

RESEARCH ARTICLE

Native trees are responsible for the high carbon density in urban natural area forests across eight United States cities

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Abstract

1. Urban natural area forests provide cities with crucial ecosystem services, including carbon storage and sequestration. Although previous work from a single city has suggested that urban natural area forests may be carbon-rich and dominated by native species, it is unclear if that pattern is widespread. Indeed, little is known about the species composition and carbon storage in these green spaces, or how urban natural area forests compared with similar rural forests.
2. Here, we use data collected by the Forests in Cities network to quantify carbon stored in urban natural area forests across 1852 plots in eight of the most populous US cities and examine patterns in woody vegetation carbon storage by tree species composition and size class. We also compare the carbon storage in these urban natural area forests to similar rural forests using USDA FS Forest Inventory and Analysis data.
3. We found that urban natural area forests store between 214 and 267 Mg C ha⁻¹, with the majority (on average 55%) in the above-ground portion of live trees and shrubs. This carbon was primarily stored by native trees and increased with the proportion of native species, as native trees tended to be larger. The proportion of non-native species was higher in smaller size classes. Overall, the woody vegetation carbon density in urban natural area forests was higher than similar forest types in rural settings, a phenomenon driven by the presence of more large trees.
4. *Synthesis and applications:* Together these results demonstrate the importance of urban natural area forests as carbon-dense ecosystems and havens for native tree species. However, because of the greater number of non-native species in smaller size classes, these forests may also be at risk of transitioning away from native-dominated systems. Therefore, greater monitoring efforts and increased

management activities such as non-native species removal will be crucial to maintaining the high carbon storage and health of these ecosystems.

KEYWORDS

forest carbon stocks, invasive species, urban forests, urban forest health, urban natural areas

1 | INTRODUCTION

Urban forests, which include trees along streets, in yards, parks, abandoned spaces, and natural areas, provide numerous ecosystem services which bolster the sustainability of cities. These benefits include improvements to local air and water quality (Livesley et al., 2016), reduction of stormwater runoff (Selbig et al., 2022), temperature regulation (Moss et al., 2019), and carbon sequestration and storage (Nowak et al., 2013). Interaction with the urban forest is also shown to correlate with improvements in the overall physical and mental health and well-being of urban residents (Reyes-Riveros et al., 2021).

One type of urban forest, which we refer to as 'urban natural area forest,' is a crucial and often undervalued component of urban green space (Vieira et al., 2018). Urban natural area forests are distinct from other parts of the urban forest, such as landscaped parks and street trees, as they exist as forest stands, rely on natural regeneration of woody plants, and do not receive regular human maintenance such as mowing or tree planting (Piana, Pregitzer, & Hallett, 2021). They occur patchily, sometimes within other green spaces (e.g., one area within a landscaped park) and they can range in size from small patches under 1 hectare, which may exist as a vacant lot or on the fringes of other land uses (e.g. roadways), to larger patches of continuous forest stands exceeding 150 hectares, which are typically found in public parks or private lands (Doroski et al., 2022). Urban natural area forest health may vary widely, both within a single city and more broadly, due to factors such as forest patch size (Doroski et al., 2022), historic land-use (Pregitzer & Bradford, 2023), and disturbance regimes (Jenkins & Howard, 2021).

Urban forests of all types face an increasing number of threats, many of which are driven or exacerbated by climate change and increasing development (Nowak et al., 2022). In part due to these threats, urban forests are often expected to be of low quality: dominated by non-native species, having lower biodiversity, poor soil health, or storing less carbon (Radford & James, 2013; Stanley et al., 2015). However, urban natural area forests are more likely to contain a higher proportion of native species than other urban forest types, such as street trees or landscaped parks (Pregitzer, Ashton, Charlop-Powers, et al., 2019), and recent work on urban natural areas in New York City (NYC) suggested that these forests store similar amounts of carbon, on a per area basis, to their rural counterparts, and that urban natural area forests are typically dominated by native tree species (Pregitzer et al., 2022). In this study, we ask whether these findings from NYC generalize to other populous cities across the U.S.

Here we use data on woody vegetation and soils collected in eight U.S. cities to quantify above- and below-ground carbon storage in urban natural area forests. We have two primary research questions. First, we ask if urban natural area forests dominated by native species store more carbon in their woody vegetation than those that have been invaded by non-native species. This might occur if non-native species tend to be smaller than native species. Such a size difference could be due to differences in age; for example, if non-native individuals were younger, and therefore smaller, than native individuals. Alternatively, a size difference could be due to differences in growth form; for example, if the non-native species in these forests tend to be smaller statured at maturity than the native species. Therefore, we also examine whether there are differences in both actual size and potential mature size between native and non-native species found in urban natural area forests. Our second question is whether urban natural area forests have a similar woody vegetation carbon stock density to nearby rural forests. Given that urban natural area forests are naturally regenerating with complex structure we expect they may store similar amounts of carbon in their woody vegetation to rural forests.

2 | MATERIALS AND METHODS

2.1 | Data collection

Data for this study were sourced from partners in eight member cities from the Forests in Cities network (Pregitzer et al., 2020): Seattle, WA; Chicago, IL; Indianapolis, IN; Baltimore, MD; St. Louis, MO; Dayton, OH; New Haven, CT; and New York City, NY (Figure 1). Members of the network followed standard methods to set up forest plots within urban natural area forests, and in some cases were able to locate pre-existing, commensurate data. Therefore, the sampling designs varied slightly from city to city, as described below and detailed in Table 1. However, the forest type (urban natural areas) and general methodology (fixed area plots where all woody stems are identified and measured) are consistent across the entire dataset.

In each city, urban natural area forests were targeted for data collection, and no other urban forest type was included. Plots were located by randomly sampling within defined areas (e.g. within a park, within municipal protected natural area forests), which differed from city to city (Table 1). Some cities include data for urban natural area forests within the single largest park (e.g., Baltimore, St. Louis), whilst others include dozens of parks (e.g., NYC, Seattle). The total number of plots also varied by city, from $n=8$ in St. Louis

