites were likely the result of a greater proportion of introduced species and higher species richness in interstitial sites, especially in the sapling layers (Table 1).

Our careful selection of sites allowed us to assess how changes in plant community composition affect soil N cycling, which is important for a variety of ecosystem services (for example, primary productivity). In our study sites, there were no

Figure 4. Canonical correlation analysis (CCA) showing similarity of woody species community composition in relation to soil parameters among interstitial and reference sites in a) Baltimore, b) Boston, c) Los Angeles, d) Miami, e) Minneapolis-St. Paul, f) Phoenix. Sites (green and yellow dots), tree species (open triangles), soil parameters (black arrows): microbial biomass C (BiomassC), microbial biomass N (BiomassN), basal respiration (Respiration), NO_3^- (NO_3), NH_4^+ (NH_4), total inorganic N (TIN), potential net N mineralization (Mineralization), potential net nitrification (Nitrification), denitrification potential (DEA), organic matter content (OM) and bulk density (BD). Distance between plot symbols indicates similarity of species composition and abundance. The proportion of variance explained by CCA1-CCA2 in each city **a** 17–10%, **b** 17–10%, **c** 35%, **d** 14–10%, **e** 16–14%, **f** 5–3%.

noticeable anthropogenic effects on soils, for example, compaction, profile disturbance or fertilization. Therefore, we were able to examine how differences in plant community composition between interstitial and reference sites were associated with variation in N availability. This finding is shown by separation of interstitial and reference sites along PCA axes of soil characteristics in Baltimore, Boston, Los Angeles, Miami and Minneapolis-St. Paul in the PCA and by relationships between N pools (NO_3^- , NH_4^+ , TIN and microbial biomass N) and woody vegetation composition in the CCA. It is important to note that there were no systematic differences in N availability between interstitial and reference sites, and no evidence that interstitial sites had artificially elevated N availability based on soil taxonomy (Table S1). Closely matching the soil series allowed us to avoid differences in soil moisture retention and having the sites interspersed across the region avoid local pollution (for example, atmospheric N deposition) gradients. Thus, careful selection of sites allows for examination of how natural variation in N availability across native reference and interstitial sites is a driver of woody plant community composition (Table S3).

As detailed below, the differences that we observed between interstitial and reference sites have implications for how forests are assessed and managed to provide ecosystem services related to native species diversity, carbon storage and ecosystem resilience to global environmental change.



Sites ● Interstitial ● Reference △ Species

How does Composition of the Woody Plant Community Differ Between Interstitial and Natural Reference Sites?

The observed differences in woody plant community composition between native reference and interstitial sites are likely the result of the expanded species pool—native and introduced—in urban areas. While there might be multiple confounding factors (for example, land-use history, plant physiology, abiotic effects), woody plant communities in the interstitial sites have developed adjacent to altered landscapes, such as residential areas with human-managed landscapes (yards and neighborhoods, transportation corridors and so on). These areas are planted and managed with highly selected species (Padullés Cubino and others 2019b, 2020) that have the potential to establish in unmanaged areas such as our interstitial sites, and disperse beyond managed areas, such as our reference sites.

Woody plant canopies in interstitial sites across the six cities were dominated by native species, while sapling layers had greater percentages of introduced species (Table 2). While this could be a function of ecological time lags (for example, phase in biological invasion; Blackburn and others 2011), it could also be the result of invasive species cultivated in highly managed urban areas that have successfully dispersed to relatively unmanaged areas (for example, Buckthorn; Heneghan 2004). However, the majority of saplings in the interstitial sites were still native (Table 1, Figure S1). Despite native woody plant canopies, previous studies suggest that the presence of introduced species in the understory layer indicates that interstitial sites are likely to develop different trajectories than the reference natural areas over time (Kowarik and others 2019; Trammell and Carreiro 2011; Trammell and others 2020b), especially if native progeny are outcompeted by introduced (exotic/invasive) species. Previous studies comparing urban forests (for example, large parks) with natural reference areas have found that the presence of introduced species was greater in forests within the urban matrix, particularly in the understory layer (Templeton and others 2019). While different factors would contribute to the presence and persistence of introduced species in different cities (for example forest age, land-use type and mechanism of introduction; Schoenenberger and Conedera 2013; Trammell and others 2020b; Jiang and others 2022), interstitial sites—which are embedded within the urban matrix—are closer in proximity to residential areas than reference sites. Padullés Cubino and others (2020) found that residential yards

