

ARTICLE

Tree communities in Baltimore differ by land use type, but change little over time

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Abstract

Across a city, tree communities are spatially heterogeneous and vary by land use type. However, it remains unclear how urban tree communities change over time and whether rates of change depend on land use type. To address this knowledge gap, we analyzed urban tree composition using long-term plot data to examine tree diversity changes across six different urban land use types in 1999, 2004, 2009, and 2014. We found that spatial differences in tree species diversity and community composition among land uses were much greater than changes over time. Number of trees increased over time, being driven by gains of non-native species. There was also a significant interaction between land use and time, with institutional and transportation land uses having greater community changes over time. Our study can inform site-specific efforts to promote and preserve urban biodiversity across public and private land uses.

KEYWORDS

land use, long-term change, species diversity, urban trees

INTRODUCTION

Urban tree diversity and community composition impact the services and disservices influencing the quality of life for local residents (Nowak & Dwyer, 2007; Roman et al., 2020). Recent urban sustainability policy goals include enhancement of tree biodiversity in order to enhance adaptive capacity to future climate conditions (Brandt et al., 2016) and to create more resilient urban ecosystems (Hale et al., 2015; Huff et al., 2020). The mosaic of urban land uses found in cities leads to varying management practices throughout the urban landscape, with resulting impacts on tree community composition (Bourne & Conway, 2014; Nitowski et al., 2016). Despite the recognized importance of diverse urban tree communities for critical biophysical and sociocultural

ecosystem services, little is known about long-term changes in urban tree community composition, which have implications for sustained provision of those services (Nitowski et al., 2016).

The spatial distribution and diversity of urban trees are affected by both biophysical and socioeconomic drivers (Avolio et al., 2015). At the global scale, variation in tree species composition among cities is impacted by climate, city age, and geographic distance, with cities that are closer having more similar tree species composition than those that are further apart (Yang et al., 2015). At a regional scale, tree species composition and diversity are more homogenous, because of similar environmental conditions and human tree preferences (Danneyrolles et al., 2020; Schulte et al., 2007). Within cities, urban tree community composition may be influenced by

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socioeconomic factors, including land use and land ownership (Dobbs et al., 2013). Bourne and Conway (2014) found differences in tree species composition to be greater between land use types than between municipalities, suggesting different mechanistic controls associated with each land use type. Swan et al. (2017) found that land uses with lower levels of human management have a higher abundance of trees and lower species turnover between sites, possibly reflecting saturation from the regional species pool compared with more actively managed land uses. Tree communities on private land (e.g., residential yards) and public land (e.g., streetscapes) may also have different species compositions, due to differences in manager preferences and perceptions of urban tree traits (Avolio et al., 2018; Conway & Vander Vecht, 2015). For example, residential land in southern California, USA, was found to have more fruiting trees, while street trees had lower water and maintenance requirements (Avolio et al., 2015). In addition to these differences in land ownership and management intensity, Jim and Zhang (2015) found tree community species composition to be significantly different between older and newer housing developments of Hong Kong, attributing this pattern to differences in development density and pre-urbanization land cover. Urban woody plant communities are also generally more diverse in wealthier neighborhoods (Avolio et al., 2018; Clarke et al., 2013; Hernández & Villaseñor, 2018), a relationship termed the “luxury effect” (Hope et al., 2003).

While differences in urban tree communities are well documented over space, less is known about how urban tree communities change over time. Historical flora presence-absence data have revealed increases in urban tree species richness from the 19th century to the present day in Plzeň, Czech Republic (Chocholoušková & Pyšek, 2003), Adelaide, Australia (Tait et al., 2005), and Halle, Germany (Knapp et al., 2008). On a shorter time-scale, a citywide analysis of Santiago, Chile, found overall abundance and diversity of urban trees were stable over 12 years (Hernández & Villaseñor, 2018). Using a space-for-time substitution, urban tree species richness has generally been found to increase with time since property development (Avolio et al., 2018; Clarke et al., 2013). Studies of compositional change within urban forested areas reveal that without active management, species composition in urban forested areas will diverge from nearby reference forests over time (Hotta et al., 2015). Templeton et al. (2019) found that species richness declined in both urban and rural forests of Baltimore, MD, USA, over 17 years, but rural forest sites became more similar to one another in terms of composition, while urban forests did not. However, such temporal trends are likely to vary among urban land uses with

substantially different levels of management activity. To our knowledge, only Tucker Lima et al. (2013) have examined changes in urban tree diversity over time among different land uses, finding that tree species diversity and richness increased over a 9-year period in San Juan, Puerto Rico, most prominently in vacant and upland forest land uses.