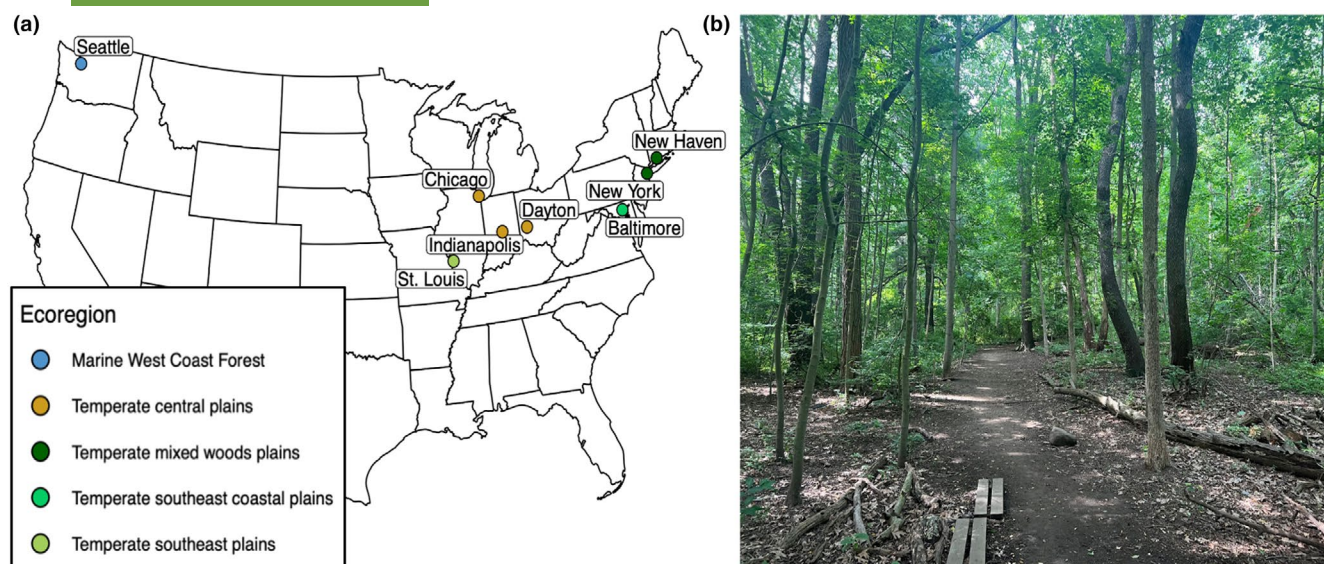


FIGURE 1 (a) Location of eight cities with urban natural areas included in this study. Colours indicate EPA level 2 Ecoregion (<https://www.epa.gov/eco-research/ecoregions-north-america>). (b) Example of an urban natural area forest in Alley Pond Park, Queens New York.

TABLE 1 Table of methodological details for urban natural area forests in each of the eight cities included in this study.

City	New Haven, CT	Dayton, OH	New York, NY	Seattle, WA	St. Louis, MO	Indianapolis, IN	Chicago, IL	Baltimore, MD
Plots	106	28	1124	276	7	30	115	186
Parks	17	9	53	71	1	3	NA	1
Study area definition	Urban forested natural area patches	Forested natural areas in Five Rivers Metroparks	Municipal protected natural area forests	Managed natural area forests	Forested natural areas in Forest Park	Forested natural areas in three parks	iTree-Eco plots in forested natural areas, plus additional forested natural areas	Forested areas in Gwynns Falls Leakin Park
Sample design	Random grid sample	Random sample, stratified by forest type	Random grid sample	Random sample	Random sample	Random sample, stratified by condition	Random sample	Random grid sample
Plot size (ha)	0.0314	0.0314	0.0314	Variable: 0.012–0.0809	0.2023	0.0314	0.0405	0.0405
Minimum DBH (cm)	2+	2+ ^a	2+ ^a	2+	2.54+	2+	2.54+	2.54+
Number of plots with soil carbon data	0	0	994 ^b	29	7	30	0	16
Data source	Danica Doroski	Eco Logic LLC and Five Rivers Metroparks	Natural Areas Conservancy	Green Seattle Partnership	Forest Park Forever	Eco Logic LLC and Indy Land Stewardship	Lindsay Darling, Morton Arboretum	Baltimore City Recreation and Parks

Abbreviation: DBH, diameter at breast height.

^aFor Dayton, OH, and New York City, all midstory stems (2–10 cm DBH) were tallied by species and the midpoint of the size range (5.5 cm DBH) was applied to each stem to calculate carbon stock.

^bFor NYC, soil carbon was taken from Pregitzer et al. (2022) which sampled soils at the plots used in this study but used somewhat different methods for the carbon calculations.

to $n=1124$ in NYC. Because of this difference in plot numbers, we have varying levels of confidence that the results represent the full range of citywide conditions in natural area forests, and therefore do not attempt to scale these data to city- or state-wide assessments. Rather we treat the data as examples of values we might see in urban natural area forests. In all cases, the data collectors (Table 1) were people or organizations with the necessary permissions to carry out this work.

Across cities, plot size varied from 0.0314 ha (majority of plots) to 0.201 ha (St. Louis plots). In general, plots were circular with a 10 m radius (0.0314 ha plots). Within each plot, live woody stems and standing dead stems were measured at 1.37-m height (diameter at breast height [DBH]) and identified to species. All stems (live and dead) greater than 2 cm DBH (Seattle, Indianapolis, Dayton, New Haven, NYC) or 2.54 cm (St. Louis, Chicago, Baltimore) were included; however, in Dayton and NYC stems from 2 to 10 cm were tallied by species (their DBH was not recorded), and therefore their midpoint DBH (5.5 cm) was used for calculations.

To investigate patterns of species composition, we assigned a native status to each species that was found in the dataset. We based these decisions on their USDA native range maps (USDA NRCS, 2024). When trees were occasionally not identified as species, their native status was considered "unknown." We used the estimate of typical mature height for each species from the USDA PLANTS database (USDA NRCS, 2024).

In four cities, soil cores were additionally collected at a subset of plots. In St. Louis ($n=8$) and Indianapolis ($n=30$), all plots were sampled, whilst a subset of plots were chosen for soil sampling, stratified by forest type, in Baltimore ($n=16$), and Seattle ($n=29$). In all cases, one 3.8-cm diameter soil core was taken to 30-cm depth at the centrepoint of each plot using a soil corer with a plastic liner. Cores were returned to the laboratory, air dried, sieved to 2 mm, and weighed. Coarse fragments (greater than 2 mm) were weighed and their volume was measured by displacement. The adjusted mass (g) and volume (mL) were then used to calculate the final bulk air dry density (g mL^{-1} or g cm^{-3}). A subsample was then analysed for percent organic carbon by the New Jersey Agricultural Experiment Station Soil Testing Laboratory at Rutgers University. We also compared these values to previously published soil carbon estimates from NYC urban natural area forests which were collected and calculated using a somewhat different methodology but which come from the sample plots used in this study (Pregitzer et al., 2022). Because the methods used to calculate soil carbon were somewhat different in NYC, we simply compared the overall mean and confidence interval from that study to the values calculated here (rather than presenting plot-level data).

