

Effects of Urbanization on Tree Species Functional Diversity in Eastern North America

Charles A. Nock,^{1*} Alain Paquette,¹ Matt Follett,¹ David J. Nowak,² and Christian Messier¹

¹Center for Forest Research, Université du Québec à Montréal, P.O. Box 8888, Centre-Ville Station, Montréal, Quebec H3C 3P8, Canada; ²Northern Research Station, c/o SUNY ESF, 5 Moon Library, Syracuse, New York 13210, USA

ABSTRACT

Urban forests provide ecosystem services for millions of people. Numerous introductions have elevated tree species richness in cities, which may enhance functional diversity. However, few studies have examined changes in tree community composition or functional diversity with urbanization, even though functional diversity, and not species number per se, is directly linked with ecosystem function and associated services. We combined tree abundance data from both urban and extra-urban forest inventory plots for seven metropolitan areas in eastern North America to analyze changes in species composition, Shannon's diversity, and functional diversity with urbanization. As expected, urban tree diversity was reduced at local scales, and the effect varied with land use. Rarefaction analysis indicated that at large scales, urban tree species pools were equal with respect to species or functional diversity compared to extra-urban

forests, but in urban areas at small scales this diversity is not realized because of low tree density. Ordination revealed that with urbanization, introduced species increased in importance, and regional variation in species composition became more homogenous. Increasing tree density and/or tree cover through changes in management practices and urban design could facilitate local scale urban tree diversity using existing species pools, which are functionally diverse. Monitoring of forests at large spatial scales that include urban areas, and the use of methods that account for abundance and functional trait variation can provide insights into the effects of urbanization on tree diversity at multiple scales.

Key words: functional diversity; land-use change; functional traits; tree species diversity; urban forest; urbanization; gradient; rarefaction.

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*Corresponding author; e-mail: charles.nock@gmail.com

INTRODUCTION

The lives of humans are increasingly urban. In most regions of the world urban trees substantially contribute to the health and well-being of millions of people living in cities. An extensive urban forest canopy can provide important ecosystem services, such as modifying city microclimate by ameliorating temperatures, reducing urban water runoff, decreasing building energy use, and reducing air pollution (Pataki and others 2011; Nowak and

others 2006). In addition to the extent of tree cover, the diversity of tree species is a key attribute of urban forests. The existence of a positive relationship between species diversity and the rates or stability of ecosystem functions (biodiversity–ecosystem functioning) and associated services is supported by seminal research in grasslands, and recently confirmed by meta-analyses over several ecosystems (Cardinale and others 2011). Some recent evidence suggests that the positive relationship between species diversity and the rates or stability of ecosystem functions extends to urban ecosystems, as the functional diversity of tree species was shown to have a positive effect on the stability of tropospheric ozone removal in the city of Rome, Italy (Manes and others 2012).

Previous research has identified a complex suite of filters that likely influence changes in tree species diversity with urbanization (McDonnell and others 1993; Walker and others 2009; Williams and others 2009). Most conspicuous is the transformation of previously forested sites to settlements comprising buildings and impervious surfaces (that is, buildings and impervious surfaces), which negatively impacts diversity via a reduction in habitat (McKinney 2006, 2008; Nowak 2010). Altered environmental conditions in the urban environment, such as anthropogenic soils, pollution, and the urban heat island (McDonnell and others 1993), may also negatively or positively affect particular tree species (for example, Searle and others 2012). Furthermore, human preferences are also likely to select for and against species (Williams and others 2009; Nowak 2010). Together, each of the above filters will interact with the pool of tree species normally found in urban areas to determine present diversity (Williams and others 2009; Nowak 2012).

Increasingly ecologists argue that it is not the number of species per se, but the diversity and identity of functional traits and the diversity of species that express them that drive ecosystem function (Tilman and others 1997; Díaz and Cabido 2001; Díaz and others 2004). Within this framework, changes in species diversity have multiple potential outcomes with respect to functional diversity (Flynn and others 2009; Williams and others 2009; Mayfield and others 2010). For example, adding a species to a community necessarily increases species richness or diversity, but its effect on functional diversity depends on its functional uniqueness or singularity, and can range from positive to negative. Alternatively, as species are removed, those communities with both high functional diversity and high functional redundancy, in which many species share similar traits, may be more resilient to changes in

their environment (Flynn and others 2009; Laliberté and others 2010). In recent studies of urban flora, despite high urban plant richness, species were generally found to be closely related and hence functionally similar, potentially decreasing the flora's capacity to respond to environmental change (Knapp and others 2008, 2012).