In this study, we used long-term data on Baltimore’s urban tree community to examine changes in species diversity across different land uses over a 15-year period. Our objectives were to (1) determine whether abundance, richness, and evenness of native and introduced tree species varied by land use over time and (2) examine changes in overall community composition by land use over time.

MATERIALS AND METHODS

Baltimore, MD, USA, is located on the banks of the Chesapeake Bay in the deciduous forest biome with a humid subtropical climate. We used i-Tree Eco plot data collected throughout Baltimore using standard i-Tree inventory protocols (Nowak, 2020). These plots were established as part of the Baltimore Ecosystem Study Long-Term Ecological Research site (Nowak, 2018). Two hundred circular 0.04-ha (0.1-acre) plots were established with a stratified random sampling approach using land use categories obtained from a 1996 municipal land use map, and data were collected every 5 years in 1999, 2004, 2009, and 2014. Plots that were not assessed at all time periods were excluded from the analysis, which led to a total of 193 plots used in the analyses (Appendix S1: Table S1).

Each plot was assigned to one of the 10 land uses by field crews: commercial, industrial, forest, institutional, transportation, residential, high-density residential, park, cemetery, and vacant. These categories were collapsed into seven categories for the purposes of this analysis as follows: commercial/industrial, forest, institutional, transportation, residential (includes high- and low-density residential), park (includes cemetery), and vacant. Because some plot land uses changed over time, the number of plots within each land use varied between years (Appendix S1: Table S1).

The species of every woody plant on each plot with a diameter at breast height (dbh) equal or greater than 2.54 cm (1 inch) was recorded as a tree in the dataset (Nowak, 2020). We used the USDA PLANTS database and Maryland Native Plant Society databases to determine native or introduced species status in Maryland. Trees only identified to the genus level were not assigned as native or introduced species in the analysis. Standing dead trees were excluded from the analysis.

All statistical analyses were conducted in R (R Core Team, 2020). First, we calculated the species richness and Simpson's evenness for each plot at a single point in time using the codyn package (Hallett et al., 2016), and overall abundance by summing the number of trees. We also did these same calculations for native and introduced tree species and considered a tree as introduced if it was only identified to genus and could have been either native or introduced.

To study overall community differences, we used multivariate methods to perform several analyses based on the Bray-Curtis dissimilarity in the vegan package (Oksanen et al., 2020). For these analyses, we summed species by each land use type for each year. First, to test whether tree community composition differed by land use, we performed permutational analysis of variance using the adonis function. Next, to test whether there were differences in dispersion around the centroid of different land use groups, we used the betadisper function. A land use type with greater dispersion around the centroid would indicate greater year-to-year changes than a land use type with little variation around the centroid. To visualize this, we used the metaMDS function to perform nonmetric multidimensional scaling. Finally, to understand the processes that led to the observed community composition changes, we used the codyn package to study changes in species ranks (e.g., reordering) and species gains and losses between consecutive time points based on rank-abundance curves (Avolio et al., 2019). For these analyses, we calculated change metrics at the plot level.

To test whether there were significant differences among land uses, time, or an interaction for both the static measures of community structure (richness, evenness, and abundance) and the change measures (species gains, losses, and rank changes), we used two-way repeated-measures ANOVAs in lme4 (Bates et al., 2015), with time and land use as fixed effects and plot as a random effect. Next, we used lmerTest package (Kuznetsova et al., 2017) to calculate *p* values and the lsmeans function to do post hoc pairwise comparisons using the Satterthwaite degrees of freedom. For the analyses of

evenness, we removed plots with no trees. Differences between means were considered significant at $\alpha = 0.05$.