2.2 | Calculations

To estimate woody vegetation carbon stock density (Mg Cha^{-1}), we followed a slightly modified version of the methods followed by

Pregitzer et al. (2022). Briefly, individual tree carbon pools were calculated based on their species and DBH using allometric equations with the following generalized forms (Jenkins et al., 2003):

$$\text{Above-ground biomass (kg)} = \exp(B_0 + B_1) \times \log(\text{DBH})$$

$$\begin{aligned} \text{Below-ground biomass (kg)} = & \exp(B_0 + B_1) \times \log(\text{DBH}) \times \text{FR} + \\ & \exp(B_0 + B_1) \times \log(\text{DBH}) \times \text{CR} \end{aligned}$$

where DBH is the diameter in centimetres at 1.37 m from the ground, B_0 and B_1 are taxon-specific coefficients from Chojnacki et al. (2014) or Jenkins et al. (2003), and FR and CR are the fine root and coarse root component ratios, respectively (Jenkins et al., 2003). We combined the above- and below-ground components for each individual tree to get whole tree biomass estimates and multiplied this by 0.5 to convert kg dry mass to kg carbon. Finally, we summed the total tree carbon within a plot and divided that by the plot area to get to the carbon density (Mg Cha^{-1}). We used the same approach to calculate carbon stocks for standing dead trees, but adjusted for the recorded decay class. For example, the carbon stock for a standing dead hardwood in decay class 2 was calculated as 80% of the carbon in a live hardwood (Harmon et al., 2011; Appendix S1).

To estimate soil carbon we first calculated the total volume of mineral soil within the plot by subtracting the coarse root volume within the plot, derived from the allometric equations, and the proportion of coarse fragments (e.g. rocks), derived from the soil samples, from the total volume of the plot to 30 cm (Crown et al., 2023). We note that although the diameter of the soil cores (3.8 cm) is commonly used for soil carbon estimation, it excludes large coarse fragments, leading to a possible overestimation of total soil volume and therefore soil carbon stocks. We additionally assumed that 60% of the coarse roots are within the top 30 cm (Yanai et al., 2008). The calculated soil volume (cm^3) was then multiplied by the percent organic carbon and the soil bulk density (g cm^{-3}), and converted to Mg Cha^{-1} . An in-depth description of these methods, including all equations and coefficient values used for tree, standing dead, and soil carbon estimation, is available in Appendix S1.

2.3 | Forest Inventory Analysis comparison

To compare the woody vegetative carbon density of urban natural area forests to rural counterparts, we used USDA Forest Service (FIA) data collected from forests surrounding each of the eight cities. To do this, we obtained all state-wide data from each state included in these zones from the publicly available DataMart (FIA DataMart, <https://apps.fs.usda.gov/fia/datamart/datamart.html>) on August 26th, 2024, and filtered the data to include only plots that are located within 200 km of each city. We also filtered the data to include only the most recent inventory. We then used the same allometric equations as above to estimate live tree carbon based on the recorded DBH, then scaled these estimates to the

plot level by summing the carbon stock of all trees within a plot and dividing by the plot area. We excluded plots that had fewer than 30 trees ha^{-1} . We assigned each urban natural area forest plot to its closest USDA FIA forest type (Burrill et al., 2021) based on the dominant canopy species. In some cases, plots did not have a rural analog: in this case, they were excluded from this analysis. We then filtered the FIA data to only include forest types that are also represented in the urban forested natural areas. This filtering resulted in a subset of plots from both the FIA dataset and our urban natural areas dataset but provides for a more direct comparison between similar forest types.

2.4 | Data analysis

All data analysis was conducted in R version 4.3.0 (R Core Team, 2023). Linear mixed-effects models were run using the 'lme4' and 'lmerTest' packages (Bates et al., 2015; Kuznetsova et al., 2017). For all statistical models, we checked the homogeneity of variance, influential outliers, normality of residuals, and normality of random effects (when relevant) using the performance package (Lüdtke et al., 2021).

First, we estimated carbon stock density in above-ground live biomass, below-ground live biomass, standing deadwood, and soil carbon across the eight cities. Since the data available differed

across cities, this was primarily done to provide a range of plausible values in urban natural areas that span a variety of characteristics, including climate, city size, and history of development rather than to compare the pools in each city statistically.

To answer our first research question, whether urban natural area forests with more native species store more carbon, we used two linear mixed-effects models to test whether total woody vegetation carbon in a plot increases with first the percentage of native basal area and second the percentage of native stems using the city as a random effect. We then used two logistic regressions to test whether the native species found in urban natural areas have (a) a larger typical mature height and (b) a greater observed DBH than the non-native species, including the city as a random effect in each case. Given the large number of plots in NYC relative to other cities, we test both the full dataset and the subset of data with NYC data excluded to ensure our conclusions are not reflecting NYC-only patterns (Tables S1 and S2).

To answer our second research question, whether urban natural area forests store similar amounts of carbon to rural forests, we again looked exclusively at the total live, woody vegetation carbon. Using the subset of urban natural area data from each city that has an analogous rural forest type in that state, we used a paired two-sample *t*-test to compare the live woody vegetation carbon in urban natural area forests to their rural counterpart. To investigate which forest characteristics might be responsible for any differences, we