In addition to its effects on plant diversity, urbanization is generally associated with the homogenization of plant assemblages, resulting from an expansion of alien plant species and declines of native species (Kühn and Klotz 2006; McKinney 2002). This process, often referred to more generally as biotic homogenization, can have important impacts on plant diversity at larger scales as the species composition of previously distinct floras from different regions converges due to increasing urbanization (Schwartz and others 2006; Olden and others 2006).

Changes in plant communities with urbanization have generally been documented by either analyzing temporal datasets (for example, Pyšek and others 2004), or by employing a gradient approach (McDonnell and others 1993). Seminal work on urban ecology in the 1990s developed the application of the ecological gradient paradigm to the study of human influences on plant communities (for example, McDonnell and Pickett 1990; McDonnell and others 1993). A number of recent studies have applied the gradient approach, but instead of focusing on species richness, have explored the effects of increasing land-use intensity on plant functional or phylogenetic diversity because of the additional information it provides (Aubin and others 2009; Flynn and others 2009; Knapp and others 2008, 2012; Laliberté and others 2010). However, in studies to date tree species have been poorly represented and few studies have included samples from urban areas.

Here, we use forest inventory data for seven urban areas in eastern North America to assess the effects of urbanization on the composition, species diversity, and functional diversity of forests. Specifically, we sought to determine: (1) the response of tree species and functional diversity to urbanization and how this depends on scale, (2) variation in tree species and functional diversity within urban areas across different land-use types, and (3) the effect of urbanization on regional variation in tree species composition.

MATERIALS AND METHODS

Study Sites and Tree Inventories

The Northeastern United States was chosen as the site for our study because it fulfilled a number of

important criteria: (1) forest was the dominant vegetation prior to European settlement, (2) large cities exist within a matrix characterized by different states of development or human influence, (3) sample-based forest inventory data allowed for comparison of tree diversity along urban gradients, and (4) functional trait data for tree species was relatively complete.

To quantify responses of tree species and functional diversity to urbanization we selected seven major metropolitan areas (Figure 1A), for which urban forest composition (identified to species and including planted and spontaneous trees) had recently been assessed using plot-based random sampling (Nowak and others 2008, $N = 875$). Dates of inventories ranged from 1996 to 2007 and land use was noted during sampling. We added additional data on forest composition from extra-urban forest inventory plots—measured by the USDA Forest Inventory and Analysis Program (FIA)—less than 100 km distance from the center of each metropolitan area ($N = 607$). Our sample of extra-urban forest plots did not include monospecific plantations. Further details on forest inventories are given in the supplementary material (Appendix 1).

Quantifying Urbanization: Intensity of Human Influence

Past studies have quantified intensity of human influence as the density of road networks or as the type of land-use cover (for example, forest, agricultural, urban). Here, we employed an approach that integrates different sources of information into a composite Index of Human Influence (IHI). IHI quantifies “the human footprint” on terrestrial ecosystems by integrating information on human settlement (population density, built-up areas), access (roads, railroads, navigable rivers, coastline), landscape transformation (land-use/land cover) and electric power infrastructure (Sanderson and others 2002). In a geographic information system (ArcGIS version 10, ESRI, Redlands, California, USA), extra-urban plots were placed in a category (low, 0–30; moderate, 30–60) based on IHI and urban plots comprised a third category (high). We did so because analyses using IHI as a continuous variable yielded equivalent results, and grouping facilitated subsequent comparison of urban and extra-urban samples with rarefaction. The number of plots in each category for each of the