RESULTS

From 1999 to 2014, overall tree species richness in Baltimore increased, while the total tree abundance decreased. A total of 112 tree species were recorded over the 15 years of this study. Most of these trees were native (over 60% of species and 79% of all trees). However, from 1999 to 2014, the number of introduced species doubled and the total number of introduced trees increased by 15% (Table 1). The overall increase in species richness included one native species and 21 introduced species (Table 1), 15 of which were found on residential land (Figure 3).

Quercus, *Fagus*, and *Acer* were the top three most common genera in Baltimore, making up more than 30% of the total tree population (Appendix S1: Table S2). The proportion of *Ulmus* grew faster than any other genus, increasing from 7.2% in 1999 to 11.3% in 2014 (Appendix S1: Table S2). *Fagus grandifolia* (American beech) was the most common species and was the only tree to make up more than 10% of the total tree population across all four time periods (Appendix S1: Table S4). The proportion of *Ulmus americana* (American elm) grew faster than any other species, increasing from ranking 9 in 1999 to ranking 2 in 2014 (Appendix S1: Table S4). *Ailanthus altissima* (tree of heaven) and *Morus alba* (white mulberry) were the most abundant introduced species. The proportion of *A. altissima* declined by 2%, while *M. alba* grew by 1.1% from 1999 to 2014 (Appendix S1: Table S4).

The urban tree community of Baltimore was relatively stable over time. *Fagus grandifolia* was the most abundant species from 1999 to 2014 (Figure 1). However, the tree community differed greatly among land use types (Figure 2). *Fagus grandifolia* was the most common species in the forested plots, while the introduced and invasive species *A. altissima* and *M. alba* were the more common species in transportation, residential, and

TABLE 1 Baltimore City tree species diversity metrics for native and introduced species over time

Metric	Native				Introduced				Total			
	1999	2004	2009	2014	1999	2004	2009	2014	1999	2004	2009	2014
Abundance	951	922	834	780	189	209	197	217	1140	1131	1031	997
Richness	58	60	54	59	18	29	31	39	76	89	85	98
Evenness	0.35	0.30	0.30	0.28	0.26	0.19	0.22	0.22	0.33	0.26	0.25	0.24

Note: Abundance is the number of trees, richness is the number of tree species, and evenness is measured using Evar, which ranges from 0 to 1 (a lower number reflects less evenness in the community).

vacant land uses (Figure 2). The size of the species pool was also affected by land use type. There were 71 species on residential land and 62 species on forested land compared with 23 species in parks, 20 in commercial/industrial, 18 in transportation, and 13 in both vacant and institutional land uses.

Plot-level species richness, evenness, and abundance significantly varied among land uses (Appendix S1: Table S6a), while only tree abundance on forested land changed significantly over time. Forested plots had higher values of species richness than all other land uses

and lower species evenness (Figure 3; $p < 0.001$). There was also a significant interaction between time and land use on abundance (Figure 3, Appendix S1: Table S6a), with abundance in forest plots being greater than in other land uses at all time periods, but forested plot abundance being lower in 2009 and 2014 compared with 1999 and 2004 (Appendix S1: Table S5).

The multivariate community analyses confirmed the patterns observed with rank–abundance curves. Urban tree communities had different species compositions depending on land uses ($F = 26.288$; $p = 0.001$; Figure 4),