had higher proportions of introduced species compared to reference natural areas in the cities we studied. It is possible that dispersal through residential yards may facilitate the spread of introduced species to interstitial sites (Vieira and others 2014). Moreover, invasive species are widely available through the horticultural industry (for example, *Rhamnus cathartica*; Nóvoa and others 2015; Beaury and others 2021). In this study, only woody plant species were included, and the presence of introduced species in other herbaceous layers may provide additional support for this idea (Trammell and Carreiro 2011; Trammell and others 2020; Deljouei and others 2017; Fratarcangeli and others 2022).

In forest ecosystems, introduced woody species that are also invasive are especially concerning due to their potential to threaten recruitment of native species (for example, shading out) and out-competing native understory over time (Reinhart and others 2006; Doroski and others 2018). For example, Templeton and others 2019 showed that urban forests tended to have greater abundance of invasive plants in both the canopy and understory layers. Other studies have found canopies dominated by native species and understories dominated by exotics (Trammell and Carreiro 2011; Pregitzer and others 2019; Trammell and others 2020), supporting the idea that exotics will become more important over time.

Among the invasive species that we observed, *Acer platanoides* and *Rhamnus cathartica* are of particular interest because they were both found in multiple cities, which suggest they have a wide-ranging distribution. *Rhamnus cathartica* has the ability to establish and persist in disturbed areas and proliferate in sites undergoing succession (Zouhar 2015), while *Acer platanoides*' strong shade tolerance allows it to dominate in closed canopies and suppress native understory seedlings (Munger 2003).

Among the six cities, introduced species were most common in Boston (Table 1) and it was the only city with a greater percentage of introduced species in reference sites than interstitial sites (Table 1). *Tilia x europaea* was both abundant and dominant in the canopy of one reference site, and it was also present in the sapling layer, along with *Rhamnus cathartica* and *Ailanthus altissima* (Table 1; Figure S2). Previous studies of temperate forests in Massachusetts have found that heavily fragmented forest patches are more susceptible to invasion of introduced species (McDonald and others 2008). Temperate forests of New England have experienced increased fragmentation over recent decades

resulting from increasing human population expansion, even at low densities (Vogelmann 1995). Therefore, not just proximity to the urban matrix, but also forest size, age and structure may play an important role in the susceptibility of forested ecosystems to plant species invasion (for example, Trammell and others 2020b). The “edges” of these fragmented forests are highly dynamic, with notably high rates of C fixation and growth, that vary with species composition (Reinmann and Hutyra 2017; Morreale and others 2021). There is thus great interest in how woody plant species composition is changing in these increasingly common fragmented landscapes.

In Minneapolis-St. Paul, the relative openness of forest stands in a prairie landscape may facilitate the spread of invasive species. One of the reference sites in this city had high abundance of *Rhamnus cathartica*, but only in the sapling layer (Table 1; Figure S2). This species is known to occur not only in disturbed areas but can also be found in open wildlands (Zouhar 2015). Given the openness of savanna landscapes, reference sites in the Minneapolis-St. Paul region may be especially susceptible to this species, which is readily dispersed by birds and tends to out-compete native understory plants by creating dark, dense thickets (Mascaro and Schnitzer 2007; Knight and others 2017). *Rhamnus cathartica* also has the advantage of “extending” the growing season through early leaf-out and delayed senescence, probably contributing to its success in the understory (Zouhar 2011). Interestingly, this reference site was the only one without any *Quercus* species (a shade-intolerant genus) and was the only one with *Ulmus pulima* in the canopy layer. This species is fast-growing, which allows it to develop rapidly once established, becoming highly invasive in prairie ecosystems (Gaskin and others 2020). The presence of this invasive species in the canopy layer may facilitate invasion by *Rhamnus cathartica* in the understory, which thrives in the shade of other trees. This species has also been found spontaneously growing in residential yards in Boston and Minneapolis-St. Paul (Cubino and others 2019a), indicating its ability to spread and establish without human intervention.