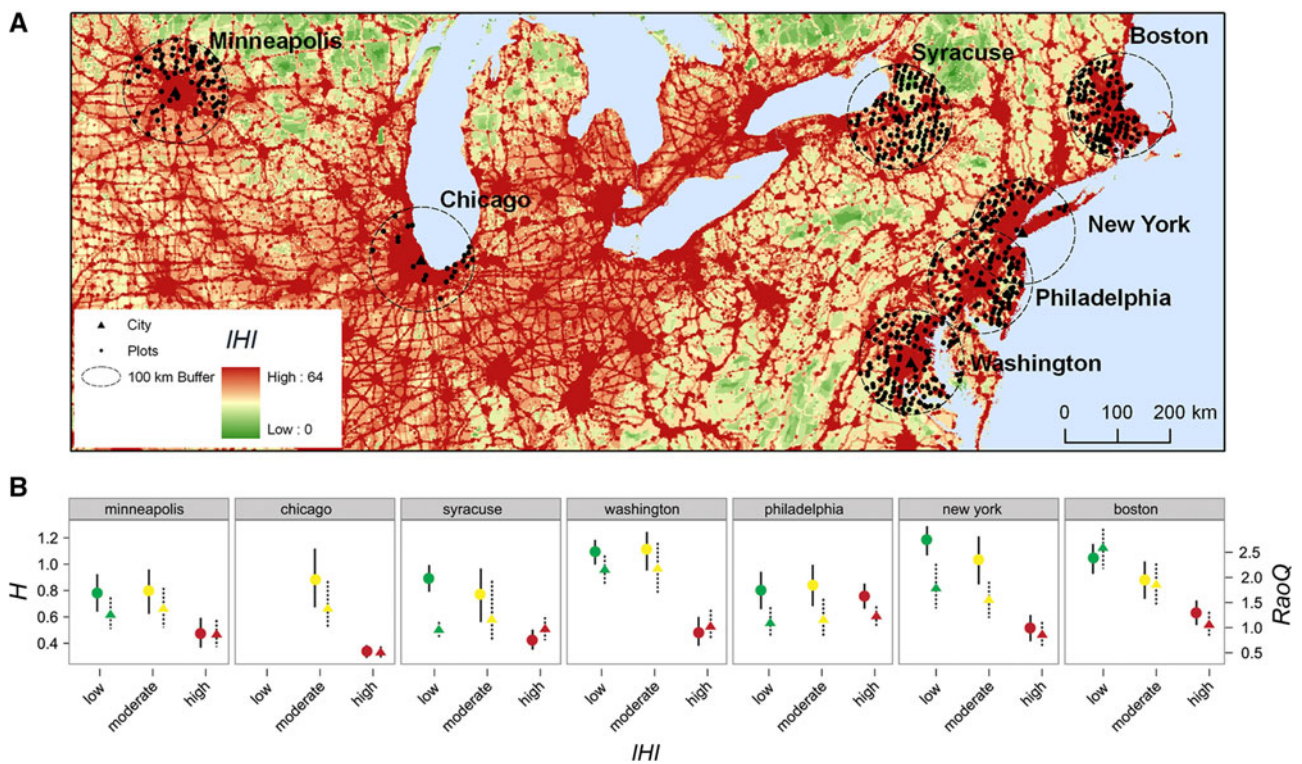


Figure 1. **A** Map of eastern North America with study areas, sample plot locations with an Index of Human Influence (IHI) on terrestrial ecosystems overlaid. Response of mean plot (**B**) tree species diversity (H , circles) and functional diversity (RaoQ, triangles) to increasing human influence with 95% confidence interval lines. Two categories were assigned to extra-urban forest plots (0–30 = low IHI; 30–60 = moderate IHI), and urban plots were assigned to a third category (high).

Table 1. Functional Traits Used in the Present Study and Related Axis of Plant Strategy

Functional trait	Units	Strategy spectrum	Brief description of strategy spectrum
Leaf nitrogen per unit mass	%N	Leaf economics (Wright and others 2004)	Construction cost, photosynthetic rates and nutrient content and leaf lifespan
Seed mass	mg	r/K (Moles and Westoby 2006)	Production of many small seeds per unit energy and low survivorship, versus fewer large seeds and higher survivorship
Wood density	g/cm ³	Wood economics (Chave and others 2009)	Construction cost, stem growth costs and mortality
Maximum plant height	m	r/K (Moles and others 2009, Moles and Leishman 2008)	Longevity, reproductive lifespans, age at first reproduction

Plants that are r selected tend to have high growth rates, produce a large number of seeds and have shorter lifespans. K selected plants are associated with slower growth rates, production of fewer but larger seeds and tend to have longer lifespans.