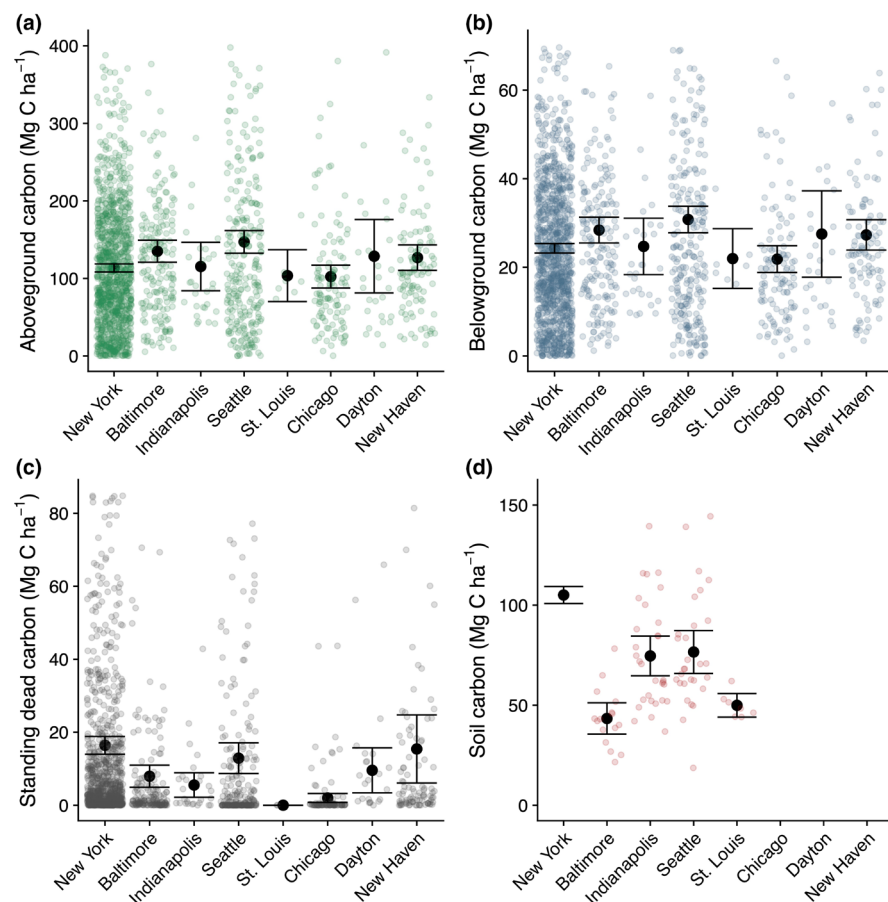


FIGURE 2 Carbon stock density in urban natural area forests for each city. (a) Above-ground live woody biomass carbon; (b) below-ground live woody biomass carbon; (c) standing dead woody biomass carbon; (d) soil organic carbon (to a depth of 30 cm). Large black circles represent the mean for the city; error bars represent the 95% confidence interval; and coloured points represent individual plot data. Some high outliers in each panel are not displayed to aid visualization [$n = 39, 63, 252$ and 0 for (a, b, c and d), respectively]. Note the different scales for the y-axis in each panel.

FIGURE 3 Live tree carbon stock density in urban natural area forests increases with the percentage of basal area that is native. Coloured points represent data for individual plots from each of the eight cities ($n = 1852$; 12 points not shown here because tree carbon values are $>600 \text{ Mg C ha}^{-1}$), but included in statistical analyses. The coloured lines represent individual mean linear regressions for each city, and the dashed black line represents the mean linear regression for the entire dataset (grey shading represents its 95% confidence interval). Model results are reported in Table 2.

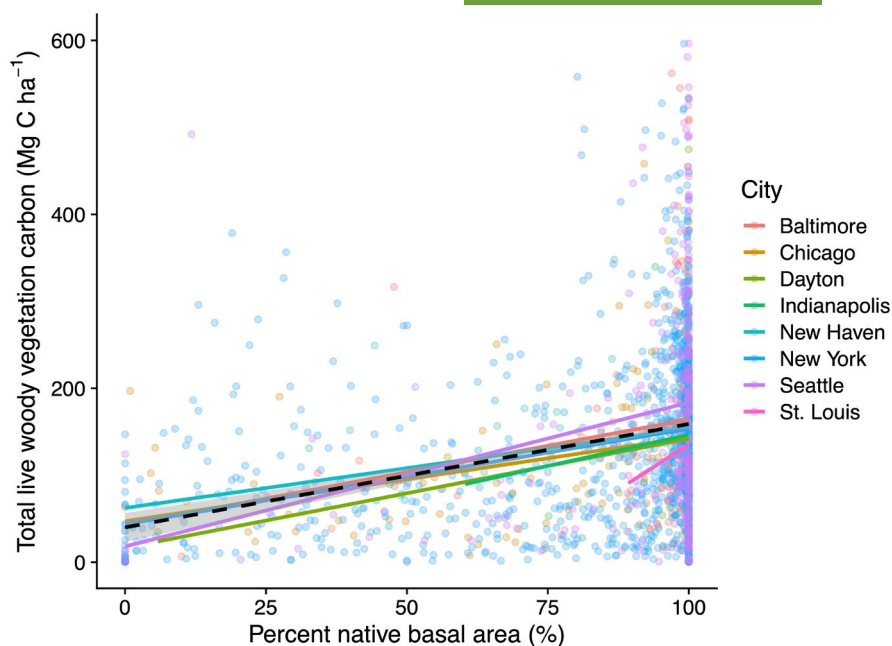


TABLE 2 Linear mixed-effect model output for predicting total live vegetation carbon in a plot using the proportion of the basal area that is made up of native species.

Predictor	Estimate (CI)	Standardized estimate (CI)	p
Intercept	42.96 (21.98–63.94)	0.01 (–0.08–0.10)	<0.001
Proportion native basal area	121.9 (101.4–142.3)	0.26 (0.22–0.31)	<0.001

Note: City is included as a random effect ($n = 8$). Overall $n = 1852$ plots. Marginal R^2 /Conditional $R^2 = 0.070/0.078$. See also Table S1.

TABLE 3 Linear mixed-effect models output for predicting typical mature height (m) and observed DBH (cm) based on plant native status (reference group in non-native).

Predictor	Typical mature height (m)	Observed DBH (cm)
	Estimate (CI)	Estimate (CI)
Intercept	14.75 (12.16–17.33)	11.27 (9.01–13.52)
Native status (native)	8.98 (6.70–11.26)	6.51 (6.23–6.79)
N	483	60,451
Marginal R^2 /Conditional R^2	0.111/0.150	0.034/0.078

Note: City is included as a random effect in both models ($n = 8$). Bold values indicate $p < 0.05$. See also Table S2.

Abbreviation: DBH, diameter at breast height.

also compared the total basal area ($\text{m}^2 \text{ ha}^{-1}$), stand density (trees ha^{-1}), and density of large trees (trees larger than 50-cm diameter ha^{-1}) using paired two-sample *t*-tests.

3 | RESULTS

Across all eight cities, the largest carbon pool in urban natural area forests was in above-ground woody biomass, which contained on average 55% of the total forest carbon. Cities varied in the size of their carbon storage pools, with Seattle ($147 \text{ Mg above-ground C ha}^{-1}$)

storing roughly 50% more above-ground carbon than Chicago ($100 \text{ Mg above-ground C ha}^{-1}$). Soils were the next largest carbon pool ($43\text{--}105 \text{ Mg soil C ha}^{-1}$), containing on average 31% of the total carbon. Below-ground woody biomass ($21\text{--}31 \text{ Mg C ha}^{-1}$) and standing dead trees and shrubs ($2\text{--}16 \text{ Mg C ha}^{-1}$) were the smallest carbon pools (Figure 2).