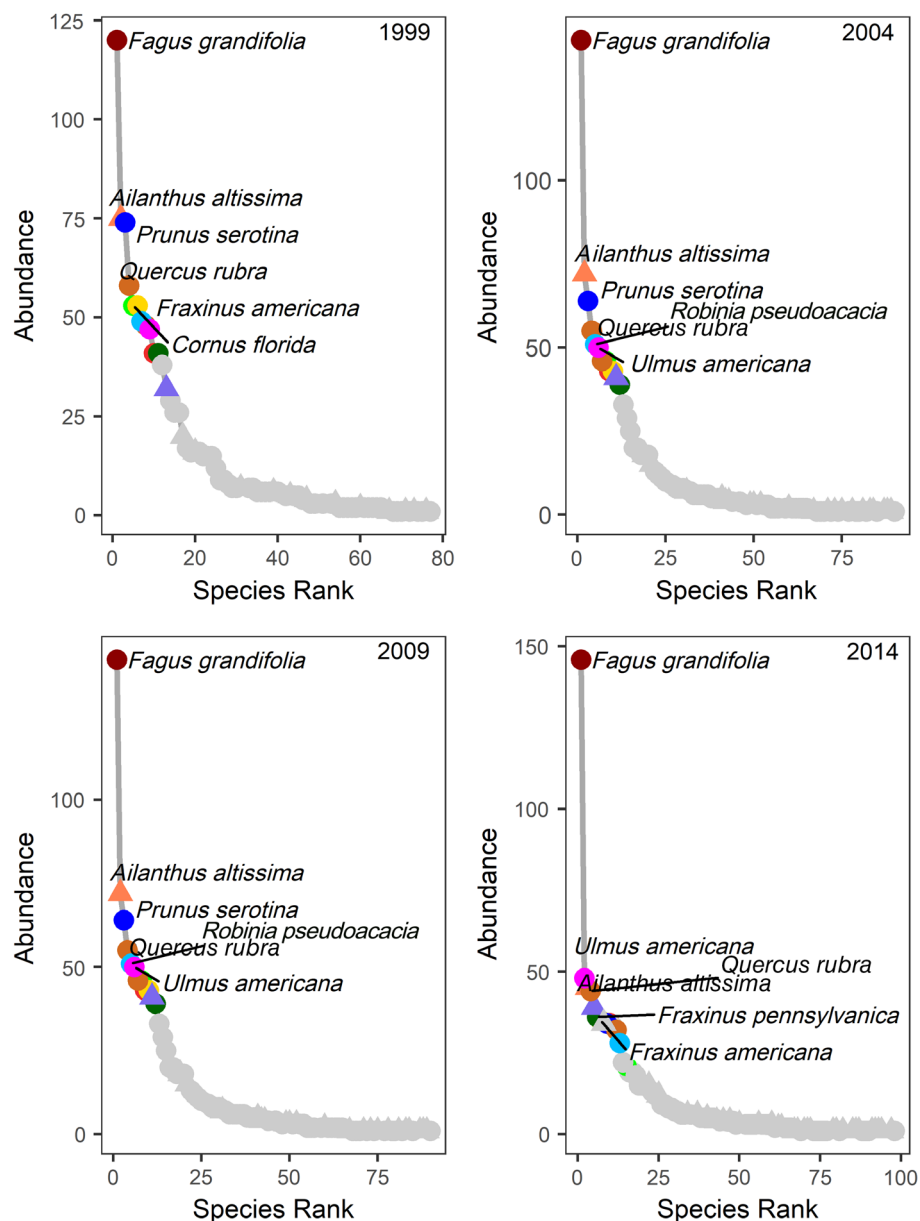


FIGURE 1 Baltimore City species rank–abundance curves, showing the relative abundance of each species versus its rank in different years. Rank–abundance curves for each year are averaged across all land uses. Note the range of y-axis varies with the temporal species abundance. The most common species in each panel are labeled and color coded. Triangle points are introduced species, and circles are native species