Table 2. Traits Used to Calculate Functional Diversity for Tree Communities in Eastern North America and Sources for Trait Information Taken from the TRY Database (<http://www.try-db.org/>)

Trait	Source(s)
Leaf nitrogen	Cornelissen (1996), Cornelissen and others (1996, 2003, 2004), Cornwell and others (2008), Craine and others (2009), Freschet and others (2010), Garnier and others (2007), Han and others (2005), Kattge and others (2009), Kerkhoff and others (2006), Laughlin and others (2010), Medlyn and others (1999), Niinemets (2001), Ogaya and Peñuelas (2003), Ordoñez and others (2010), Preston and others (2006), Quested and others (2003), Reich and others (2008), (2009), Willis and others (2010), Wright and others (2004)
Seed mass	Cornelissen and others (1996), Díaz and others (2004), Garnier and others (2007), Green (2009), Kleyer and others (2008), Kühn and others (2004), Laughlin and others (2010), Moles and others (2005), Paula and others (2009), Preston and others (2006), Royal Botanical Gardens Kew (2008), Sack (2004)
Wood density	Chave and others (2009), Cornelissen and others (2003), Ogaya and Peñuelas (2003), Ordoñez and others (2010), Preston and others (2006), Reich and others (2009)
Maximum height	Cornelissen and others (2004), Díaz and others (2004), Laughlin and others (2010), Moles and others (2004), Ordoñez and others (2010), Preston and others (2006), Wirth and Lichstein (2009)

metropolitan areas is given in the supplementary material (Appendix 2).

Quantifying Species and Functional Diversity

Functional diversity was calculated using traits that are coarse indicators of plant functional strategies, and represent multiple axes of functional differentiation in trees (Table 1). Specifically, low to high leaf nitrogen, and high to low wood density, describe a continuum from fast-growth and an acquisitive growth strategy with

fast returns on investment to a slow-returns, slow-growth and more stress-tolerant strategy. Maximum height describes the adult light niche, and seed mass describes a continuum from many small seeds per unit energy invested to few large seeds (Table 1). Functional trait data were mostly obtained from the TRY database (Table 2; Kattge and others 2011), and a small portion of trait data was obtained from additional literature or from congeneric species (supplementary material—Appendix 3).

For urban and extra-urban plots we used living trees larger than 12.7 cm in diameter at breast height to calculate species (Shannon's, H) and

functional diversity (Rao’s quadratic entropy, RaoQ, Botta-Dukát 2005), both were weighted using the percent relative abundance of each species, calculated from numbers of individuals. H and RaoQ were calculated using the R packages vegan (Oksanen and others 2011; version 1.17-8) and FD (Laliberté and Shipley 2011; version 1.0-11) respectively. After excluding rare species with missing functional trait data, we accounted for approximately 90% and approximately 85% of individuals in extra-urban and urban datasets, respectively. Mean plot tree species diversity (H and RaoQ) was compared by bootstrapping the means and calculating 95% confidence intervals using the statistical program R, version 2.15.2 (R core development team 2012) and the package simpleboot (Peng 2008; version 1.1-3). Pearson correlation coefficients were calculated to describe the relationship between plot-level tree diversity, tree density and the percentage of plot surface area taken up by buildings or hard surfaces.