At the plot level, increases in the proportion of native trees were correlated with a small increase in carbon storage (Figure 3; Table 2). This pattern was consistent across the eight cities, which varied in their abundance of native species: whilst only 35% of all individual stems in Chicago natural areas were native, 70%

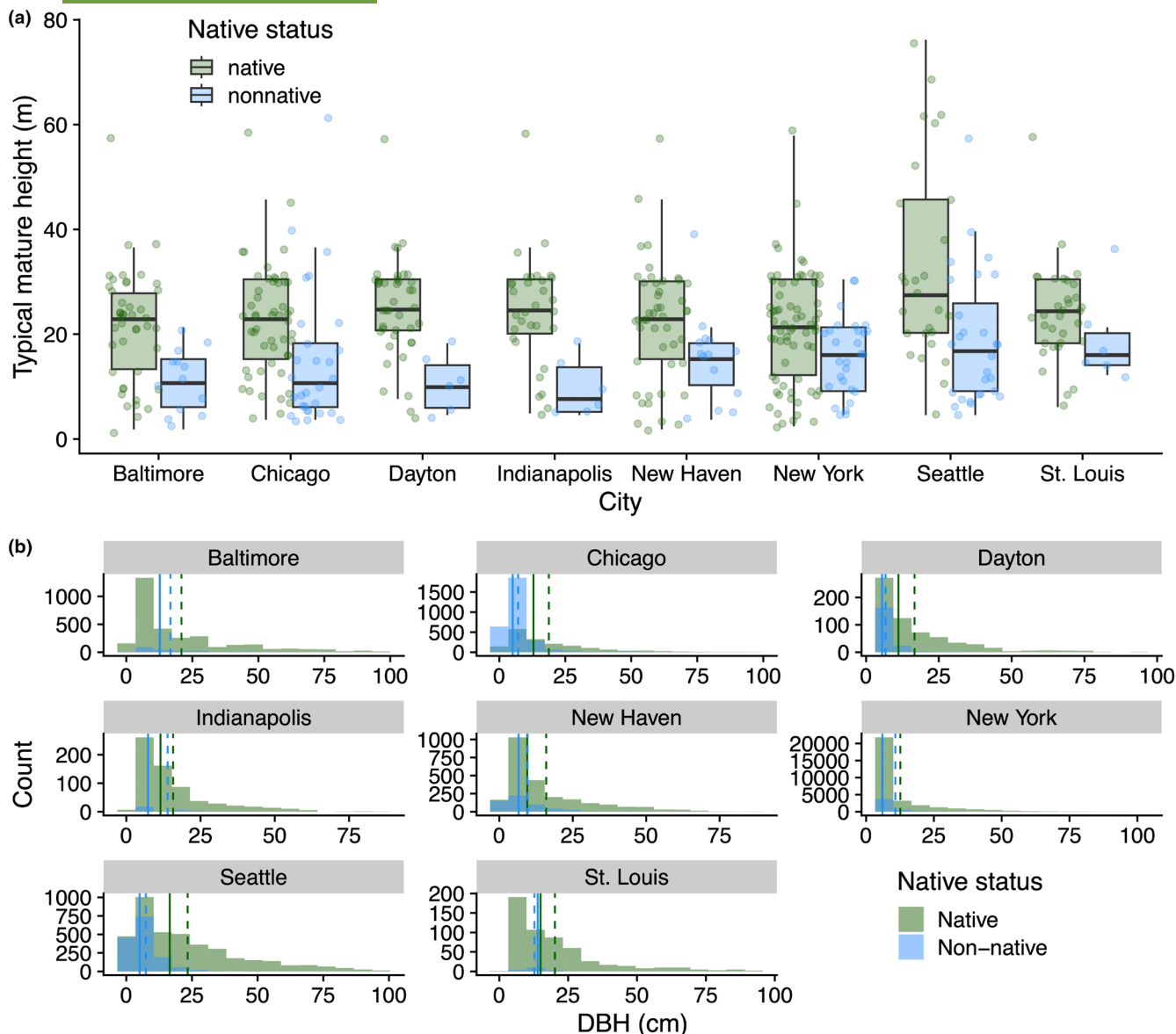


FIGURE 4 Native species (green points) found in urban natural area forests tend to be larger than non-native species (blue points). (a) Native species tend to have larger mature heights than non-native species. Each point represents the typical mature height of a species (USDA NRCS, 2024) that is found in the urban natural area forests surveyed in these eight cities ($n=475$). (b) Frequency histograms of the DBH of all individual stems grouped by their native status. Solid lines represent group medians, dashed lines represent group means. Data are only shown for stems identified to species and up to a DBH of 100 cm (5230 stems not shown out of 60,451 total). Note the different scales on x- and y-axes. See Table 3 for model output. DBH, diameter at breast height.

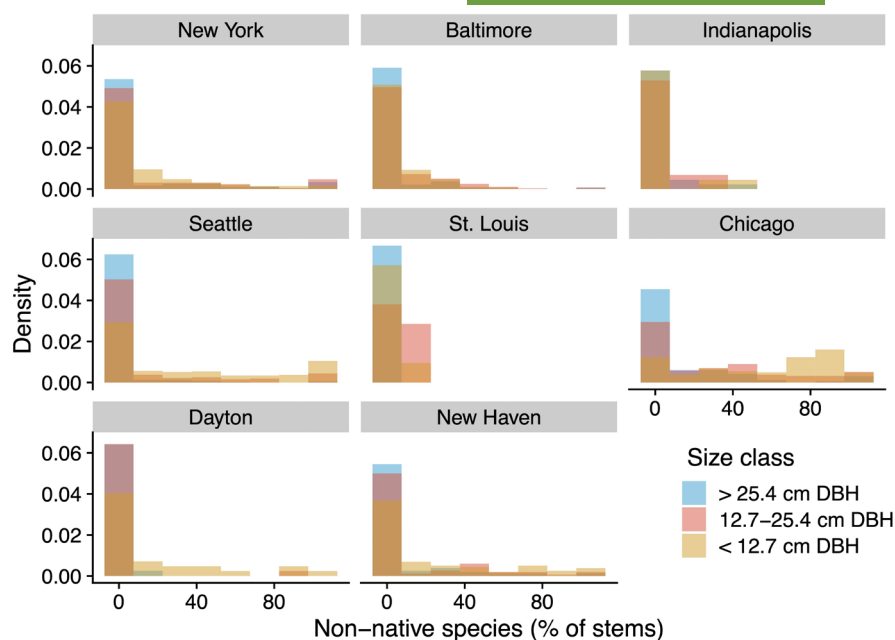
were native in Seattle, 77% in New York, 79% in Dayton, 80% in New Haven, and more than 90% in St. Louis, Baltimore, and Indianapolis. Despite these differences in the abundance of native species, 85%–99% of the carbon stored by woody vegetation in urban natural area forests of all eight cities was stored by native species.

Native species had an average typical mature height of 23.3 m, significantly greater than the 15.4 m average of non-native species (Table 3; Figure 4a). Relatedly, the average size (DBH) of native individuals (regardless of growth habit) is on average greater than that of non-native individuals (Table 3; Figure 4b). Across the entire dataset, the mean DBH of native individuals was 15.2 cm and the mean

DBH of non-native individuals was 9.4 cm. Thus although the largest tree size classes are dominated by native species, this dominance decreases in the smaller size classes where greater proportions of non-native species are found (Figure 5).

