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ARTICLE

Socio-Ecological Systems

The influence of urban and agricultural landscape contexts on forest diversity and structure across ecoregions

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Abstract

Forest patches in urban landscapes make outsized contributions to biodiversity, ecosystem function, and human health and well-being. However, urbanization can alter environmental conditions that underpin forest health. Most studies of forest health in urban landscapes have focused on few forest patches across a single metropolitan region, and synthesis is needed to understand broader patterns. We assessed variation among measures of forest health across land cover gradients and ecoregions by determining (1) whether the degree of urban, agricultural, and forested land surrounding a forest patch was reflected in differences in tree community composition, diversity, and structure and (2) whether these differences were consistent across ecoregions. We synthesized data from 17 observational studies (3334 plots) and remotely sensed land cover (1-km buffer) across four metropolitan regions (Baltimore–Washington DC, Chicago,

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New York City, and Philadelphia) spanning five ecoregions of the eastern deciduous forest of North America. Land cover surrounding forest patches differed among ecoregions, and forests were surrounded by heterogeneous land cover even in the most urbanized areas. Patterns of tree species composition and forest structure reflected landscape context. Forest patches surrounded by high canopy cover had greater or equal tree species diversity, density, basal area, and diversity of tree sizes relative to patches surrounded by highly agricultural or highly impervious landscapes. In contrast, there was little difference in structure and diversity between forests in highly agricultural and impervious settings. Tree species composition varied among ecoregions, yet tree community assemblages of forests in intensively urbanized areas were consistently distinct from those of forests in other contexts. Forest patches in the most urban and most agricultural landscapes shared predominantly native species communities and were characterized by low tree species diversity, basal area, and size class diversity, as well as high non-native tree abundance, highlighting commonalities among these intensive anthropogenic landscapes. These results point to both common challenges to forest health and common opportunities for forest stewardship in urban and agricultural landscapes.

KEYWORDS
data synthesis, ecoregion, landscape ecology, non-native species, plant community, urban forest, urbanization, urban–rural gradient, woodland

INTRODUCTION

As urban land use and the proportion of humanity living in urban areas increases, patches of forest in cities have an increasingly disproportionate importance compared with the small fraction of land they occupy. Urban forest patches are spontaneously regenerating and self-organizing forest communities that occur within an urban landscape matrix that are important contributors of ecological function, biodiversity conservation, and human–nature interactions (Johnson, Johnson, et al., 2020). They arise from historical legacies, management priorities, socioeconomic conditions, and social values (e.g., Payne et al., 2002; Roman et al., 2018; Sonti et al., 2020), reflecting urban history (Dow, 2000; Ogden et al., 2019) and evolving land use governance (Morzillo et al., 2016, 2022). They may be older forests that remain as their surroundings are developed, or areas where forests regrow on previously cleared or developed land (Sonti et al., 2024). Other urban forest site types, such as street trees or yard trees, are not considered urban forest patches, as management of those areas inhibits spontaneous regeneration. However, urban forest patches are socio-ecological systems, and their biological communities reflect influences of human actions and governance, native and non-native species, and abiotic components (Johnson, Johnson, et al., 2020).

Growing awareness of the importance of urban natural areas to ecological functioning and sustainability of cities (Elmqvist et al., 2015; Kowarik, 2011), the well-being of urban residents (Berg et al., 2007; Hauru et al., 2012; Korpela et al., 2010; Song et al., 2016; Tyrväinen et al., 2005), and regional biodiversity (Müller et al., 2018; Piana, Hallett, Johnson, et al., 2021; Piana, Pregitzer, et al., 2021; Rebelo et al., 2011; Schwartz et al., 2002; Soanes et al., 2019) has drawn attention to the need to integrate urban forest patches into land management decision-making. Urbanization alters the conditions that underpin forest health at multiple scales. Temperatures within urban environments are influenced by global climate change and urban warming, making them a window onto the potential effects of future climate on forests (Alcoforado & Andrade, 2008; Carreiro & Tripler, 2005). Altered hydrology and chemical inputs shift the distribution and quality of water inputs to forests (Welty, 2009). Cycles of ecological disturbance central to plant community dynamics may be altered or completely removed by urbanization. In the forests of eastern North America, for example, exclusion of fire has led to shifts in tree composition favoring moisture-adapted, shade-tolerant species (Dey et al., 2019), while herbivores proliferate in the absence of large predators, and introduced earthworms speed up rates of leaf

litter decomposition and nitrogen cycling (Steinberg et al., 1997)—collectively facilitating invasive plant species establishment and spread (Aronson & Handel, 2011; Frelich et al., 2019).

Species vary in their responses to these conditions and to environmental change itself (Lopez et al., 2018; McDonnell & Hahs, 2008), with consequences for the composition of local and regional species pools (Aronson et al., 2016), genetic diversity of native species (Johnson et al., 2018; Ricotta et al., 2011), and regeneration potential of native trees (Piana et al., 2019). At the same time, urban areas are hotspots of species introductions (Pennington et al., 2010; Sorte et al., 2014)—from intentional agricultural, commensal, and horticultural introductions to invasive species, predators, and pests. These factors combine to shape the composition and structure of urban forest patches.

Such diversity creates complex situations where the generalization of forest management guidelines across cities with differing contexts and histories may lead to misguided decision-making and suboptimal land use planning outcomes. Therefore, understanding the dynamics and drivers of change across multiple urban areas and differing intensities of urbanization is essential to developing effective and targeted approaches to the conservation and management of urban forest patches.

Because quantitative documentation of forest composition and structure prior to and during urbanization is scarce (Goring et al., 2016), analyses focused on urbanization gradients have been developed to test how varying intensities of surrounding urbanization are related to forest health. The urban-to-rural gradient approach applies the gradient paradigm (Whittaker, 1967) to understand urbanization as a spatially varying effect (McDonnell & Pickett, 1990). This approach has advanced understanding of the effects of urbanization on a variety of taxa, processes, and the physical environment, including soils (Pouyat et al., 1995; Pouyat & McDonnell, 1991), plant communities (Guntenspergen & Levenson, 1997; Medley et al., 1995; Wang et al., 2020), bird diversity (Blair, 1996), mammal habitat utilization (Bowers & Breland, 1996), invertebrate communities (Klausnitzer & Richter, 1983; Niemelä & Kotze, 2009), amphibians (Pillsbury & Miller, 2008), nutrient cycling (Pouyat et al., 1997), water quality (Schoonover et al., 2005), and pollution (Callender & Rice, 2000; Gingrich et al., 2001). While linear distance from the city core is perhaps the most readily visualized and easily measurable gradient, urban spatial patterns and typologies often are not concentric (Kaminski et al., 2021; Theobald, 2004, 2005; Zhang et al., 2017) but rather are heterogeneous in form and pattern (Cadenasso et al., 2007).

Research exploring relationships between urbanization and vegetation began centuries ago with catalogs of urban flora across entire cities (Sukopp, 2008). Most research to date on urban forests has been similarly broad—encompassing street trees, parks, and other manicured spaces as well as natural areas (e.g., Konijnendijk et al., 2006; Pincetl, 2010). With increasing attention to and understanding of the importance of urban ecosystems to biodiversity and local provision of ecosystem services, approaches comparing vegetation of different habitat types have emerged, revealing homogenization of highly managed landscapes (i.e., yards) in relation to native vegetation including forests (Padulles Cubino et al., 2019; Pearse et al., 2018; Swan et al., 2017; Wheeler et al., 2017). At the same time, however, cities retain their unique biogeographical and cultural heritage at regional and global scales due to native species found in natural areas embedded in these urban landscapes (Aronson et al., 2014, 2015; Trammell et al., 2020; Trammell & Carreiro, 2011).

Research examining forest patches in urban landscapes has primarily been conducted at the scale of a single metropolitan area. Effects of urbanization on forest soils were among the first ecosystem impacts discovered using single-city urbanization gradient approaches (McDonnell et al., 1997; Pouyat & McDonnell, 1991). Other work at this scale has revealed differences in forest structure and species composition with greater urbanization, including tree density, total basal area, species richness, shifts in proportion of native and introduced species, and composition of trees, seedlings, and saplings (Medley et al., 1995; Ortega-Álvarez et al., 2011; Pennington et al., 2010; Piana et al., 2019; Templeton et al., 2019; Wang et al., 2020). The tree communities of forest patches, which can include both remnant pre-urban vegetation and influences of diverse human activities over time, have been demonstrated to be compositionally unique relative to other types of urban tree communities, such as trees planted along streets or found in residential yards (Jiang et al., 2022; Steenberg, 2018).

Multi-city studies examining the effects of urbanization on forest patches using measures of urbanization intensity are fewer. To date, these studies have reported that highly urbanized areas showed both greater and lower tree diversity than nearby less urbanized areas, with lower diversity linked to lower stem density, larger tree size, and an increase in abundance and importance of introduced species (Blood et al., 2016; Nock et al., 2013). Multi-city studies have also pointed to the importance of differences in surrounding landscape context and history on forest patches, including ecological province, latitude, and forest age (Blood et al., 2016; Trammell et al., 2020). Although surrounding landscapes and historical contexts are clearly relevant for understanding relationships between urbanization and dimensions of forest biodiversity (Blood et al., 2016; Trammell

et al., 2020; Williams & Winfree, 2013), this analysis is the first to examine relationships between landscape context and indicators of forest health across intensities of urbanization in multiple regions.

Research objective and specific questions

In this study, we examined the influence of urbanization intensity on forest tree composition, diversity, and structure, and the consistency of these effects across five ecoregions within the eastern deciduous forest of North America encompassing five major cities. We examined how landscape context of forest patches greater than 0.8 ha varied across ecoregions, and how differences in the degree of urbanization and other predominant land covers surrounding observational plots were related to forest tree community composition and structure. We categorized landscape context based on three predominant land cover types: impervious surface, tree canopy, and agricultural land, and focused our analysis on forest plots embedded in landscapes with high levels of these land covers.