Species pools for extra-urban and urban forest communities, and for different land uses within

cities, were compared using rarefaction curves. Rarefaction curves are produced by repeatedly re-sampling the pool of N individuals or N samples at random and plotting the average number of species, or the average diversity (Shannon’s, H) represented by $1, 2, \dots, N$ individuals or samples (samples can also be re-scaled to area sampled). Thus, rarefaction generates the expected number of species or value for diversity in a collection of n individuals (or n samples) drawn at random from the large pool of N individuals (or N samples). Data for the seven metropolitan areas were pooled together, and rarefaction curves were calculated on both an individual and an area basis for species (H_{ind} , H_{area}) and functional diversity (RaoQ_{ind}, RaoQ_{area}). EstimateS was used to calculate H_{ind} and H_{area} (Version 7.5, <http://purl.oclc.org/estimates>), and RaoQ_{ind} and RaoQ_{area} were calculated with a slightly modified version of the function rare_Rao presented in Ricotta (2012), so that the R package FD and rare_Rao calculated Rao’s quadratic entropy using identical procedures.

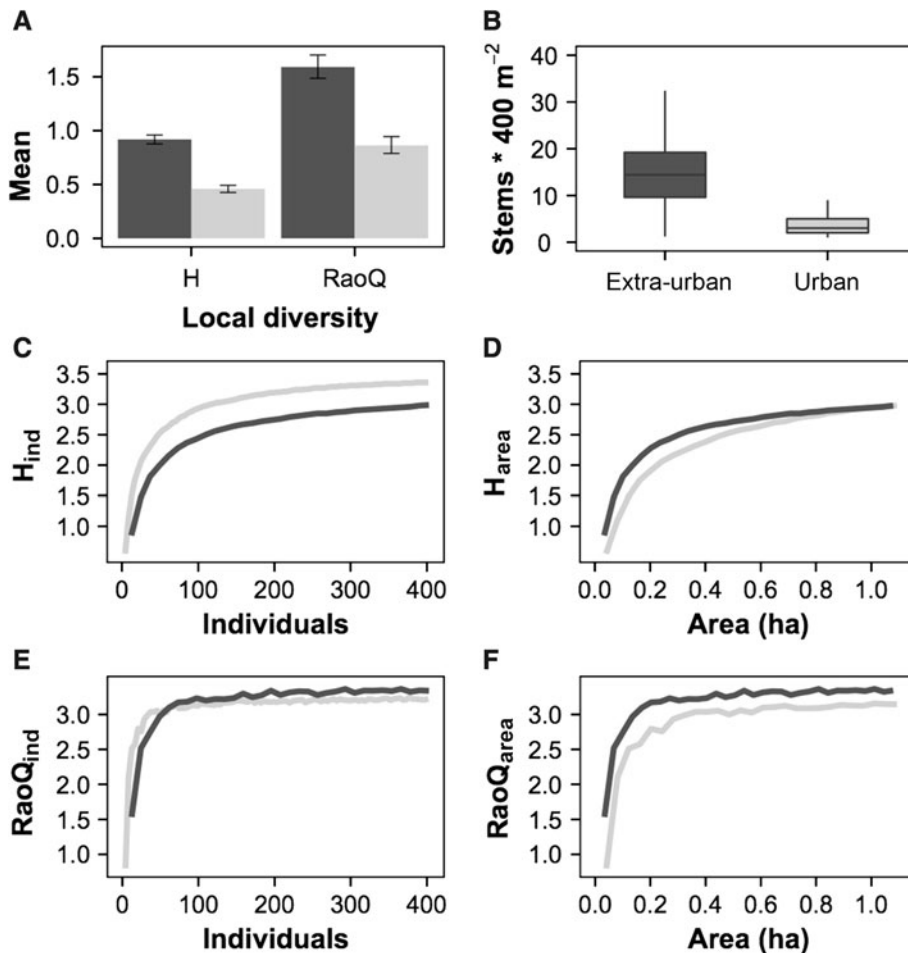


Figure 2. Differences in mean plot level Shannon’s (H) and functional diversity (RaoQ) (A) and stem density for extra-urban (red) and urban (blue) forest plots (B). Rarefaction analysis showing changes in expected Shannon’s and functional diversity with number of individuals (C, E) or area sampled for (D, F). Confidence intervals (95%) in (A) calculated by bootstrapping the mean.