Urban natural area forests on average store similar or greater amounts of carbon in live woody vegetation relative to non-urban forests (Figure 6a). Although some forest types exhibit greater carbon storage in rural areas, on average urban natural area forests contain 85% greater live woody vegetation carbon density than their rural counterparts ($t_{121} = -9.09$, $p < 0.001$). This difference is due to the greater basal area per hectare in the urban natural areas ($t_{181} = -7.88$, $p < 0.001$; Figure 6b). Urban natural area forests do not

FIGURE 5 Relative frequency of native species across different size classes in urban natural area forest plots within each city. Each observation represents the percentage of all stems of that size class present in a plot ($n = 1805$ total plots) that are non-native species. Each plot is therefore represented in each of the three overlapping histograms in each facet unless that size class was absent.



necessarily contain a larger number of trees than their rural counterparts: indeed in some states (Washington, Maryland), rural forests have higher stand densities (Figure 6c). Rather, the greater basal area (and therefore greater woody vegetation carbon) is due to the presence of more large trees ($t_{164} = -8.07$, $p < 0.001$; Figure 6d), which contribute disproportionately to the carbon stock. We also note that although the urban natural area carbon estimates at the plot level contain some very high values, likely due to the small size of the plots, the range of vegetation carbon values at the plot level is similar for urban and rural forests (Figure S1).

4 | DISCUSSION

Our analysis finds that across multiple cities, urban natural area forests store considerable carbon per hectare, with live woody vegetation stock generally equivalent to or higher than similar rural forest types. This work extends a previous, single-city analysis in NYC (Pregitzer et al., 2022), which estimated that mean woody carbon density in urban natural area forests was $135.4 \text{ Mg C ha}^{-1}$ in NYC. This estimate falls in the middle of the range we observed across the eight cities (120.8 in Chicago to 177.3 in Seattle). These natural area forest-focused estimates are higher than those derived using methodologies that assess carbon storage by combining all trees in a city. Specifically, prior city-level assessments randomly sampled all trees growing in cities, including multiple, lower carbon density, urban forest site types such as street trees or landscaped areas (Hutry et al., 2011; Nowak et al., 2013). Because of their more clumped distribution, natural area forests may be under-sampled in these city-scale urban forest assessments compared with more uniformly distributed canopy types, such as street or landscaped yard trees. Such designs can underestimate the number of

trees and forest carbon storage in cities whilst overestimating the relative abundance of non-native versus native tree species (Pregitzer, Ashton, Charlop-Powers, et al., 2019). Our work supports the idea that natural area forests are carbon hotspots within urban landscapes (Raciti et al., 2014), and that non-stratified sampling efforts may underestimate total urban forest carbon storage given that, on average, native-canopy urban forests have high carbon storage.

We found that overall, the biomass of urban natural area forests was dominated by native species, with 85%–99% of the carbon stored in live woody vegetation carbon found in native trees and shrubs: a result consistent with work from NYC that found urban natural area forest canopy was composed of 82% native species on average (Pregitzer, Charlop-Powers, Bibbo, et al., 2019). Despite perceptions that urban forests should be reconceived as novel systems co-dominated by natives and non-natives (Gaertner et al., 2017; Hobbs et al., 2006), we find that native species dominate.

We also found that native species in urban forests tended to be larger than non-native species, helping to explain why we see an increase in carbon storage with increasing native dominance. We show that this is for two reasons: the native species that occur in urban natural area forests have greater size potential, as shown by their greater typical mature height. Additionally, the observed size of native species tends to be larger. Together, this means that although non-native-dominated areas in our study may be at an earlier successional stage (as indicated by their smaller observed size), their carbon stock is unlikely to “catch up” to native-dominated areas as they have lower storage potential. That is, with fewer native individuals in the mid- and understory, there is a risk that as native-canopy trees die, they will be succeeded by the smaller statured, non-native species that are currently more common in the understory. Such a dynamic is consistent with diverging regeneration conditions in