Our strategy in addressing these questions was to first determine the relationships between forest trees and land cover within each ecoregion. We then looked across ecoregions to see whether these relationships were consistent across the study area or whether they varied from ecoregion to ecoregion. We did not delve into direct comparisons of forest tree communities between ecoregions as they are defined based on climatic and physical characteristics that influence tree distributions.

Our research addresses three broad questions:

1. Is landscape context consistent across ecoregions, or do ecoregions have a different mix of canopy, agricultural, and impervious land cover surrounding forest patches?
   a. We expected landscape context to vary substantially across ecoregions due to differences in land use history.
2. Is surrounding landscape context related to tree species composition and diversity of forest patches?
   a. Are forest patches within each type of landscape context (high impervious, agricultural, or canopy cover) consistent and distinct in their composition? Based on ordination analysis, we expected to find a distinct tree species composition in highly urban and highly agricultural contexts.
   b. Does landscape context relate to tree species diversity? We expected lower tree diversity in highly urban and highly agricultural contexts.
   c. Does landscape context influence the proportion of non-native species represented in the tree community? We expected a greater abundance of introduced tree species in highly urban and highly agricultural contexts.
3. Do forest patches in different landscape contexts have a different forest structure?
   a. Does landscape context influence tree density and basal area? We expected forest structure to be composed of younger trees and lower structural diversity in highly urban and highly agricultural contexts.
   b. Does landscape context influence tree size distribution? We expected lower size diversity in highly urban and agricultural contexts.

METHODS

This analysis is a result of the "Socio-Ecological Drivers of Change Over Time in Urban Woodlands" working group (Johnson, Johnson, et al., 2020; Morzillo et al., 2022) at the US-based National Socio-Environmental Synthesis Center (SESYNC; Palmer et al., 2016). The 20 members of this group included ecological and social science researchers and leaders in urban forest patch management within our study areas (Figure 1). This synthesis project encompasses five major cities in the North American Eastern Deciduous Forest (human population in parentheses; total for study area 52 million): Baltimore (590,000), Chicago (2.7 million), New York City (8.8 million), Philadelphia (1.6 million), and Washington, DC (690,000; US Census Bureau, 2020). To delineate study area boundaries, we extended the combined metropolitan statistical area boundaries for each city by an additional two counties to capture surrounding nonurban landscapes.

Data synthesis

In order to explore the relationship between land cover and forest composition and structure, we first assembled standardized tree and land cover datasets. To characterize forest conditions, we compiled and synthesized forest tree community composition and structure data from 17 observational studies. We used remote sensing–derived measures of land cover to characterize landscape context. The data we used have been produced by public agencies, universities, and institutions that are part of the SESYNC Urban Woodlands working group described above and/or are publicly available.

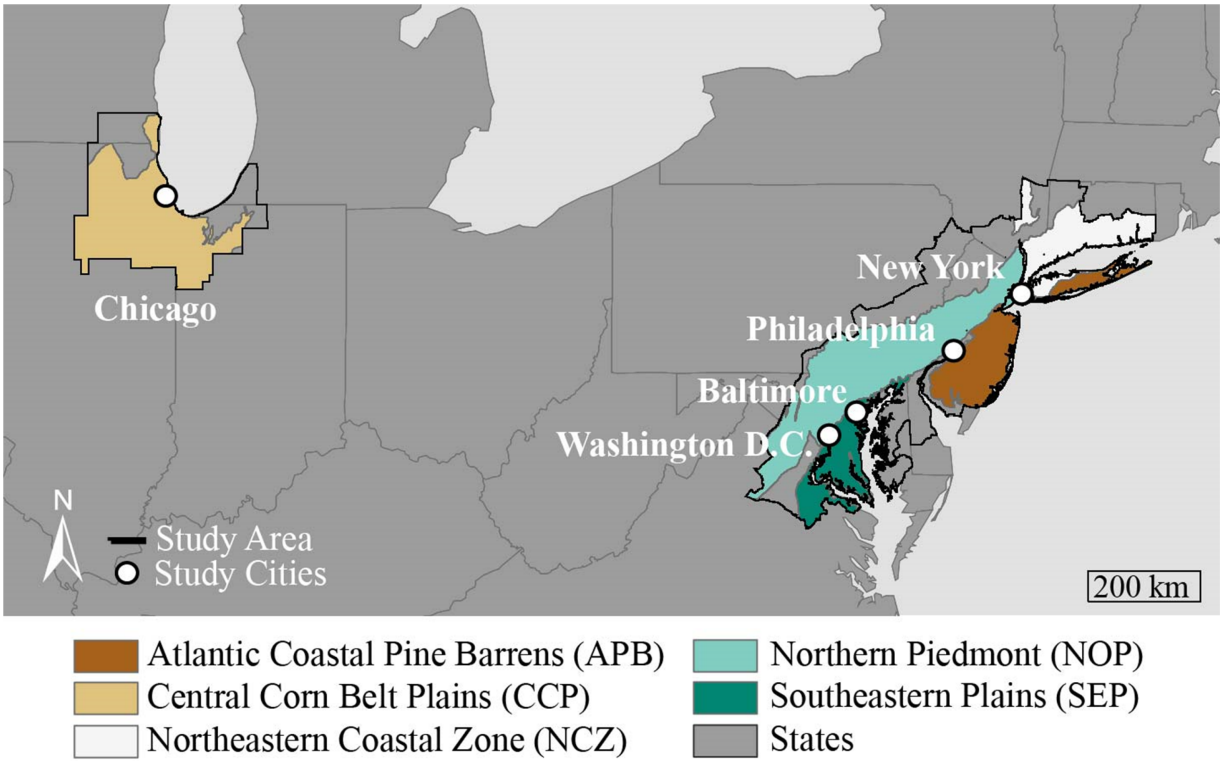

FIGURE 1 Study area, cities, and EPA Ecoregions (Level III) considered in this study.

Forest vegetation

Forest vegetation datasets (Appendix S1: Table S1) included species identification and measurements (dbh) of all trees in randomly located plots of known size that were not subjected to an experimental treatment. Due to our interest in the influence of urban land cover, we made a particular effort to acquire datasets characterizing forest vegetation in highly urbanized settings. We focused this effort on urban forest patches (see definition above; Johnson, Johnson, et al., 2020); therefore, plots sampling street trees and trees located in other urban and agricultural land uses (e.g., mowed parks, residential yards, agricultural fields) were excluded. Some data sources only sampled forested areas, whereas others sampled a range of land covers and uses. To account for this, we only selected plots from each dataset that met our definition of forest (see Appendix S1: Data Sources for criteria for each study). Only data collected after the year 2000 were used, and for studies with repeated visits to the same plots, only the most recent visit was used. Although the USDA Forest Service's Forest Inventory and Analysis program had the most data available, it traditionally has not sampled intensively in urbanized areas, necessitating our use of additional datasets.

Given the large spatial extent of our analysis, we were concerned that the effects of landscape context could be confounded with geographic differences in species composition. To help control for species composition, each plot was assigned to an ecoregion using the EPA's Level III Ecoregions of the United States (Commission for Environmental Cooperation, 1997; Omernik, 1995, 2004; Omernik & Griffith, 2014; Appendix S1: Table S1). Although the study area spanned 14 EPA Level III Ecoregions, many of those ecoregions contained very few plots. Therefore, we subset the data for this analysis to include only the five ecoregions in which the greatest number of plots (3334) were located: the Central Corn Belt Plains (CCP—296 plots), Atlantic Coastal Pine Barrens (APB—415), Northeastern Coastal Zone (NCZ—841), Northern Piedmont (NOP—1349), and Southeastern Plains (SEP—433) along the Atlantic Coast (Table 1).

We used Taxonomic Name Resolution Service Version 5.0 (Boyle et al., 2013) to standardize species taxonomy across datasets. We followed Cornelissen et al. (2003) to assign species to growth forms and included only trees in this analysis. Some input datasets differentiated between trees and saplings based on dbh, but the diameter threshold varied across datasets. Therefore, we chose the largest threshold measurement among all datasets, 12.7 cm dbh, to divide trees from saplings. Some datasets considered individual stems of a multistemmed plant to be separate trees, whereas others treated them as a single tree but recorded data for each stem. For this

TABLE 1 Distribution of forest plots and land area by ecoregion and city.

Ecoregion	City	Area (km^2)	Plots
Northern Piedmont (NOP)	Baltimore–Washington, DC	1,473,734	415
Southeastern Plains (SEP)	Baltimore–Washington, DC	809,719	318
Central Corn Belt Plains (CCP)	Chicago	2,300,361	296
Atlantic Coastal Pine Barrens (APB)	New York City	587,241	190
Northeastern Coastal Zone (NCZ)	New York City	1,048,126	841
Northern Piedmont (NOP)	New York City	455,820	548
Atlantic Coastal Pine Barrens (APB)	Philadelphia	593,846	225
Northern Piedmont (NOP)	Philadelphia	914,377	386
Southeastern Plains (SEP)	Philadelphia	27,381	115

analysis, each stem that met the dbh threshold was treated as an individual tree, including cases where two or more such stems were joined at their base.

Forest plot landscape context

To examine forest characteristics across urbanization intensity and assess consistency across ecoregions, we first needed to define urbanization indicator gradients. Based on an initial exploratory analysis, we determined that percent impervious surfaces within 1 km of a forest plot would serve as our primary urbanization gradient metric (see Appendix S1: Exploratory Analysis of Urbanization Indicators section for further details).

Our initial plan was to contrast impervious surface with canopy cover, which we viewed as an indicator of areas with less urbanization. To quantify the degree of imperviousness in the 1 km surrounding each plot, we calculated the average value of the 2016 National Land Cover Dataset (NCLD, Table 2; Dewitz, 2019) percent developed imperviousness layer. To quantify tree canopy cover, we did the same with the 2016 National Land Cover Dataset (NLCD) tree canopy cover layer. We then plotted percent impervious surface relative to percent canopy cover in the landscapes surrounding forest plots. It was evident that a simple urban-to-forest cover gradient did not adequately capture the variation in landscape context in the vicinity of forest patches. Instead, at any given point along the urbanization gradient, forest plots were surrounded by a mix of tree canopy, cities, sub- and ex-urbia, and agricultural land. Furthermore, the range of canopy and impervious cover was not consistent between ecoregions, but rather some had more intense urbanization than others.