Table 3. Pearson Correlation Coefficients for Relationships Among Species Diversity (Shannon’s Diversity Index; *H*), Functional Diversity (Rao’s Quadratic Entropy; RaoQ), Tree Density and Urban Forest Plot Characteristics

	RaoQ	<i>H</i>	Tree density	%Grass
RaoQ				
<i>H</i>	0.75			
Tree density	0.38	0.57		
%Grass	-0.02 ^{NS}	-0.13	-0.25	
%Building and hard surface	-0.36	-0.47	-0.53	-0.13

Correlations are highly significant ($P < 0.001$) unless indicated. Not significant (NS) at $P = 0.05$. Exact *P* values and sample sizes given in Table A4 in supplementary material.

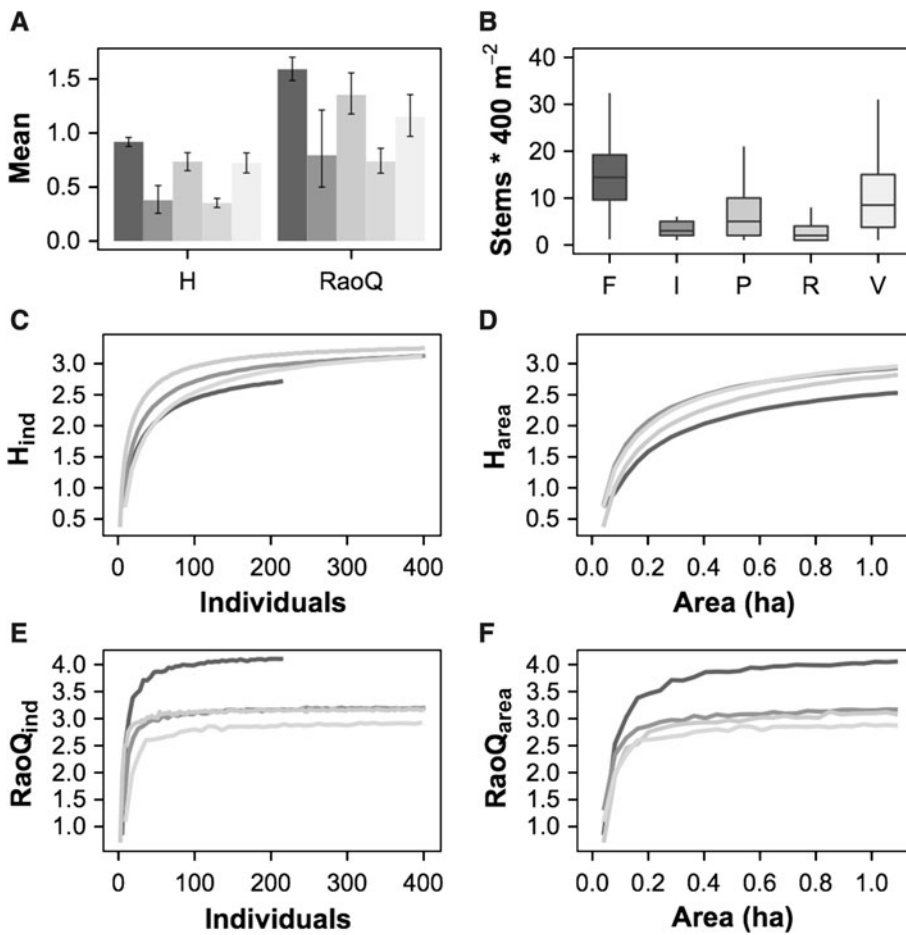


Figure 3. **A** Mean Shannon’s (*H*) and functional diversity (RaoQ) and **(B)** tree density compared for extra-urban (F) and urban forest plots classified according to varying land uses: institutional (I), parks (P), residential (R), and vacant (V). Rarefaction of Shannon’s **(C, D)** and functional diversity **(E, F)** for differing land uses within urban areas by area and individuals sampled. Confidence intervals (95%) in **(A)** calculated by bootstrapping the mean. Colors for bars and curves in all panels are the same as in **(B)**.