Despite the abundance of introduced and invasive species in interstitial and some reference sites, native species dominated most sites across cities (Table 2; Figure S1; Figure S2). Still, there were important differences in native species dominance between interstitial and native sites. For example, reference areas in Baltimore were dominated by *Quercus* species (for example, *Quercus michauxii*,

Quercus alba, *Quercus velutina*) and co-dominated by *Liriodendron tulipifera* (Table 2; Figure S2). However, *Quercus michauxii* was not present in any of the interstitial sites, and *Fraxinus Pennsylvanica* was co-dominant in two interstitial sites, but not present in any reference sites. *Quercus michauxii* is shade-intolerant and requires openings for establishment allowing it to survive in the understory, while *Fraxinus Pennsylvanica* is tolerant to shade and adaptable in many landscapes (Gucker 2005), including urban environments, where it is commonly planted as part of municipal planting campaigns (Doroski and others 2020) and in residential yards (Wheeler and others 2017). This indicates that there might be different ecological sorting processes occurring in some interstitial sites that allow for different species than those found in reference sites to establish and dominate stands. For example, Schurman and others (2012) found that environmental constraints, such as N availability and soil moisture regime, influenced the species distribution of younger trees in temperate forests, but stand age was more likely to predict mature tree distribution. In addition, the loss of late successional species impacts the structure and functions of forested ecosystems such as microclimate, biomass and chemical processes (Ellison and others 2005; Thompson and others 2013).

Comparison of interstitial and reference sites in our most arid cities (Phoenix and Los Angeles) produced an interesting contrast to mesic cities. Woody plant species richness was very low in these cities, with most sites in Phoenix dominated by a single species (Table 1; Figure S1; Figure S2). Additionally, all the species in both the reference and interstitial sites within these cities were native and dominated by the same species. For example, in Los Angeles, *Malosma laurina*, which was highly abundant in interstitial sites and one reference site in Los Angeles, is a successful colonizer following disturbance (for example, fire; Howard 1992), making it a resilient species. These results suggest that forests developing on interstitial sites in Los Angeles may have similar trajectories to current native reference sites.

Is Variation in Woody Plant Community Composition Related to Variation in Soil C and N Cycle Processes?

A major objective of our study was to determine if community assembly processes in urban interstitial areas are leading to the development of novel ecosystems that have the potential to spread within and beyond urban areas. We found little evidence

for unique urban effects on soils in the interstitial sites in this study. However, evaluation of plant–soil interactions in urban ecosystems is complicated by extensive alteration of soils by human activities. This alteration can limit the use of urban ecosystems as analogs of global environment change (McDonnell and Pickett 1990). For example, if soil profiles at a site are altered by the presence of human-altered or human-transported materials such as coal ash or municipal trash (Mejía and others 2022), they cannot be used to learn about the effects of interacting factors such as changes in climate, atmospheric chemistry and local species pool. In this study, interstitial sites were selected to avoid areas with extensive alteration. Consistent with this effort, we did not see significant differences between interstitial and reference sites for any N cycling variable across cities, suggesting that these sites were suitable for studying the effects of altered urban climate, atmospheric chemistry and species pools on community assembly (McDonnell and Pickett 1990). However, we did observe significant variation in soil processes within individual cities that sheds light on the causes of variation in N cycle processes such as the presence of introduced species, and the influence of these processes on woody plant dynamics (Figure 3; Figures S3–S8). In drier regions, these variations may be affected by local N cycling patterns (for example, deposition), such as those observed in California (Fenn and others 1996, 2010).