To explore this variation, we examined the land cover proportions in a 1-km buffer around each plot center (Appendix S1: Table S3). We found that after forest cover (NLCD classes 41, 42, 43, and 90; 51%) and developed land (classes 22, 23, and 24, not including developed open space; 18%), agriculture (pasture/hay and cropland, classes 81 and 82; 13%) was the most important land cover across the study area (Appendix S1: Table S4), so we focused subsequent analyses on relationships between these three landscape gradients. We divided the agricultural area based on NLCD classes in the 1-km buffer by the total area of that buffer to calculate the percentage of land that is agriculture around each plot. Hereafter, cover by forest canopy, agricultural, and impervious cover as defined above within the 1-km buffer are referred to as the *landscape context* of a plot (Figure 2).

Because the composition of land cover surrounding forest plots varied widely across ecoregions, a plot's buffer might contain low value in one class (e.g., forest canopy) along with a range of values for other land covers. In order to unambiguously explore associations of the three major land covers with forest vegetation composition and structure, we selected a subset of 993 plots in each ecoregion (APB, 123 plots; CCP, 87; NCZ, 252; NOP, 402; SEP, 129) that fell within the top 10% of values for each landscape context (i.e., agricultural, canopy, and impervious). In no case was a plot in the top 10% of more than one of these land covers. Therefore, for these analyses, forest plots were categorized as belonging to one of the three primary landscape settings, referred to as (1) high-agricultural, (2) high-canopy, or (3) high-impervious settings.

Ecoregion landscape context

Having defined parameters for landscape context at the level of a forest plot, we wanted to determine whether landscape context differed among ecoregions in our study area (Question 1). We used NLCD data to determine the landscape context (land cover within a 1-km radius) for

TABLE 2 Summary of landscape metrics from the National Land Cover Dataset (NLCD) considered in this study.

Measure	Data source	Year	Resolution	Data type	Spatial aggregation	Reference
Impervious	NLCD Impervious	2016	30 m	Continuous raster	Mean impervious %	NLCD, Dewitz (2019)
Canopy	NLCD Canopy	2016	30 m	Continuous raster	Mean canopy %	NLCD, Dewitz (2019)
Agricultural lands	NLCD Land Cover	2016	30 m	Categorical raster	% land covered by agricultural categories	NLCD, Dewitz (2019)

Note: All metrics were aggregated to a 1-km buffer around each forest plot. Agricultural land cover types included crop and pasture.

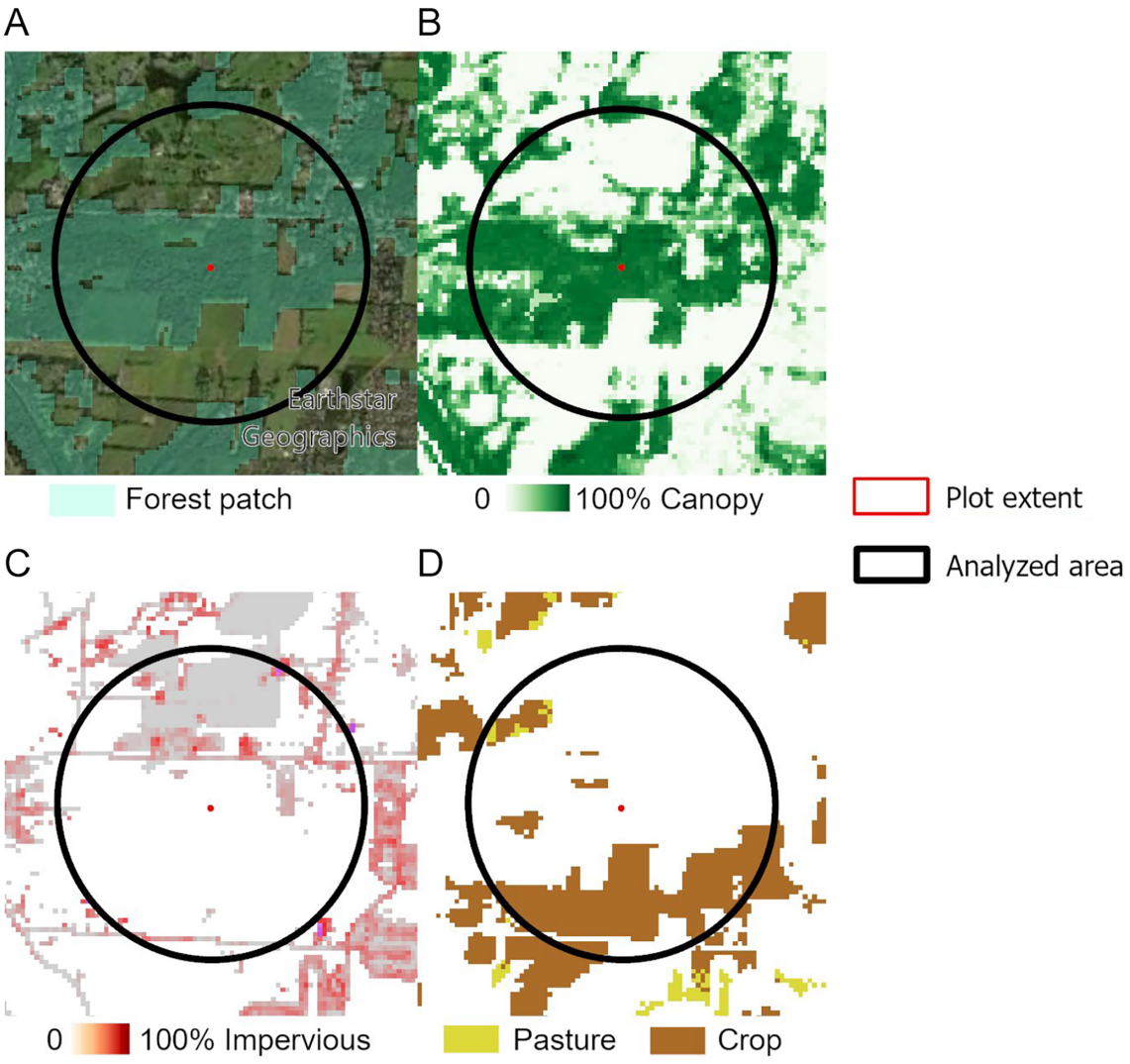

FIGURE 2 Example calculation of landscape context of a forest plot. The red circle indicates the extent of a single forest plot, and the black circle is the area assessed for landscape context. (A) National Agriculture Imagery Program (NAIP) imagery of a sample plot. (B) Percent canopy cover from National Land Cover Dataset (NLCD) Canopy raster. (C) Percent impervious cover from NLCD Impervious raster. (D) Crop and pasture cover from NLCD Land Cover raster. The 1 km around this sample plot has on average 40% canopy cover, 2% impervious cover, and 26% agricultural cover.

every forested pixel that occurred within a forest patch across all ecoregions.

To identify all forest patches in the study area, we used the 2016 NLCD forest canopy layer to create a forest patch layer using a morphological spatial pattern recognition approach (MSPA; Alonzo et al., 2021; Soille & Vogt, 2009; Sonti et al., 2024) within Guido's Toolbox (Vogt & Riitters, 2017). The NLCD canopy layer was reclassified to a binary forested layer, and all pixels with greater than 20% canopy cover were considered

forest. This layer was input into the MSPA, which categorized forest edge, core, and connector using the following criteria: Forest core included all pixels surrounded on all four sides and diagonals by at least one forest pixel, edge included all forest pixels along the perimeter of each group of forest core pixels, and connectors comprised all pixels connected to forest core pixels by an unbroken chain of forest pixels. Pixels that were categorized as core or edge were considered to be a part of a forest patch, and our analysis focused on them. Similarly to the analysis of landscape context around plots, we calculated the percent canopy and impervious cover and percent abundance of agricultural land as described above in a 1-km buffer around each forest pixel using a neighborhood analysis in ArcGIS Pro 3.0 (ESRI, 2022).

Statistical methods

After deriving our landscape context and forest tree vegetation measures, we used a variety of analyses to address our research questions. Differences in landscape context between ecoregions and comparisons between the plot and overall ecoregion landscape context (Question 1) were assessed graphically. We did not perform any statistical analyses for this question as we are interested in differences between entire distributions, rather than in differences in summary metrics, such as means or SDs.

We used ordination and regression analysis to assess the relationships between landscape context and tree communities (Question 2a). Ordination was used to assess community shifts related to landscape setting at the ecoregional level. We conducted nonmetric multidimensional scaling (NMS) ordination on a matrix of plot-level basal area by tree species in each of the five ecoregions. NMS ordinations were performed in PC-ORD v.5.31 (Grandin, 2006) using the "slow and thorough" autopilot setting, which uses 250 runs of real data and 250 Monte Carlo randomizations to assess the robustness of the solution. Permutational multivariate ANOVA (PERMANOVA) was used to test whether species composition differed significantly among landscape settings and was conducted with PC-ORD using the Bray–Curtis dissimilarity measure (McCune & Grace, 2002). Variation in species composition within each landscape setting was compared using the mean dissimilarity among plots in each grouping for each ecoregion.

We used Bayesian linear models to examine the relationship between landscape setting and species diversity and nativity (Question 2b,c), and tree abundance, basal area, and size diversity (Question 3; Table 3). An offset of log plot area was used in the regression models of abundance and basal area. Offset terms are frequently used in generalized linear models to account for differences in sampling effort, such as the variable plot sizes in this study (Kéry, 2010). Size class diversity and species diversity were calculated on a per plot basis using the Shannon index (Shannon, 1948). Size class diversity was calculated by first binning trees into 5-cm dbh classes (e.g., 12.7–17.7 cm, 17.7–22.7 cm) and then calculating a Shannon diversity index (Staudhammer & LeMay, 2001). Nativity was quantified using the proportion of non-native trees as the response variable.