Comparing Tree Community Composition

Ordination was used to examine the effects of urbanization on tree species composition and to test for homogenization among cities by comparing: (1) extra-urban to urban plots, (2) among urban plots grouped by metropolitan area, and

(3) among extra-urban plots grouped by metropolitan area. Ordination of tree community composition was performed using non-metric multidimensional scaling, with Bray–Curtis distance, using the function metaMDS in the R package vegan. Further details on the methodology and analyses are presented in supplementary material (Appendix 1).

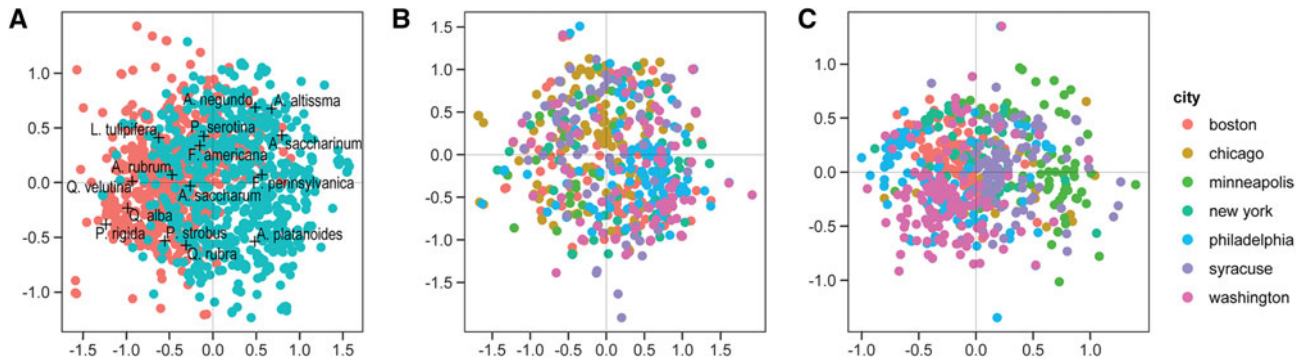


Figure 4. Ordination of tree community composition from inventory plots for seven metropolitan areas in eastern North America: **A** extra-urban (red) compared to urban forest plots (blue) with abundant species indicated. **B** Urban plots only with different colors for different metropolitan areas, and **C** extra-urban plots only with different colors for different urban areas. Note legend for cities applies to **B** and **C**.

RESULTS

Changes in Tree Species and Functional Diversity with Urbanization

H and RaoQ generally decreased with IHI, with most of the decrease occurring from moderate to high IHI (Figure 1B). Decreases in H and RaoQ were large for some metropolitan areas (Washington, Boston), whereas others exhibited no trend (Philadelphia). H and RaoQ generally changed in concert, although for Syracuse H decreased with IHI, whereas RaoQ did not (Figure 1B). Given the minor differences between the two categories of extra-urban plots (Figure 1B, low and moderate IHI), they were combined for subsequent analysis. At the plot level, tree diversity for urban plots was approximately half that of extra-urban plots for both H and RaoQ (Figure 2A). Tree density was also much lower in urban plots compared to extra-urban plots (Figure 2B).

There were strong positive correlations between tree density and RaoQ and H ($r = 0.38$ and $r = 0.57$ respectively, $P < 0.001$, Table 3), and strong negative correlations between the percentage of urban plot surface area accounted for by hard surfaces or buildings and RaoQ and H ($r = -0.36$ and $r = -0.47$ respectively, $P < 0.001$, Table 3). Finally, tree density was also negatively correlated with percentage of urban plot surface area covered by grass ($r = -0.25$, $P < 0.001$; Table 3) and strongly negatively correlated with the percentage of urban plot surface area accounted for by hard surfaces or buildings ($r = -0.53$, $P < 0.001$; Table 3). Sample sizes and P values are provided in supplementary material (Appendix 4).

Rarefaction curves were similar for H_{ind} and RaoQ_{ind}—diversity in samples containing the same number of individuals was approximately equal

(Figure 2C, E; confidence intervals not shown). For the area-based rarefaction, H_{area} and RaoQ_{area}, similar results were also obtained (Figure 2D, F).