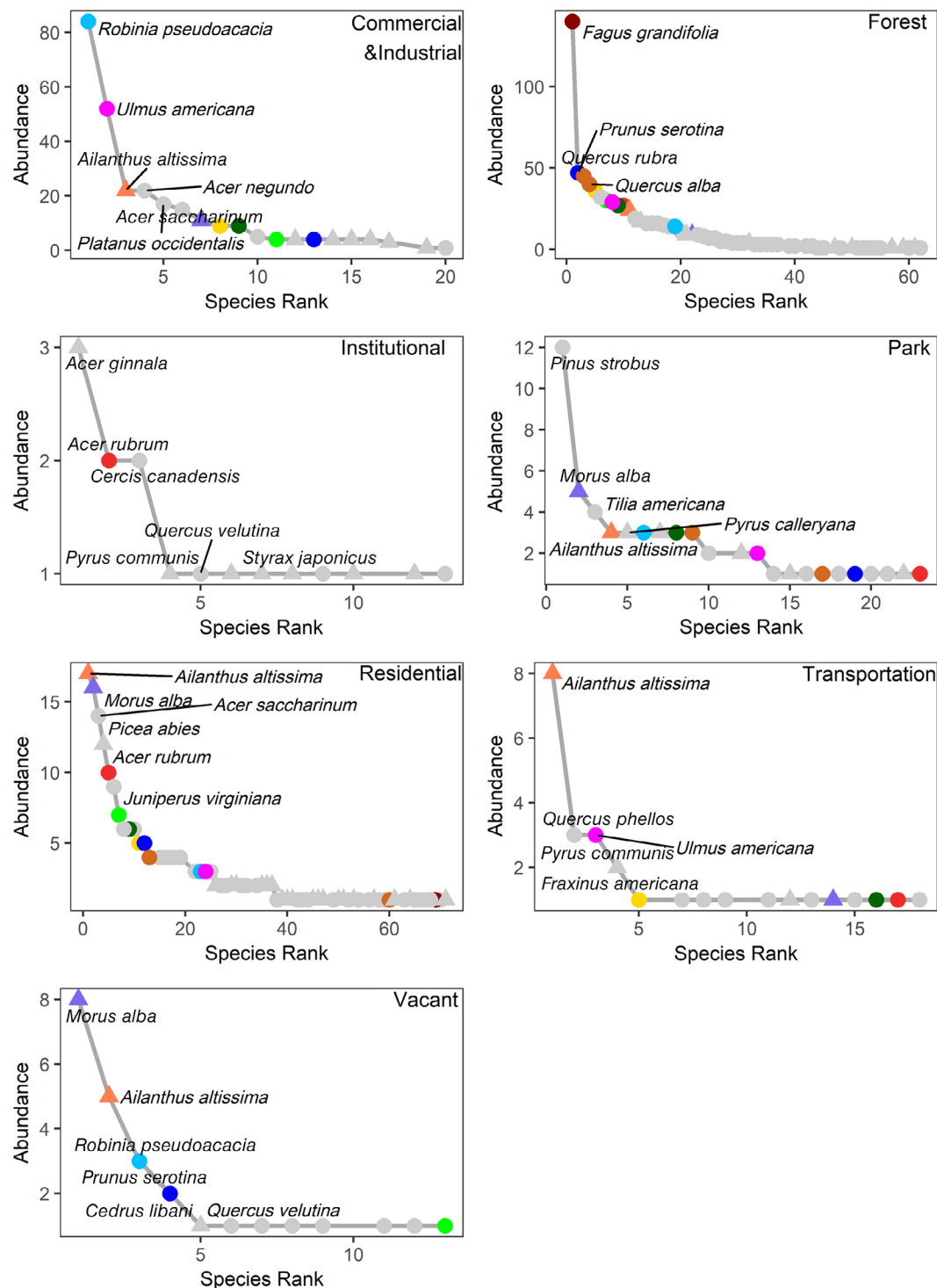


FIGURE 2 Baltimore City species rank–abundance curves, showing the relative abundance of each species versus its rank in different land uses. Rank–abundance curves for each land use are averaged across all years. Note the range of y-axis varies with the spatial species abundance. The most common species in each panel are labeled and color coded. Triangle points are introduced species, and circles are native species

and institutional and transportation plots had greater dispersion around the mean, indicating greater differences across years in the community composition ($F = 3.14$; $p = 0.01$). Finally, we investigated processes of community

composition change. Reordering of species was different by land use; there was less community reordering in parks compared with all other land use types except institutional and vacant land uses (Figure 4). Species gains