The use of a Bayesian framework allowed us to directly model the effect of landscape setting on both the mean and the variance of each response variable. Models had the general form of:

$$\begin{aligned}\text{Response (or scale parameter)} \sim\ & \beta_0 + \beta_1 \\ & \times \text{landscape setting}_i + \beta_2 \times \text{ecoregion}_j + \beta_3 \\ & \times \text{landscape setting}_i \times \text{ecoregion}_j + \log(\text{PlotArea}_k) \\ & + (1|\text{Protocol}_k) + \varepsilon_{ijk}\end{aligned}$$

where landscape setting is a categorical variable indicating whether a plot is in a high-agricultural, high-canopy, or high-impervious setting and ecoregion is a categorical variable indicating the EPA level III ecoregion. Protocol is a categorical variable indicating the data source of the vegetation data (e.g., FIA, National Park Service) that is used as a random intercept to account for any differences

TABLE 3 Regression models.

Response	Error distribution	Offset	Additional parameters
Question 2b: Shannon index on tree species diversity	Gaussian	None	Sigma
Question 2c: % non-native trees	Zero–one inflated beta	None	Phi, zoi, coi
Question 3a: Count of trees per plot	Negative binomial	Mean, shape	Shape
Question 3a: Total basal area per plot	Gamma	Mean	Shape
Question 3b: Shannon index on tree size	Gaussian	None	Sigma

Note: Statistical details for the Bayesian linear models for each question.

between sampling protocols that were not eliminated during the data standardization process. ε is an error term.

The choice of error distribution and the additional parameters modeled varied depending on the data. Modeling the associations between landscape cover class and ecoregion on the scale parameters allowed us to examine how these factors influenced the variance as well as the mean of the response variables. Note that in addition to the scale parameter *phi*, the zero–one inflated beta distribution has two additional parameters: *zoi*, the probability that 0% or 100% of the trees on a plot are non-native, and *coi*, which indicates the probability that a plot has 100% non-native trees, given that either all or none of the trees are non-native. These were fit using the same model as the shape and scale parameters above.

For each response variable, we fit a single model, including data from all five ecoregions. This approach had the benefit of producing more realistic estimates of the random effects of protocol, as several protocols were used in multiple ecoregions. The variances were allowed to differ by ecoregion and cover class category so that could test whether the landscape setting influenced the variability of the response variables.

Models were fit using the brms 2.16.1 (Bürkner, 2017, 2018) interface to Stan 2.29 (Stan Development Team, 2019) in R 4.1.1 (R Core Team, 2023). Default priors were used, with the following exceptions: (1) for all models, the prior for the random effect of protocol had a student_t (20,0,0.5) distribution; (2) for the analysis of basal area and Shannon indices, the prior for the mean was a normal (0,1) distribution; (3) for the analysis of % non-native trees, the mean, *coi*, and *zoi* had a normal (0,3) prior, and *phi* had a student_t (3,0,2.5) prior. Each model was fitted using four Markov chain Monte Carlo (MCMC) chains of 10,000 steps with a warm-up of 1000 steps. Default settings were used except that adapt_delta was set to 0.99.

After fitting the models, we checked for convergence using trace plots and verifying that the point scale reduction factor (R-hat, Gelman & Rubin, 1992) was less than 1.05; in all cases, they were 1.00. Model fits were assessed using graphical posterior predictive checks. These included comparison of the actual and predicted distribution of the response variable and scatterplots of the actual and predicted mean and SD of the response.

We determined the effects of landscape setting by using the brms hypothesis function to query the MCMC chains. Variances were calculated from the models using the standard methods for each distribution. We considered the mean or variance to be significantly different between two landscape settings if 95% of MCMC steps were higher or lower in one landscape setting than another.

We only conducted hypothesis tests for outcomes within individual ecoregions (see above list of research questions), as differences between ecoregions were not the focus of the study.

RESULTS

Landscape context

Landscape context of forests differed among ecoregions (Question 1; Figure 3, Forest Pixels). Agricultural cover was a more common part of the landscape contest for forests in the CCP and NOP ecoregions. Canopy cover was less common in the landscape context of the CCP than in other ecoregions. While impervious cover was relatively rare in the landscape contexts, it was particularly so in the SEP.

The landscape context of the forest vegetation sampling plots was similar to that of forest pixels across the ecoregions in which they were found, with some systematic differences (Figure 3, All Plots). Consistent with our focus on acquiring data for urban forest patches, the distribution of impervious land cover surrounding plots (All Plots) was higher than that of forest pixels in their ecoregion, but to a lesser extent in the APB. Conversely, landscapes surrounding all plots had a lower distribution of agricultural cover than forest pixels in their ecoregion, except in APB. Canopy cover surrounding all plots was similar to that of forest patches, with the exception of the NCZ, where plot distributions skewed lower than those of forest pixels. Forest plots in contexts with high values of one of the three major land covers (Figure 3, Analyzed Plots) often had heterogeneous landscape context, with over one-third of their 1-km buffer composed of other land cover types in addition to the three predominant ones.

The landscape context of plots in each of the three landscape settings was distinct (clustered graphically in Figure 4) although important differences can be seen between ecoregions. For example, plots in high-impervious settings varied in maximum percent of impervious cover (53% in SEP to 73% in CCP and NCZ) and in the amount of surrounding canopy cover (as low as 0% in CCP to as high as 36% in APB). Across all ecoregions, plots in high-impervious settings consistently had very little (<10%) surrounding agricultural cover.

Plots in high-agricultural settings in CCP had a higher proportion of agricultural cover surrounding forest plots than in the other ecoregions (>75%; Figure 4). Compared with CCP, the highest agricultural cover in the surrounding landscape was much lower in NCZ (range 5%–43%) and SEP (range 21%–46%) and extremely variable in APB (range 33%–82%) and NOP (range 49%–91%). In most ecoregions, plots in high-agricultural settings were contextually distinct from the other two settings, whereas in NCZ, which had the

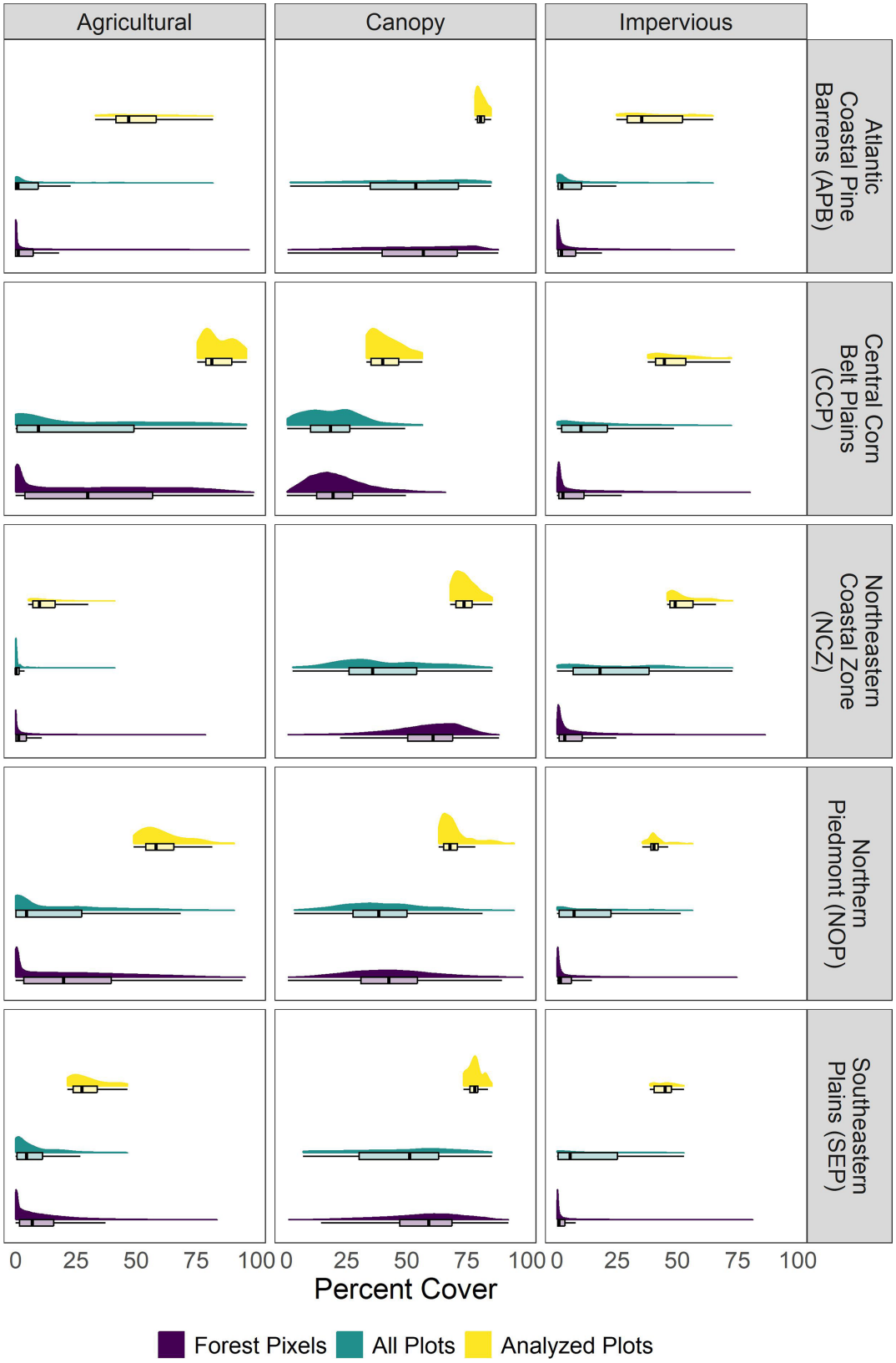

FIGURE 3 Land cover within each ecoregion. "Forest Pixels" show the distribution of each land cover within a 1-km radius around every morphological spatial pattern recognition approach (MSPA)-derived forest pixel in our study area. "All Plots" shows the land cover within a 1-km radius of each forest plot ($n = 3334$) whereas "Analyzed Plots" shows the land cover within a 1-km radius of the 993 plots with the top 10% of values for each cover type. Ecoregions differed in the distributions of their landscape context (see text). Forest plots generally captured the range of variation seen within each ecoregion.