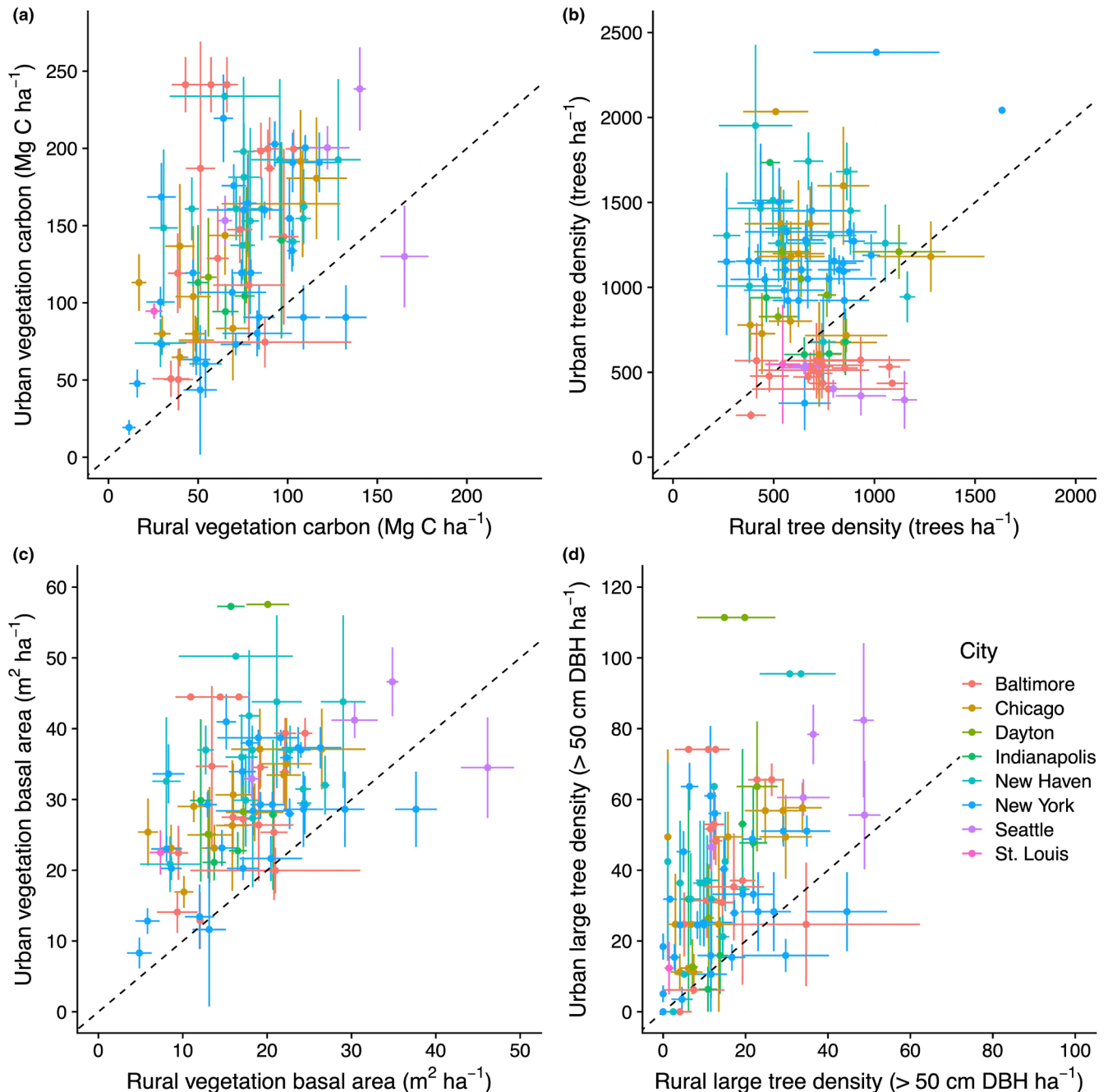


FIGURE 6 Rural and urban natural area forest live vegetation characteristics. Each point ($n=88$) represents the mean value for a single forest type is found in both the urban natural area forests (y axis) and the FIA data within 200 km of that city (x-axis). Carbon stock in above-ground and below-ground biomass of live trees (a), stand density in trees ha^{-1} (b), basal area in $\text{m}^2 \text{ha}^{-1}$ (c), and the number of large (>50 cm DBH) trees ha^{-1} (d). Horizontal and vertical error bars represent the standard error of rural (FIA) and urban (our data) forests, respectively. The black dashed line represents the 1:1 line. DBH, diameter at breast height; FIA, Forest Inventory Analysis.

urban versus rural forests, with urban natural area forests exhibiting greater barriers to the natural regeneration of native species (Piana, Hallett, et al., 2021; Trammell & Carreiro, 2011).

Together, these results have several management implications. Greater monitoring of tree growth and turnover in urban natural area forests is needed to predict future carbon stocks. Our observation of greater non-native species presence in the understory suggests, but does not prove, that these forests are at risk of succession

to non-native-dominated forest. Monitoring would help determine whether these forests are indeed in the process of transitioning away from native dominance. This is of particular importance as municipalities are increasingly including estimates of tree carbon storage and sequestration in climate action plans and net carbon emissions goals. Monitoring would provide additional evidence for additional management activities, such as the removal of short-statured, non-native species from the understory.

Woody vegetation carbon density was greater on average in urban natural area forests than in comparable rural forests. We found that this difference was due primarily to the presence of more large trees in urban natural areas, relative to similar forest types growing rurally, consistent with previous work (Pregitzer, Charlop-Powers, Bibbo, et al., 2019; Sonti et al., 2022). Overall, the differences are likely due to a combination of factors, which are not possible to disentangle from our data: urban natural area forests may be older (as is suggested by the presence of more large trees) than their average rural counterparts, and their management histories likely differ. For example, the preservation of large trees may be more common in urban natural area forests, where management activities typically focus on invasive species and trash removal (Pregitzer, Charlop-Powers, Hipple, et al., 2019) rather than the silvicultural treatments that are common in rural forests, which tend to remove more basal area. Future work that identifies management strategies that balance the carbon advantage of urban natural area forests with the potential need for non-native species removal is sorely needed. Increased temperatures and nutrients in urban areas, and lower ozone damage, can in some cases stimulate and sustain tree growth (Briber et al., 2015; Gregg et al., 2003; Pretzsch et al., 2017).

5 | CONCLUSIONS

Although urban forested natural areas represent a small fraction of all forested land and therefore do not represent a major climate mitigation strategy at national scales (Piana, Pregitzer, & Hallett, 2021), these forests are native-dominated, carbon storage hotspots. To maintain the health of these ecosystems, increased monitoring, and non-native plant removal are likely needed to counter potential succession away from native dominance. Our work also highlights the need for national-level, urban forest assessment efforts that are stratified by canopy type. Such efforts could guide the management of urban natural area forests and would facilitate the inclusion of these carbon-rich systems in national and global forest carbon accounting.

AUTHOR CONTRIBUTIONS

Clara C. Pregitzer, Crystal A. Crown, Jeffrey A. G. Clark, Fiona Jevon, and Mark Bradford conceived the ideas and designed the methodology; Danica A. Doroski, Grace Dietsch, Lindsay Darling, Nancy F. Sonti, and Ian D. Yesilonis collected the data; Fiona Jevon and Crystal A. Crown analysed the data; Fiona Jevon led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.1g1jwsv3p> (Jevon et al., 2024).

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REFERENCES

- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Briber, B. M., Hutrya, L. R., Reinmann, A. B., Raciti, S. M., Dearborn, V. K., Holden, C. E., & Dunn, A. L. (2015). Tree productivity enhanced with conversion from forest to urban land covers. *PLoS One*, 10, e0136237.
- Burrill, E. A., DiTommaso, A. M., Turner, J. A., Pugh, S. A., Christensen, G., Perry, C. J., & Conkling, B. L. (2021). *The forest inventory and analysis database: Database description and user guide for phase 2 (version 9.0.1)*. U.S. Department of Agriculture, Forest Service.
- Chojnacky, D. C., Heath, L. S., & Jenkins, J. C. (2014). Updated generalized biomass equations for North American tree species. *Forestry*, 87, 129–151.
- Crown, C. A., Hanna, C., & Pregitzer, C. C. (2023). *Aggregated methods for calculating tree carbon stock and sequestration rate, and soil carbon stock from field collected fixed radius plot data*. Forests in Cities Resource Library. <https://fic.naturalareasnyc.org/docs/carbon-budget-calculation-methods>
- Doroski, D. A., Bradford, M. A., Duguid, M. C., Hallett, R. A., Pregitzer, C. C., & Ashton, M. S. (2022). Diverging conditions of current and potential future urban forest patches. *Ecosphere*, 13, e4001.
- Gaertner, M., Wilson, J. R. U., Cadotte, M. W., MacIvor, J. S., Zenni, R. D., & Richardson, D. M. (2017). Non-native species in urban environments: Patterns, processes, impacts and challenges. *Biological Invasions*, 19, 3461–3469.
- Gregg, J. W., Jones, C. G., & Dawson, T. E. (2003). Urbanization effects on tree growth in the vicinity of New York City. *Nature*, 424, 183–187.