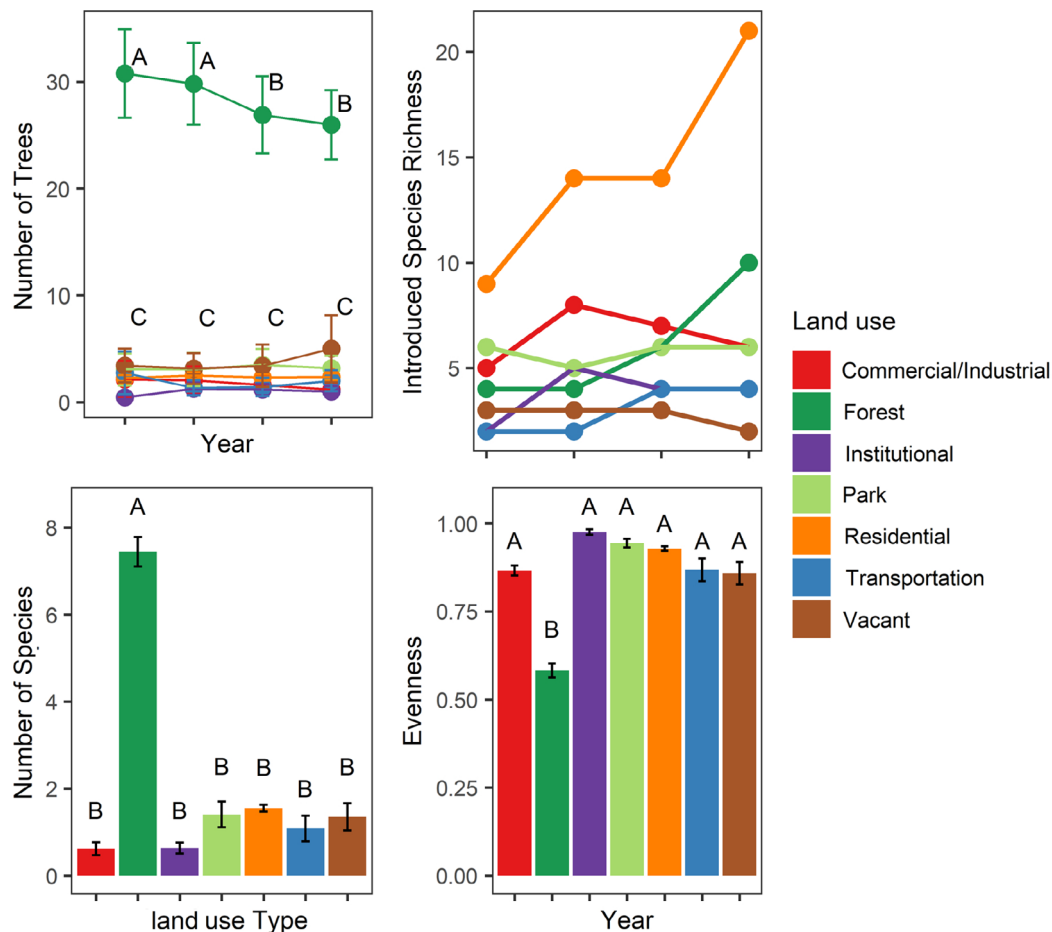


FIGURE 3 Number of trees per plot by land use and over time, overall introduced species richness by land use and over time, number of species per plot by land use, and evenness by land use. Shown are means $\pm$ SE. Different letters denote significant differences at $p < 0.05$

showed a land use-by-time interaction, where during 1999–2004, institutional, commercial, and residential land uses had greater gains than forests and parks, and from 2009 to 2014, transportation had greater gains than other land uses but vacant (Figure 4, Appendix S1: Table S6b). Vacant and transportation land uses went from among the lowest rates of species gains during 1999–2004 to the highest rates from 2004 to 2014 (Figure 4). There was no effect of land use or time on species losses, and rates of species losses were relatively low (0.14 ± 0.26).