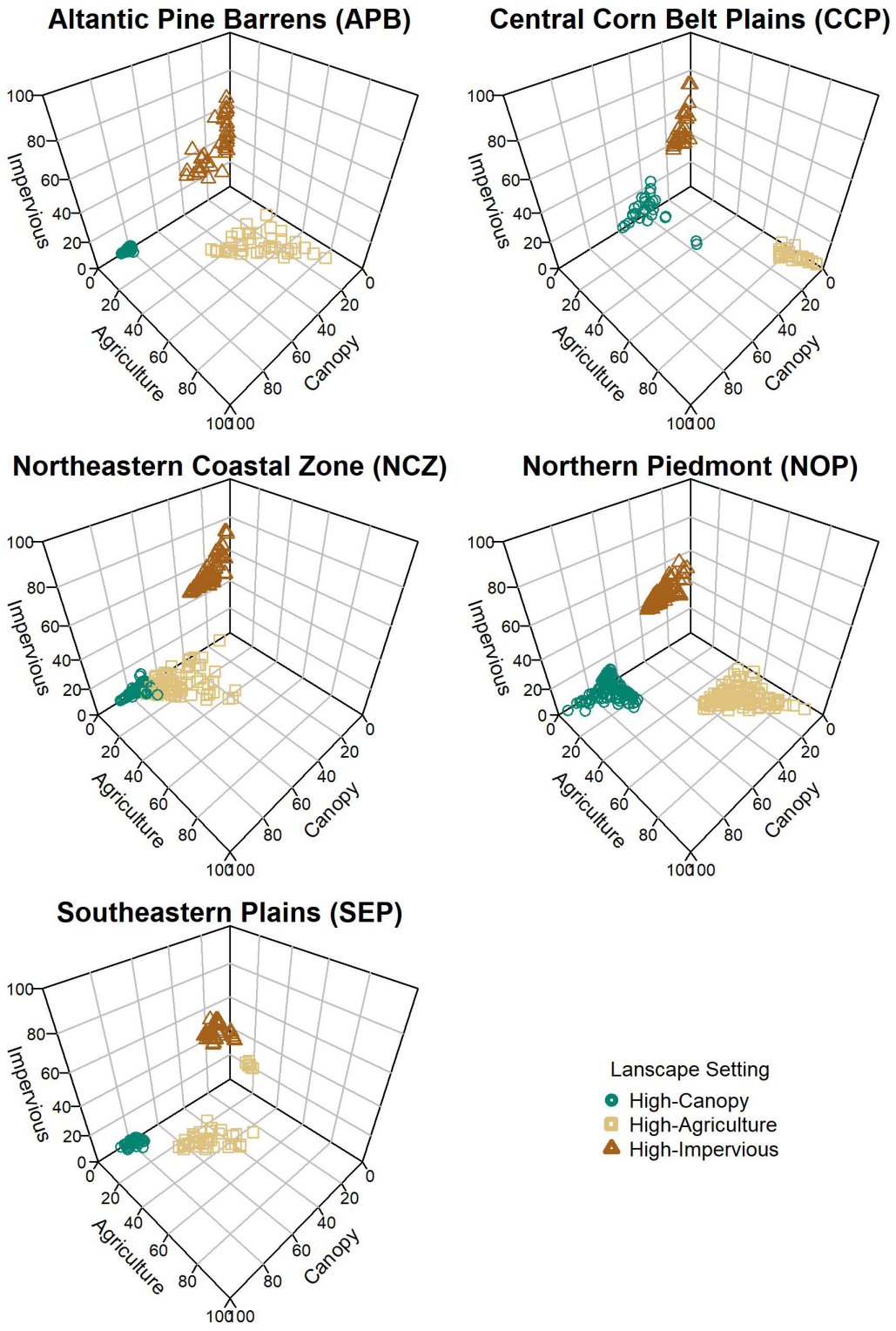

FIGURE 4 Proportional cover of 1-km buffers surrounding selected forest plots with the top 10% of ecoregional values for forest canopy, agricultural land, and impervious surface.

least agricultural cover, they clustered with plots in the high-canopy setting. Canopy cover in high-agriculture settings was consistently low in the highly agricultural CCP ecoregion (range 0%–11%), but in other ecoregions typically exceeded 25% (range 4%–73%). Across all ecoregions, impervious cover surrounding plots in high-agricultural settings was 12% or less, with the exception of six plots in SEP with approximately 30% impervious cover.

Plots in high-canopy settings were more consistent in terms of landscape context, both within and among ecoregions. Other than in CCP, these forests were surrounded by 63%–95% canopy cover, less than 10% agricultural land, and less than 13% impervious cover. CCP had many high-canopy setting plots with less than 50% canopy (range 33%–57%) and up to 22% impervious cover and 39% agricultural cover in the surrounding landscape.

Tree community composition

In all five ecoregions, species composition of tree communities in plots in high-impervious settings were relatively distinct from the other two classes as illustrated by separation in ordination space in NMS analysis (Figure 5) and quantified based on PERMANOVA (see below). In three of the ecoregions (APB, CCP, NCZ), the high-impervious setting cluster was diffuse, indicating considerable compositional variation among plots. In the remaining two ecoregions (NOP, SEP), the plots in high-impervious surface settings were somewhat more tightly clustered. Although this pattern was consistent across ecoregions, the difference in community similarity among contexts was especially stark in the APB and CCP regions, where there was especially low similarity among plots in the high-impervious setting. There was much greater within-context community similarity in the high-canopy areas than in the high-impervious or high-agricultural settings across ecoregions (Table 4).

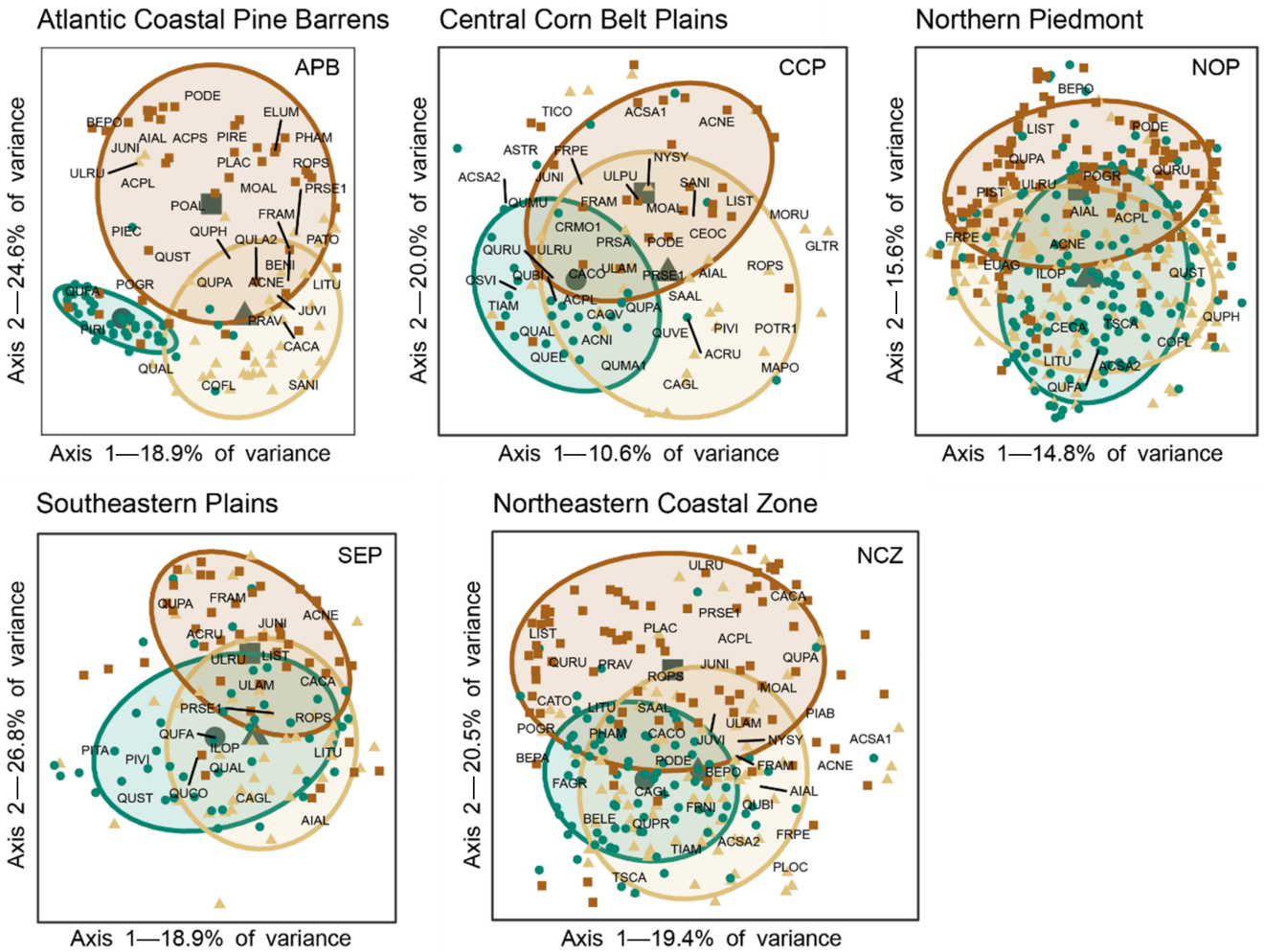

FIGURE 5 Similarity of tree community composition in forest plots in high-impervious (brown), high-agricultural (yellow), and high-canopy (green) settings by ecoregion. Ellipsoids encapsulate 75% of points, symbols illustrate centroids of different landscape contexts groups, and species associations are represented by four-letter species acronyms. The selected nonmetric multidimensional scaling (NMS) solutions had final stress values of APB, 20.7; CCP, 22.7; NOP, 24.0; SEP, 21.3; and NCZ, 25.3; and all solutions were significant based on Monte Carlo tests ($p < 0.01$). The full NMS solution explained the following levels of variance in the original data matrices: APB, 56.6%; CCP, 46.9%; NOP, 44.2%; SEP, 64.0%; and NCZ, 58.0%; and values associated with individual axes are indicated.