Although we did not see significant differences between interstitial and reference sites for any N cycling variable across cities, city-by-city analysis of relationships between N dynamics and tree community composition supports the idea that there are relationships between these variables that cut across interstitial and reference sites. For example, in Baltimore, two interstitial sites located farther outside the confidence interval in the vegetation NMDS were the same sites outside the confidence intervals in the soil PCA. Similarly, in Boston, two reference sites clustered in the vegetation NMDS were also clustered in the soil PCA. In Los Angeles, one interstitial site was distinct on both vegetation (NMDS) and soil (PCA) analyses. In addition, these patterns were supported by the CCA that illuminated multiple soil variables (basal respiration, NO_3^- , total inorganic N, microbial biomass N, potential nitrification and N mineralization, denitrification potential, organic matter, bulk density) that had significant relationships with community composition across interstitial and reference sites. However, these dynamics varied by city, indicating that the mechanisms driving the variation in N

dynamics, and the relationships with woody plant community composition are context-dependent. Factors such as soil texture, pH and water-holding capacity influence N availability in soils and have been well studied in rural context (Pastor and others 1984; Pastor and Post 1986), but less so within urban areas (Groffman and others 2006). The spread of invasive species can also affect nutrient cycling (Ehrenfeld 2003; Mueller and others 2018). There is a clear need for further analysis of these uncertainties as the N cycle is affected by multiple components of environmental change that will need to be considered when evaluating future trajectories of urban (and beyond) forests (Mason and others 2022).

While the PCA showed significant and coherent variation in N cycling among sites, variation in soil C cycle processes was less marked, that is, there were few significant correlations between soil C cycle processes and the two PCA axes from soil characteristics. Moreover, we did not observe significant differences between interstitial and reference sites for any C cycling variables across cities. The lack of difference in C dynamics between interstitial and reference sites was surprising given their differing proximity to human-dominated landscapes and the effects of this proximity on woody plant communities and N cycling. In both site types, organic matter quality appears to be high enough to support high levels of microbial biomass and respiration, which are indices of the nature and extent of soil C cycling activity (Powlson and others 2017). These C dynamics are controlled to a large extent by abiotic factors, such as temperature and moisture, that vary geographically. Cities are also subject to biological factors that affect soil C dynamics, such as the presence of earthworms (Pouyat and others 2002). Our results support the idea that there is high variation in organic matter content within forests embedded in the urban matrix (Zhu and Carreiro 2004). Unraveling the controls of this variation will be important for understanding the composition and C sequestration capacity of future forests.

What are the Implications of Differences in Woody Plant Community Composition in the Interstitial Sites for the Structure and Function of Future Forests Within and Beyond Urban Areas?

Our results suggest that novel woody plant communities are assembling in interstitial areas in cities across the USA. These communities may affect the ecosystem services provided by urban forests (for

example, wildlife habitat, water quality, climate regulation; Solomou and others 2019; Berglihn and Gómez-Beggethun 2021), and the resilience of these forests to environmental change. To the extent that environmental changes currently occurring in cities are harbingers of changes that will occur more broadly across the landscape (McDonnell and Pickett 1990), these communities may spread beyond urban areas and influence forest structure and function across large areas of North America. Johnson and Handel (2016) found that successional trajectories of urban forests have diverged between forests that underwent restoration (for example, invasive species removal) and invaded forests that were not restored, indicating that novel communities that emerge in unmanaged areas can become dominant over time. Species invasions create temporal and ecological processes that differ from native communities (Blackburn and others 2011), which suggests that effective management of invasive species is critical to prevent and mitigate their spread within and beyond urban areas (Simberloff and others 2010; Dickie and others 2014; Krumm and others 2016; Brundu and others 2020).

Our results also suggest that the assembly of novel communities in urban interstitial areas varies markedly in cities with different climates. For example, only native species (albeit very few) were found in interstitial sites in hot and dry climates of Los Angeles and Phoenix. In hot and wet Miami, a much larger pool of both native and introduced species was present. Pearse and others (2018) showed that species from both native and exotic pools were present in both cultivated and spontaneous communities in residential yards in the cities we studied, highlighting the dynamic interactions between direct and indirect human activities and a variety of natural biodiversity controls consistent with global trends in urban environments (Gaertner and others 2017).