DISCUSSION

In this study, we found greater spatial heterogeneity among land uses in tree community composition than over time and greater changes in diversity among land uses than over time, although tree community composition and diversity were more dynamic in some urban land uses than others. We also found a doubling in the

number of introduced tree species over the 15-year study, while the number of native tree species did not change.

Similar to other studies, we found that urban tree diversity and community composition differ by land uses (e.g., Bourne & Conway, 2014; Swan et al., 2017). Among land use types, forested land consistently had the highest plot-level abundance and species richness, while residential land had the highest total species richness citywide. Similarly, greater tree species diversity has also been found on residential land compared with forest patches in Halifax, Nova Scotia (Turner et al., 2005) and Chongming Island, China (Zhao et al., 2013). Tree communities on residential land are influenced by a larger number of individual landowners making independent decisions about land management and tree species selection than other land uses (Avolio et al., 2015; Bourne & Conway, 2014; Kendal et al., 2010). Forested land has a much greater density of trees than other urban land use types, leading to higher species richness at the plot level, but is generally dominated by a few native species across an urban area, indicated by their low evenness.

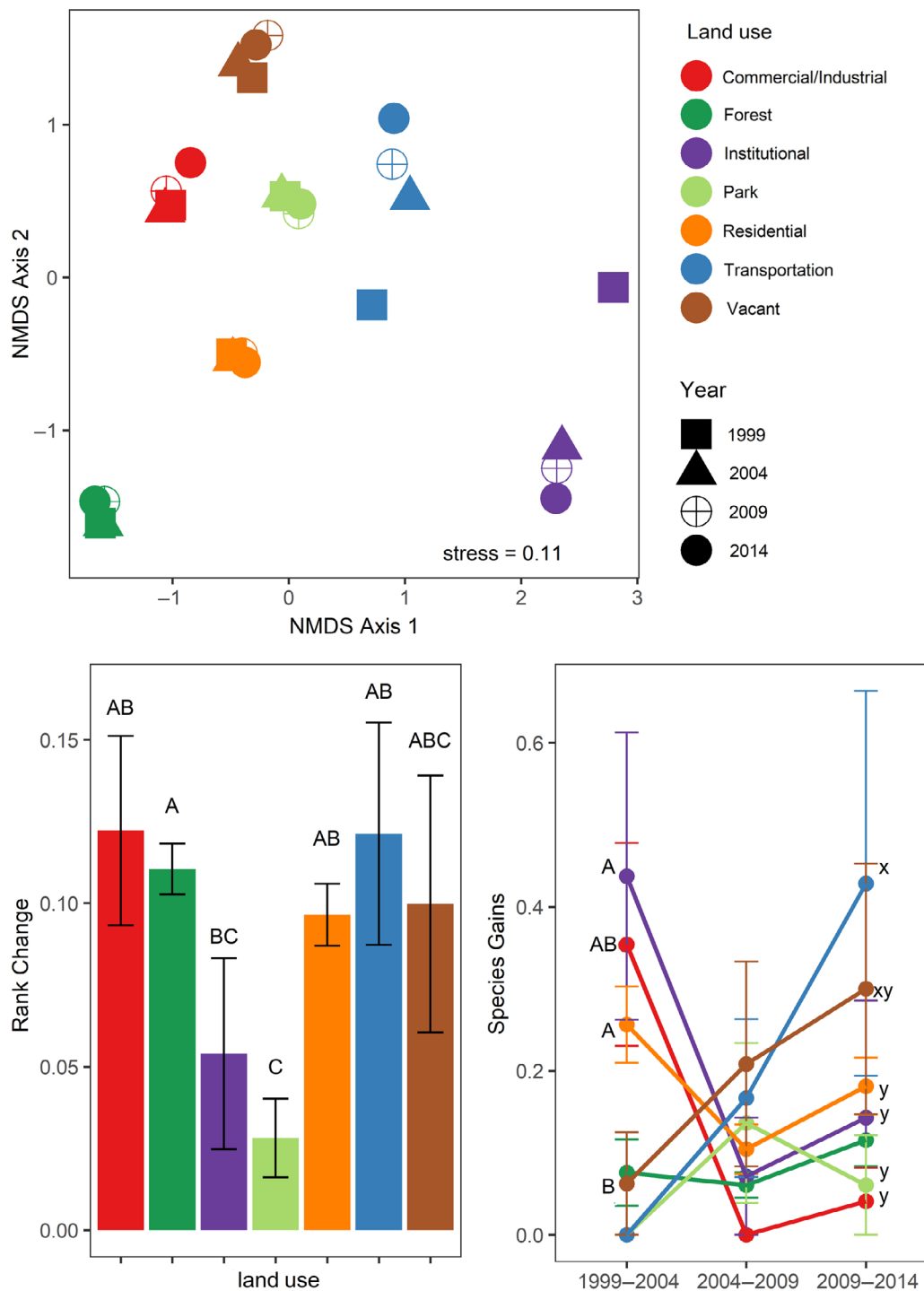


FIGURE 4 Composition of species across different land uses in 1999, 2004, 2009, and 2014 (each point denotes the community composition in a year) and rank changes and species gains for the three 5-year sampling intervals. Shown are means $\pm$ SE. Different letters denote significant differences at $p < 0.05$. Rank changes are scaled from 0 to 0.5, where 0.5 means complete reordering among species. Species gains the proportion of species gained given the size of the species pool and ranges from 0 to 1. For gains, letters are only within-year comparisons

Despite local policy aimed at increasing Baltimore's tree canopy cover, citywide tree abundance decreased from 1999 to 2014, while species richness increased. The decrease in abundance mainly occurred on forested land,

which also experienced a decrease in plot-level species richness over time. This finding is in contrast to Tucker Lima et al. (2013) and may reflect greater disturbance pressures in Baltimore forest patches than in San Juan,

Puerto Rico. The decrease in tree abundance on forested land was driven by declines in abundance of *Prunus serotina* and *Cornus florida* (both native species), which may be related to increases in deer herbivory (Kribel et al., 2011), or canopy closure and subsequent mesophication in the case of *P. serotina* (Templeton et al., 2019). The increase in species richness over time was driven by introduced species, which doubled over 15 years, primarily on residential plots. We did not find that the increase in introduced species displaced native species. However, trees are long-lived, and it is possible that over a longer time frame, the introduced tree species may cause a decline in native biodiversity (Tait et al., 2005).