Tree community similarity between plots from high-canopy and high-agricultural settings was not consistent across ecoregions. In APB, high-canopy communities clustered distinctly, indicating high compositional dissimilarity in tree composition from agricultural settings. In NOP, NCZ, and SEP, however, communities in high-canopy and high-agricultural settings overlapped almost entirely in ordination space, while in CCP, there was a lesser degree of overlap. Visually, the degree of community separation in NMS ordination (Figure 5) was similar to the landscape context pattern (Figure 4). PERMANOVA indicated that species composition differed significantly across landscape settings in all five ecoregions, but there was variation in the degree to which landscape setting predicted variance in species composition among plots (Table 4). In general, the proportion of variance explained by landscape setting was relatively low, peaking at 18% in the APB ecoregion. Analysis of within-landscape-setting similarity among plots indicated that high-canopy plots had lower dissimilarities, particularly in the APB ecoregion, whereas plots in high-agricultural or high-impervious landscape settings tended to exhibit greater compositional variability (Table 4).

Native and non-native tree species

Forest plots in high-canopy settings consistently had a significantly lower proportion of non-native tree stems (1%–2%) and lower variance in proportion of non-native stems than plots in high-agricultural (3%–8%) and high-impervious settings (6%–30%; Figure 6; Appendix S1: Tables S5 and S6). In contrast, forests in high-agricultural and high-impervious settings had similar proportions of non-native tree stems. In two ecoregions, APB and NCZ, plots in high-agricultural settings had a significantly lower proportion of non-native trees (APB 8% vs. 30%, NCZ 3% vs. 26%) and lower variance (APB 0.06% vs. 0.18%, NCZ 0.01% vs. 0.13%) than plots in high-impervious settings.

Tree species diversity

In most ecoregions, forest plots in high-canopy settings had significantly greater species diversity than those in high-agricultural and high-impervious settings (Figure 6; Appendix S1: Tables S5 and S7). There were no significant differences in diversity between plots in high-agricultural and high-impervious settings, except for APB where diversity was higher in the high-agricultural setting. There were also no significant differences in the variance in diversity (Shannon index variance) among plots in different landscape contexts, other than a high variance in the canopy setting in NCZ, a lower variance in high-agricultural than in high-canopy settings in NOP, and a greater variance in the high-impervious than in high-agricultural settings in SEP (Figure 6).

Forest structure

In all ecoregions, the mean tree density (Figure 7; Appendix S1: Tables S8 and S9), mean basal area (Figure 7; Appendix S1: Tables S8 and S10), and mean size class diversity index (Figure 7; Appendix S1: Tables S8 and S11) of plots in landscapes with high canopy cover were equal to or significantly greater than those in high-agricultural and impervious settings. Overall, there were few differences in these structural parameters between forest patches in high-agricultural and high-impervious settings, except that forests in the high-agricultural setting in NCZ had greater mean tree density and tree size diversity, whereas plots in the high-impervious setting in NOP had greater mean basal area.

Variances in density and basal area were equal across all three settings, with the exception of a greater variance in tree density in high-agricultural than in high-canopy settings in CCP, lesser variance in tree density in high-impervious settings in NCZ, a greater basal area variance in high-agricultural than in high-canopy settings in

TABLE 4 Results of analysis of community similarity using Bray–Curtis dissimilarity within landscape settings and separation of community composition among landscape settings within ecoregions using permutational multivariate ANOVA.

Ecoregion	Canopy	Agricultural	Impervious	*F*	df	*p*	Percentage variance
Atlantic Coastal Pine Barrens (APB)	0.616	0.896	0.945	10.132	2, 20	0.0002	18.216
Central Corn Belt Plains (CCP)	0.782	0.916	0.929	4.218	2, 84	0.0002	9.987
Northeastern Coastal Zone (NCZ)	0.778	0.838	0.904	12.086	2, 249	0.0002	11.659
Northern Piedmont (NOP)	0.833	0.921	0.852	12.871	2, 399	0.0002	8.138
Southeastern Plains (SEP)	0.803	0.812	0.834	4.277	2, 126	0.0002	7.081

Note: The *p* values are based on 5000 bootstrap replicates.

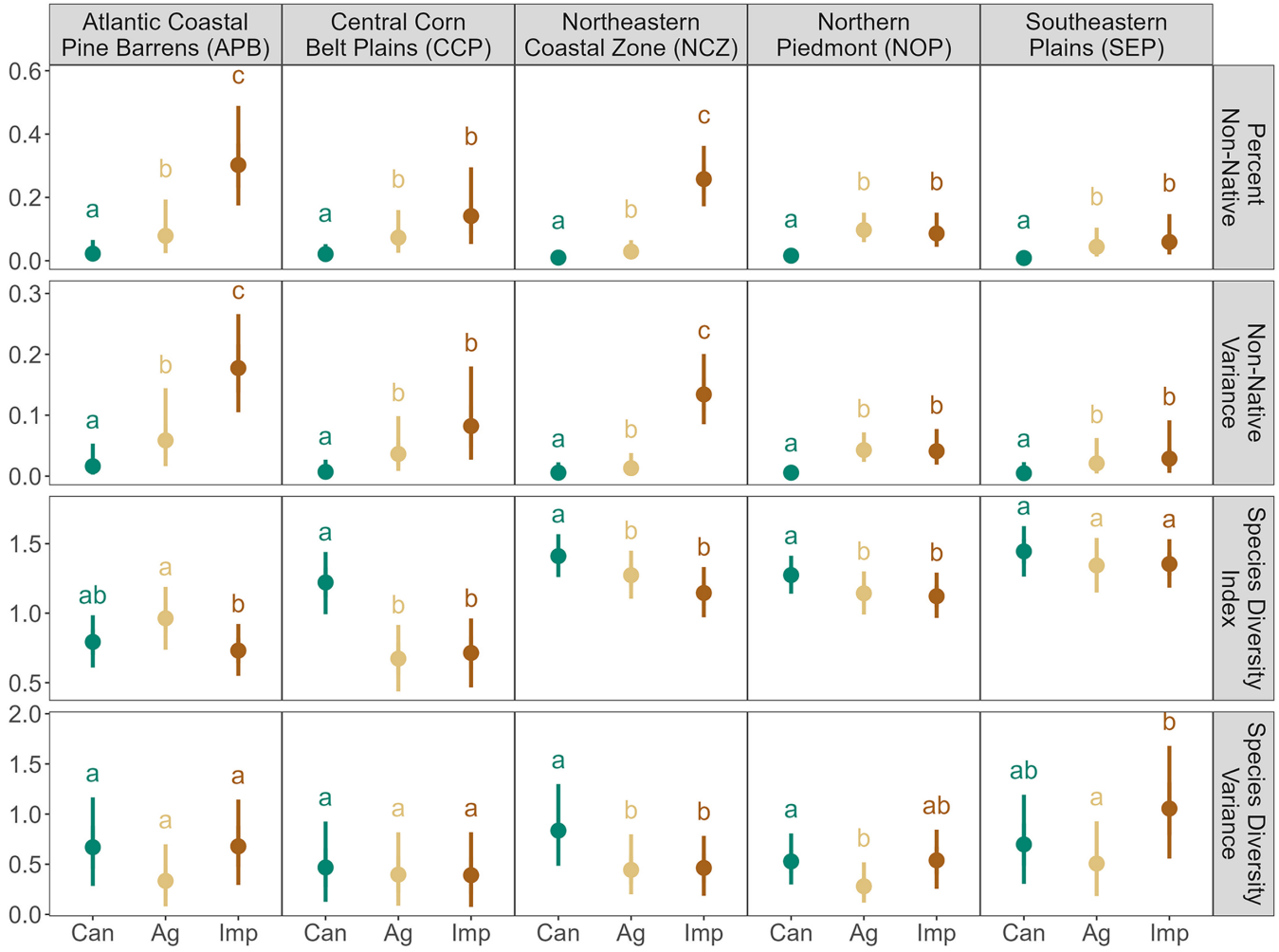

FIGURE 6 Forest composition. Mean and variance of percent non-native stems and species diversity of forest plots in high-agricultural, high-impervious, and high-canopy settings by ecoregion. Different letters indicate significant differences within an ecoregion. Points, mean values; lines, 95% credible intervals. Ag, high-agricultural setting; Can, high-canopy setting; Imp, high-impervious setting.

APB, and a greater basal area variance in high-impervious than in high-canopy settings in NCZ. Plots in high-canopy settings had higher variance in tree size diversity in all ecoregions, except in NCZ where there was no significant difference between high-canopy and high-agricultural settings, and in NOP where there was no difference between high-canopy and high-impervious settings. High-agricultural and high-impervious settings had similar variances in tree size diversity, except that in NOP the high-impervious setting had a significantly higher variance.

DISCUSSION

This synthesis of forest vegetation and land cover data across major metropolitan areas of eastern North America is the first to examine relationships between landscape context and indicators of forest health in multiple regions and to simultaneously consider multiple land cover types. We examined patterns and drivers of an underexplored dimension of urban biodiversity—forest patches—about which there is a scarcity of information to support management decision-making. Our findings have implications for the management of forest patches in landscapes under intensive human use, from cities to farmlands.

Our analysis revealed that ecoregions had distinct land cover signatures and that forest patches were surrounded by heterogeneous land cover. Forest tree community composition and structure across four metropolitan areas and five ecoregions conformed to neither a linear gradient of urbanization nor canopy cover, but rather varied in relation to surrounding agriculture and to other land covers.