- Harmon, M. E., Woodall, C. W., Fasth, B., Sexton, J., & Yatkov, M. (2011). *Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species*. USDA Forest Service Northern Research Station.
- Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R., & Zobel, M. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, 15, 1–7.
- Hutyra, L. R., Yoon, B., & Alberti, M. (2011). Terrestrial carbon stocks across a gradient of urbanization: A study of the Seattle, WA region. *Global Change Biology*, 17, 783–797.
- Jenkins, J. C., Chojnacki, D. C., Heath, L. S., & Birdsey, R. A. (2003). National-scale biomass estimators for United States tree species. *Forest Science*, 49, 12–35.
- Jenkins, M. A., & Howard, B. S. (2021). Forest vegetation response to white-tailed deer population reductions in a large urban park. *Natural Areas Journal*, 41, 114–124.
- Jevon, F., Crown, C., & Pregitzer, C. (2024). Urban natural areas forest carbon [Data set]. Dryad. <https://doi.org/10.5061/dryad.1g1jwsv3p>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26.
- Livesley, S. J., McPherson, G. M., & Calfapietra, C. (2016). The urban Forest and ecosystem services: Impacts on urban water, heat, and pollution cycles at the tree, street, and City scale. *Journal of Environmental Quality*, 45, 119–124.
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6, 3139.
- Moss, J. L., Doick, K. J., Smith, S., & Shahrestani, M. (2019). Influence of evaporative cooling by urban forests on cooling demand in cities. *Urban Forestry & Urban Greening*, 37, 65–73.
- Nowak, D. J., Greenfield, E. J., & Ellis, A. (2022). Assessing urban forest threats across the conterminous United States. *Journal of Forestry*, 120, 676–692.
- Nowak, D. J., Greenfield, E. J., Hoehn, R. E., & Lapoint, E. (2013). Carbon storage and sequestration by trees in urban and community areas of the United States. *Environmental Pollution*, 178, 229–236.
- Piana, M. R., Hallett, R. A., Aronson, M. F. J., Conway, E., & Handel, S. N. (2021). Natural regeneration in urban forests is limited by early-establishment dynamics: Implications for management. *Ecological Applications: A Publication of the Ecological Society of America*, 31, e02255.
- Piana, M. R., Pregitzer, C. C., & Hallett, R. A. (2021). Advancing management of urban forested natural areas: Toward an urban silviculture? *Frontiers in Ecology and the Environment*, 19, 526–535.
- Pregitzer, C. C., Ashton, M. S., Charlop-Powers, S., D'Amato, A. W., Frey, B. R., Gunther, B., Hallett, R. A., Pregitzer, K. S., Woodall, C. W., & Bradford, M. A. (2019). Defining and assessing urban forests to inform management and policy. *Environmental Research Letters*, 14, 085002.
- Pregitzer, C. C., & Bradford, M. A. (2023). Associations between recent land use history and urban forest composition. *Urban Forestry & Urban Greening*, 90, 128134.
- Pregitzer, C. C., Charlop-Powers, S., Bibbo, S., Forgione, H. M., Gunther, B., Hallett, R. A., & Bradford, M. A. (2019). A city-scale assessment reveals that native forest types and overstory species dominate New York City forests. *Ecological Applications: A Publication of the Ecological Society of America*, 29, e01819.
- Pregitzer, C. C., Charlop-Powers, S., Hipple, A., Gunther, B., & Bradford, M. A. (2019). *Untapped common ground: The care of forested natural areas in American cities*. Natural Areas Conservancy.
- Pregitzer, C. C., Hanna, C., Charlop-Powers, S., & Bradford, M. A. (2022). Estimating carbon storage in urban forests of New York City. *Urban Ecosystems*, 25, 617–631.
- Pregitzer, C. C., Plitt, S., & Charlop-Powers, S. (2020). Realizing the potential of urban forests: Forests in cities workshop themes and City case study descriptions. *Cities and the Environment*, 13, 2.
- Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Schütze, G., Perkins, D., Rötzer, T., Caldey, J., Koike, T., van Con, T., Chavanne, A., du Toit, B., Foster, K., & Lefer, B. (2017). Climate change accelerates growth of urban trees in metropolises worldwide. *Scientific Reports*, 7, 15403.
- R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Raciti, S. M., Hutyra, L. R., & Newell, J. D. (2014). Mapping carbon storage in urban trees with multi-source remote sensing data: Relationships between biomass, land use, and demographics in Boston neighborhoods. *The Science of the Total Environment*, 500–501, 72–83.
- Radford, K. G., & James, P. (2013). Changes in the value of ecosystem services along a rural-urban gradient: A case study of Greater Manchester, UK. *Landscape and Urban Planning*, 109, 117–127.
- Reyes-Riveros, R., Altamirano, A., De La Barrera, F., Rozas-Vásquez, D., Vieli, L., & Meli, P. (2021). Linking public urban green spaces and human well-being: A systematic review. *Urban Forestry & Urban Greening*, 61, 127105.
- Selbig, W. R., Loheide, S. P., 2nd, Shuster, W., Scharenbroch, B. C., Coville, R. C., Krueger, J., Avery, W., Haefner, R., & Nowak, D. (2022). Quantifying the stormwater runoff volume reduction benefits of urban street tree canopy. *The Science of the Total Environment*, 806, 151296.
- Sonti, N. F., Riemann, R., Mockrin, M. H., & Domke, G. M. (2022). Expanding wildland-urban interface alters forest structure and landscape context in the northern United States. *Environmental Research Letters*, 18, 014010.
- Stanley, M. C., Beggs, J. R., Bassett, I. E., Burns, B. R., Dirks, K. N., Jones, D. N., Linklater, W. L., Macinnis-Ng, C., Simcock, R., Souter-Brown, G., Trowsdale, S. A., & Gaston, K. J. (2015). Emerging threats in urban ecosystems: A horizon scanning exercise. *Frontiers in Ecology and the Environment*, 13, 553–560.
- Trammell, T. L. E., & Carreiro, M. M. (2011). Vegetation composition and structure of woody plant communities along urban interstate corridors in Louisville, KY, U.S.A. *Urban Ecosystems*, 14, 501–524.
- USDA NRCS. (2024). *The PLANTS database*. National Plant Data Team, Greensboro, NC, USA. <http://plants.usda.gov>
- Vieira, J., Matos, P., Mexia, T., Silva, P., Lopes, N., Freitas, C., Correia, O., Santos-Reis, M., Branquinho, C., & Pinho, P. (2018). Green spaces are not all the same for the provision of air purification and climate regulation services: The case of urban parks. *Environmental Research*, 160, 306–313.
- Yanai, R. D., Fisk, M. C., Fahey, T. J., Cleavitt, N. L., & Park, B. B. (2008). Identifying roots of northern hardwood species: Patterns with diameter and depth. *Canadian Journal of Forest Research*, 38, 2862–2869.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Methods for carbon estimation.

Table S1. Results of linear mixed effects models predicting plot level total live tree carbon stocks as a function of the percent of stems in each plot that are native.

Table S2. Linear mixed effect models output for predicting typical mature height (m) and observed DBH (cm) based on plant native status (reference group in non-native), with NYC data excluded.

Figure S1. Histograms of plot level total live woody vegetation carbon in rural forests (pink bars—FIA) and urban natural area forests (blue bars—UNAF) in each of the eight cities and their surrounding forests (as defined by forests within 200km of the city center).

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