The process of novel community assembly will also vary with land-use legacies and forest patch size which have a direct effect on a site's susceptibility to species invasions and soil nutrients (Hall and others 2013; Ziter and Turner 2018; Ward and others 2020). Forests growing on land that was under previous land use (for example, agriculture or timber) have lower abundance of native woodland species when compared with reference forests (Peña and others 2016). These differences between land use also point to the importance of soil conditions (for example, nutrient content; Baeten and others 2010) as a regulator of community assembly. Young forest patches are more likely to have

invasive plants and increased pH and Ca than older patches, regardless of land-use context (Trammell and others 2020b, 2021). As noted above, forest fragmentation creates edge effects that expose tree communities to disturbances that may affect stand microclimate and species physiology (Reinmann and Hutryra 2017; Morreale and others 2021). Trammell and others (2022) showed that edge effects and other environmental factors had greater influence on species invasion than land-use context in forest patches. Garvey and others (2022) found that edge effects had a strong effect on soil respiration in both urban and rural forests. The interaction of these factors will have a great effect on future forest structure and function within and beyond urban areas. These effects are being experienced in forests around the globe (Essl and others 2020), especially from the spread of woody invasive species (Jäger and others 2007; Ayanu and others 2015; Le Maitre and others 2020).

Forests embedded in the urban matrix are exposed to stressors from the surrounding matrix that can produce effects that may be different from those in less disturbed landscapes (Trammell and others 2022). These effects can include altered soil chemistry, elevated temperatures and light regimes, altered foliage (for example, caterpillars) and soil fauna (for example, earthworms), pollination and seed dispersal agents, and changes in the nature and frequency of disturbance (Pouyat and others 2007, 2010; Lerman and others 2021b). Further research in forests along urban to rural gradients is needed to assess these effects and their relevance to forests beyond urban areas.

CONCLUSIONS

Our results show that urban land-use change has resulted in alterations to natural ecosystems embedded in the urban matrix, creating conditions for novel woody plant assemblages to emerge with potentially altered functions that persist in the absence of human intervention. These results have implications for how we assess and manage the urban forests across the USA. As novel communities emerge, there will be a need for assessments of how they function relative to demands for specific ecosystem services, and decisions about whether management actions can affect these outcomes will need to be made.

For example, urban forest restoration efforts in many cities focus on invasive species removal (Pregitzer and others 2019). Invasive species can change soil conditions and/or adapt to altered soils, but whether soil conditions drive community

dynamics or vice versa is still poorly understood (Ward and others 2020). Our results support the idea that these community dynamics are associated with variation in local soil conditions, especially N availability (Smith and others 2020, 2021; Mejía and others 2022). There is a clear need for further research on how soil conditions interact with changing climate, herbivory pressure (for example, deer) and other environmental changes (Templeton and others 2019) to influence the trajectories, functions and services of forest communities.

Our results suggest that urban interstitial communities are a useful experimental venue for investigating the structure and function of future forests. These communities are highly variable and dynamic and illustrate a wide range of possible future forest trajectories that have the potential to spread beyond urban areas under changing environmental conditions. As human activities expand at the residential–wildland interface, unmanaged interstitial areas are likely to function as mediators of native, exotic, cultivated and spontaneous species pools (Pearse and others 2018), potentially altering natural habitats on regional scales and influencing the structure and function of future forests well beyond urban areas.

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DATA AVAILABILITY

Data are available as Supporting Information. Data are also available in Environmental Data Initiative (EDI) Data Portal at <https://doi.org/10.6073/pasta/8b29dc7fd536f4649f8cf6a536421fc9> (DOI) reference number edi.309.1, and <https://doi.org/10.6073/pasta/c1f9302b4cce46cbe003ac41f58ef4a> (DOI) reference number edi.374.2.

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