By simultaneously considering gradients of canopy cover, impervious cover, and agricultural land, we found

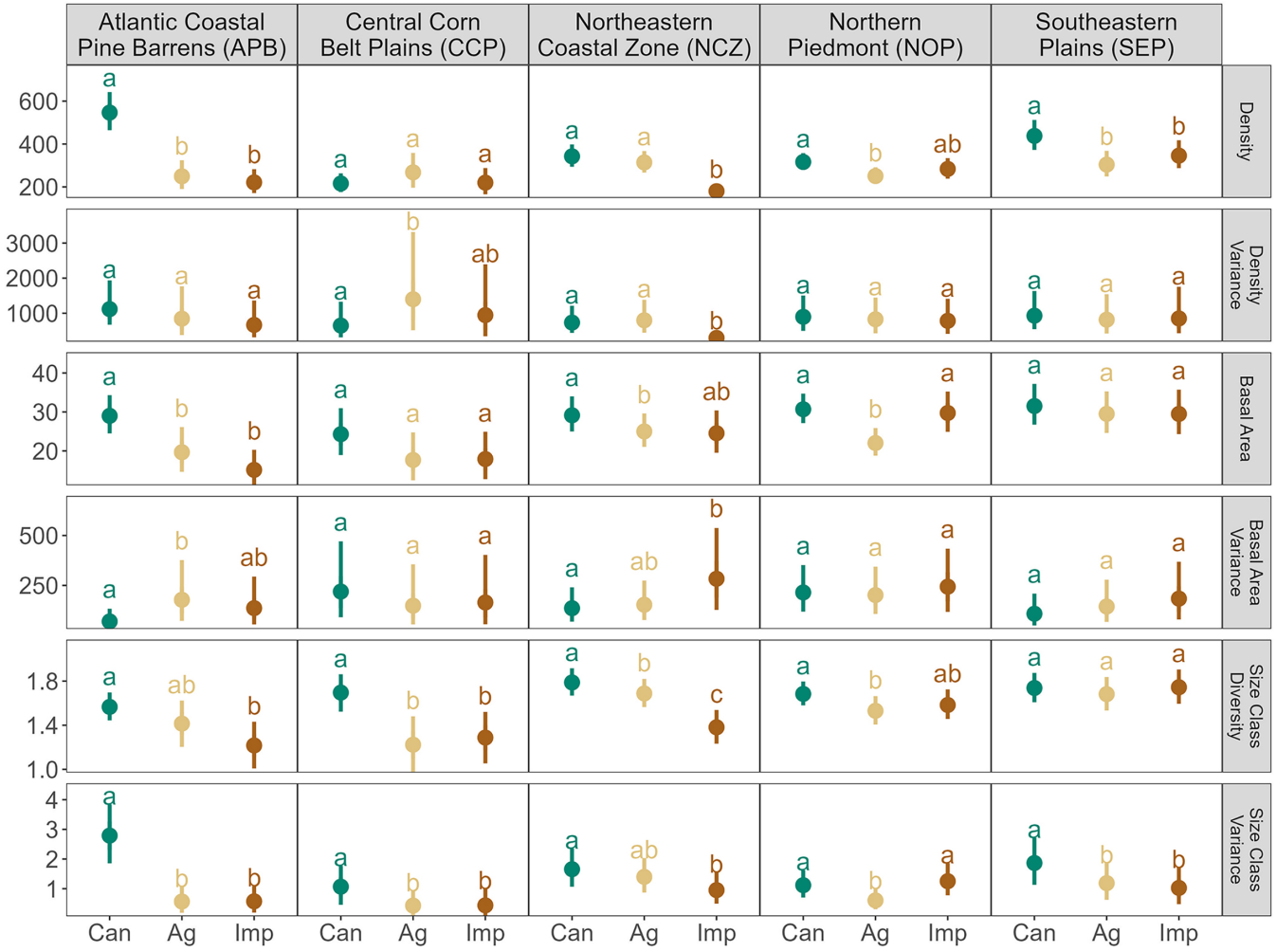

FIGURE 7 Forest structure. Mean and variance of tree density (in number of trees per hectare), basal area (in square meters per hectare), and size class diversity of forest plots in high-agricultural, high-impervious, and high-canopy settings by ecoregion. Different letters indicate significant differences within an ecoregion. Points, mean values; lines, 95% credible intervals. Ag, high-agricultural setting; Can, high-canopy setting; Imp, high-impervious setting.

potentially important relationships between landscape context and tree communities in forest patches. Forest patches in highly impervious landscapes were compositionally different from their counterparts embedded in highly agricultural or high-canopy landscapes. Despite differences in land cover among ecoregions, forest patches in high-canopy settings had species diversity, tree density, basal area, and size diversity equal to or greater than those within high-agricultural or high-impervious landscape settings. In contrast, there were few structural differences and similar levels of diversity among forests in high-agricultural and high-impervious settings. Lower species diversity, basal area, and size class diversity combined with greater non-native tree abundance in both high-impervious and high-agricultural settings highlight commonalities between these intensively anthropogenic landscapes.

The fact that these patterns repeated across ecoregions implies that similar drivers may be at work despite differences in species identities and regional physiography. This may have as much to do with legacies of past land use and related socio-environmental factors as with modern land cover classes. In both urban and agricultural landscapes, differences in forest structure and dampened ecoregional diversity indicate common signals of impaired forest health and shared opportunities for forest stewardship. Previous research in these cities (Morzillo et al., 2022) demonstrates that new ecological understanding has led managers to modify ecological goals and develop new constituency building with local stakeholders. Landscape context may constrain management options, but increasing collaboration and communication among land managers facing similar challenges across the urban to rural gradient may lead to improved outcomes and new understandings. By considering landscape context when confronting conservation challenges, forest

managers can develop more realistic goals for management action.

Landscape context

These data encompass variation in landscape contexts of forested natural areas across an urban–rural gradient, yet those landscapes could not be described neatly by gradients of impervious surface or canopy cover. Instead, forest patches were surrounded by a heterogeneous mix of land covers in both urban and rural landscapes at a local, 1-km scale. This finding aligns with recent work describing urban landscape typologies in New England (Kaminski et al., 2021) and with single-city studies of landscape context that emphasize within-city landscape heterogeneity (Godefroid & Koedam, 2007; Pickett et al., 1997, 2017).

Broader regional landscape patterns are also important. For example, agricultural land is a major component of forest context in some ecoregions—such as the CCP, where forests were surrounded by up to 95% agricultural land—but a minor component elsewhere (e.g., NCZ, where the maximum proportion of agricultural cover was only ~50%). Conversely, canopy cover often made up over 50% of the landscapes surrounding forest plots in ecoregions other than CCP. The drivers of these patterns may include differences in social-ecological factors such as the distribution of useful natural resources, suitability of land for agriculture, and the timing of social and land use change (Grove & Burch, 1997). These patterns may derive from historical factors such as the role of abandoned agricultural land in Eastern forest succession and more recent urbanization of areas that were previously wooded or agriculture in the Midwest, as during the massive, national-scale suburbanization that followed WWII (e.g., Boone et al., 2010; Lowry et al., 2012). Other research has suggested that land cover change can be particularly dynamic in suburban areas (Zhou et al., 2011) and that agricultural land use history can have important effects on forest vegetation and soils (Kelly & Ray, 2023). Our findings indicate the important integrated role of local and biophysical drivers of land cover variation among and between ecoregions (e.g., climate, topography, soils) as well as geographical and historical socio-ecological interactions at regional scales when examining relationships between urbanization and ecological systems.

Tree community composition and diversity

Local native tree species of each ecoregion were found in forest plots across all major land cover settings. These species were most strongly associated with high forest canopy contexts, yet they were also found in forest patches of urban and agricultural landscapes. This finding indicates that despite high proportions of non-native stems in urban and agricultural forest patches, forest canopies across landscape settings are maintaining their ecoregional distinctiveness.

At the same time, the composition of tree communities in high-impervious settings had limited overlap with those in high-agricultural and high-canopy settings within the same ecoregion (Figure 5), indicating a distinct influence of urbanization on forest tree communities across ecoregions. Differences in urban forest composition may be linked to myriad interacting factors deriving from human activity inherent in urban areas, including pollution, urban warming, current land use, species introductions, distinct choices by humans, disturbance frequency and successional stage, policy and planning, landscape history, and fragmentation (Johnson, Johnson, et al., 2020). For example, in Chicago, current tree communities vary based on pre-settlement vegetation patterns and historic land use (Fahey et al., 2012).

Non-native species are often associated with highly urbanized landscapes (Aronson, 2007; Aronson et al., 2015; Blood et al., 2016; Nock et al., 2013; Pennington et al., 2010; Steenberg, 2018; Wang et al., 2020). We found that while approximately 80% of tree stems in forest patches in high-impervious settings belonged to native species, these urban forest patches also had the greatest density of non-native tree stems. The higher density of non-native stems we observed in high-impervious settings aligns with recent studies of forest patches in urban regions (Alonzo et al., 2023; Baker et al., 2025; Johnson, Trammell, et al., 2020; Pennington et al., 2010; Piana, Hallett, Aronson, et al., 2021; Pregitzer et al., 2019; Trammell et al., 2020). These studies also suggested that forest understories may be dominated by non-native invasive shrubs or creeping vines and that regenerating trees may result in different future forest canopies (Baker et al., 2025; Johnson & Handel, 2016; Piana, Hallett, Aronson, et al., 2021; Trammell et al., 2020; Trammell & Carreiro, 2011).

Although plots in high-impervious and high-agricultural settings had more non-native stems and greater compositional variation between plots (beta diversity; Figure 5), plot-level species diversity (alpha diversity) was not greater than in high-canopy settings. Lower urban plant diversity has been reported in annual herbs in Shanghai (Wang et al., 2020) and in North American trees (Nock et al., 2013), but these studies compared a variety of urban land uses, including forests to exurban ones and did not focus solely on urban forest patches. Our contrasting results support forest patch tree diversity being influenced by an interaction between land cover and scale such that the effects of land

cover may vary depending on the scale of the analysis (Danneyrolles et al., 2021).