We also found significant changes in tree abundance on forest lands over time (Figure 3). Compared to the other land uses with greater anthropogenic impacts, forest compositional change may be more related to environmental processes such as climate change and succession (Hall et al., 2002). We also found greater temporal changes in the tree communities on institutional and transportation lands, illustrated by greater dispersion in the multivariate analysis and greater species gains than other land uses. Institutional and transportation lands often occupy large parcels of land, where species introductions may be more likely either through intentional management or by natural succession (Nowak et al., 2004; Pothier & Millward, 2013). Our results indicate that tree urban community composition varies more by land use than it does over time, although some land uses (i.e., transportation and institutional lands) may be more dynamic than others. Urban plant communities may be emergent, planted, or remnants of native vegetation (Williams et al., 2009), and processes that affect community composition likely differ by management intensity (Avolio et al., 2021). For example, transportation or vacant land is likely to have less human management and more opportunities for spontaneous tree communities to arise. If enough time passes for processes of natural succession to occur, these areas may resemble native remnant vegetation. However, trees are long-lived and changes in community composition may take decades to become apparent. This also means that present-day biodiversity patterns likely reflect legacy effects of past site histories in addition to current management practices (Grove et al., 2017; Roman et al., 2018).

Long-term study of the processes by which urban tree communities change across different land uses can be used by policymakers, and urban planners ensure continued provision of ecosystem services across public and private lands. Our findings confirm that different strategies or policies may be necessary to increase or maintain

diversity on different land use types and to keep introduced species from displacing native trees. However, continued temporal analysis of urban tree communities across different climate zones, political regimes, and socioeconomic contexts will be critical to understand whether these patterns are more universal.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are already published and publicly available, with those publications properly cited.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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