Many trees found in urban environments thrive in disturbed, fragmented, and high-light environments, including globally introduced species like *Acer platanoides* and *Ailanthus altissima*. In our study area, native species of highly urban contexts included fast-growing ruderal species (e.g., *Acer negundo*), wind- and bird-dispersed pioneer species (e.g., *Liquidambar styraciflua*, *Acer rubrum*, *Prunus* spp.), and species that do well in high-nutrient environments (e.g., *Ulmus* spp., *Juglans* spp.). Riparian tree species frequently planted as street trees (e.g., *Quercus palustris*, *Populus deltoides*) as well as some mesophytes mentioned above were also associated with high-impervious settings. Similar results have been reported from studies of urban forests more broadly—including for street trees (Nock et al., 2013; Pennington et al., 2010). Such outcomes suggest propagule flow from planted species into forest patches (Tartaglia et al., 2018) and emphasize that species tolerant of high levels of ecological disturbance are successful in urban environments. The prevalence of riparian species may also indicate a relatively high proportion of stream and riverine forests in urban environments due to the poor suitability of these areas for development.

As in urban environments, species associated with agricultural landscapes in our study plots included fast-growing, shade-intolerant, bird- and wind-dispersed, and riparian trees, suggesting that young forests resulting from frequent disturbance and land use change are shaped by intensive human activity in both urban and agricultural systems. In contrast, native trees with heavy, animal-dispersed seeds such as oaks and later-successional shade-tolerant species characterized plots in forest patches in high-canopy settings. These species included late-successional canopy species often associated with drier environments, such as *Quercus* spp. in all ecoregions, as well as mesic *Fagus grandifolia* and *Acer saccharum*.

Ecoregions differed in the degree of tree community similarity among major land cover settings, and the greatest differentiation occurred in the high-canopy setting of the Atlantic Pine Barrens, where a distinct local flora is supported by sandy soils over a large area. In this ecoregion, urban development has concentrated in more fertile areas proximal to river floodplains that support more mesic species. Furthermore, land conservation efforts may also be reflected in these patterns. Much of the APB in New Jersey was conserved by the establishment of the Pinelands National Reserve in 1978 and the NJ State Pinelands Protection Act in 1979, resulting in over 445,000 conserved ha (1.1 million acres; NJ Pinelands Commission, 2023). Tree community composition of forests in high-agricultural settings more closely resembled that of their associated high-canopy settings when there was a low proportion of agriculture in the landscape (lowest agricultural maxima; NCZ, SEP), as compared with ecoregions with higher agricultural maxima (e.g., forests isolated in crop fields vs. a matrix of crop and forest patches in the CCP).

Forest structure

Forest structure corresponded to land use in a generally consistent manner across ecoregions. Plots in high-canopy settings typically had higher tree density, basal area, and tree size diversity—indicating a tree community more likely to have a diverse age structure—than plots surrounded by agricultural or urban land covers within the same ecoregion. These differences were less pronounced between the high-canopy and high-agricultural settings in NCZ and SEP, which lacked plots with a high proportion of agriculture in their landscape context. The impacts of structural diversity on ecosystem function are poorly understood (Ali, 2019), but in temperate forests, high structural diversity has been associated with higher aboveground carbon storage (Fotis et al., 2018; Yuan et al., 2018) and higher species richness (Bohn & Huth, 2017). Changes in forest structure may therefore be one of the ways by which urbanization and agricultural land use alter ecosystem function.

Similar results have been found in single-city studies by Styers et al. (2011) who found that urban forest patches in the Georgia Piedmont had a lower hardwood density than more rural forest patches, and in Massachusetts (Reinmann et al., 2020; Reinmann & Hutyra, 2017), rural forests had a higher tree basal area. Nock et al. (2013) also found lower stem density in urban forests than in forests outside of cities across seven metropolitan regions, although this effect was smaller in spontaneous forests than in planted street and park trees. However, not all studies of urban forests have found similar conclusions. Urban oak-hickory forests in New York have a higher tree basal area than protected rural forests (Piana, Hallett, Aronson, et al., 2021), and forests in the wildland urban interface have a higher aboveground biomass and stem density than forests outside of the wildland urban interface (Sonti et al., 2023). Fahey et al. (2012) found that the basal area in urban forests in Chicago reflects both current and historical land use.

While surrounding land use is one way in which forest patches differ between rural and urban areas, other factors have also been shown to influence forest structure. Theoretically, forest patches in low-canopy cover settings are likely to be more isolated and therefore

be more influenced by edge effects (Collinge, 1996). Recent work has compared tree demographics between forest edges and interiors. Compared with interiors, forest edges—where light availability, temperature, wind, nitrogen deposition, and water availability are altered—can have similar mortality rates and higher stem densities, growth rates, and basal areas (Morreale et al., 2021; Reinmann et al., 2020; Reinmann & Hutyra, 2017). At the same time, numerous studies examining the impact of edge on vegetation have found that among other effects, tree mortality and windthrow are higher near edges (reviewed in Franklin et al., 2021). Furthermore, trees near forest edges in our study area are more likely to be colonized by climbing vines, and once colonized, those trees are more likely to die once the vines reach the crown of the tree (Baker et al., 2025; Matthews et al., 2016).

Additionally, tree mortality and recruitment rates can be altered in urban forest patches. For example, mortality rates in Baltimore (5.9%, Nowak et al., 2004) have been shown to be higher than in forests in nonurban areas (1.3%–2.1% outside of Front Royal VA, Gonzalez-Akre et al., 2016; <2.5% based on eastern FIA data, Lines et al., 2010). Piana, Hallett, Aronson, et al. (2021) found that in New York City, early establishment barriers for seedlings were higher in urban areas than in rural areas, but that once established, transitions to the sapling stage may occur at higher rates in urban environments. Changes in these rates can lead to long-term regeneration debt (Miller & McGill, 2019).

Implications for forest patch management

1. A single linear urban gradient does not explain patterns in forest structure and composition.
   Ecoregions vary in their land cover composition. Canopy cover at the local scale does not necessarily increase as urbanization decreases—or vice versa. Agriculture is a key component of landscapes. It is critical to consider the heterogeneity of the landscapes surrounding both urban and rural forests, the interspersion of different land development and land covers across urban areas, and of the social and ecological drivers of landscape pattern and forest structure and composition at ecoregional scales.
2. Forests in intensively urbanized areas have distinct tree community assemblages.
   with more non-native trees. Studies that have documented non-native species to be more abundant in urban areas have examined the broad urban flora—including street trees, vegetation of yards, and other managed landscapes. This study suggests that there is a flow of introduced species into spontaneously occurring urban forests. Managers of urban forest patches must contend with a legacy of past introductions and propagule flow from the surrounding landscape. They can also expect future species introductions.
3. Urban forests are more like rural forests than might be expected.
   The composition and structure of urban forest patches are more like native forests of their ecoregion when they are surrounded by more canopy. Most urban forest patches are too small to fill 75% of a 1-km circle—the typical cover for high-canopy plots. However, this may not be true of the interior of large parks in urban and suburban settings, such as the Cook County Forest Preserves of Chicago, Rock Creek Park in Washington DC, and Van Cortlandt Park in New York City. Forest patches across the urbanization spectrum can be evaluated as potentially high-quality forests and could be prioritized for forest conservation and restoration efforts.
4. This study provides rationale and support for collaboration among forest managers across intensively used landscapes.
   Managers of urban, exurban, peri-urban, and rural forests face common challenges because intensive landscape transformations have similar implications for forest health. Forest patches in urban and agricultural landscapes share communities that are predominantly native, but with more non-native trees, young trees, and species adapted to disturbance. They share frequent and intense disturbances, such as forest clearing followed by abandonment. At the same time, forests across these intensively used landscapes can serve as reservoirs of native biodiversity and sources of propagules for regeneration and restoration.
   Care should be taken when comparing urban forests with rural ones for the purpose of selecting a baseline or target for urban forest management. Forest size and age influence many structural characteristics, while differences in species composition reflecting tolerance of urban conditions in soils, climate, and disturbance may limit the usefulness of rural forest composition for use as a benchmark or goal. Comparison with less-disturbed forests can, however, give valuable insight into what might be possible, what might be missing, and why.
   Collaboration among researchers and practitioners across ecoregions may facilitate development of knowledge and effective practices to preserve and restore forest biodiversity. Initiatives like the Northeast Urban Silviculture Network (Piana, Pregitzer, et al., 2021), the Forests in Cities network

(Charlop-Powers et al., 2020), and similar efforts to bring together urban and rural community forestry (Sullivan, 2022) are important steps in this direction.

AUTHOR CONTRIBUTIONS

All authors participated in conceiving and designing the manuscript, conceptualizing the model, and reviewing the manuscript. Lea R. Johnson and Michelle L. Johnson conceived and supervised the SESYNC pursuit. Dexter H. Locke, John Paul Schmit, Lindsay Darling, Lea R. Johnson, Matthew Baker, Nancy F. Sonti, Robert Fahey, and Tara L. E. Trammell participated in data collection and modeling. Anita T. Morzillo, Dexter H. Locke, John Paul Schmit, Lindsay Darling, Lea R. Johnson, Matthew Baker, Myla F. J. Aronson, and Robert Fahey drafted the manuscript, and all authors contributed to manuscript revision. John Paul Schmit, Lindsay Darling, Lea R. Johnson, and Robert Fahey produced the figures and tables.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Schmit, Johnson, et al., 2024) and code (Schmit, Darling, et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.14454177 and https://doi.org/10.5281/zenodo.14452675, respectively. Exact locations of monitoring plots are not publicly available; contact and query details for retrieving this information are described in the Data Sources section of Appendix S1.

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SUPPORTING INFORMATION

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

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