Variation in Species and Functional Diversity with Land Use Within Cities

H and RaoQ varied among land-use types within cities (Figure 3A). For park and vacant land uses H and RaoQ approached that of extra-urban plots, but for residential and institutional land uses H and RaoQ were much lower (Figure 3A). Tree density varied with land use mostly in the same way as H and RaoQ (Figure 3B). Rarefied Shannon diversity, H_{ind} and H_{area} , were quite similar for different land uses (Figure 3C, D; confidence intervals not shown). RaoQ_{ind} and RaoQ_{area} were greater for institutional compared to other land uses (Figure 3E, F), and RaoQ_{ind} and RaoQ_{area} were lowest for vacant.

Effects of Urbanization on Species Composition

Ordination revealed an overall shift in tree species composition with urbanization, as well as significant overlap in composition (Figure 4A). Specifically, a distinguishing feature was the importance of introduced species for urban plots: for example, Norway maple (*Acer platanoides* L.) and Tree of Heaven (*Ailanthus altissima* Mill. Swingle). Examining the compositional similarity of urban plots further, we found little evidence of tight clustering, but instead diffuse patterns for the different cities (Figure 4B), suggesting that urban forest composition is relatively similar among cities. In contrast, for the extra-urban plots there was much more evidence of clustering according to their metropolitan area of origin (Figure 4C).

DISCUSSION

For seven major metropolitan areas in eastern North America, we examined tree diversity in urban and nearby extra-urban forest plots along gradients constructed using an index of human influence. Our primary goal was to examine how tree species and functional diversity were influenced by urbanization. We also examined how species and functional diversity varied with different land uses within cities and how urbanization-influenced tree species composition.

Urban areas are often described as hotspots of plant species richness (Knapp and others 2008; Walker and others 2009) and tree species richness is also generally elevated in urban areas relative to proximate “natural” habitats (Nowak 2010). Here, by comparing with plot data from proximate extra-urban forests trees species richness was found to be elevated in cities as expected. In this study the pooled tree species richness across the seven cities included 177 species, and for the extra-urban plots the pooled species richness included 101 species (data not shown). Does this increased richness lead to an increased diversity in function? Despite the high species richness, species (Shannon’s) and functional diversity were strongly reduced by urbanization at the local scale (Figure 2A). A dramatic and expected effect of urbanization was the reduction of tree density (Figure 2B), which is driven by the replacement of potential growing space by buildings, impervious surfaces and mown lawns. The percentage of plots occupied by buildings and impervious surfaces was strongly negatively correlated with tree density, as were species and functional diversity at the local scale (Table 3).

Comparison of the rarefaction curves in this study suggests that despite the striking differences in diversity at the local scale, at larger scales (greater area or number of individuals sampled) the species diversity of urban and extra-urban species pools was similar. This finding is consistent with results from a recent study examining the effects of urbanization on plant species diversity in Phoenix, Arizona, where Walker and others (2009) similarly found large decreases in local plant species diversity (plot level) with urbanization, but also found that species pools were larger in the city due to a large number of introduced species. However, whereas we found that reductions in individual density, and in turn diversity, were strongly correlated with the availability of growing space (negatively correlated with infrastructure), Walker and others (2009) found little evidence for such a relationship and suggested that plant density may be limited by

human choices other than infrastructure design. Effects of individual density are an important aspect of diversity assessment, because plant density in urban areas may reflect growing conditions, available growing space in built environments and/or human preferences.

Our results suggest that urban tree species pools were as functionally diverse as forest species pools (Figure 2E, F). In contrast, Knapp and others (2008) found that cities in Germany were hot spots of plant species richness, but included many closely related and functionally similar species, suggesting a decreased capacity in urban areas to respond to environmental changes. Our use of abundance data (vs. presence/absence) and the exclusion of rare species may account for the difference in results. We focused on relatively common species, and have also included planted individuals, for they are likely to strongly influence important ecosystem processes. Our results also suggest that caution should be used in interpreting changes in functional diversity in urban areas from species richness data, due to the large number of rare species that may not strongly influence ecosystem processes.

A surprising result was that tree diversity in parks and vacant areas of cities approaches that of forest plots (Figure 3A, B), indicating limited urban influences (for example, air pollution, soil compaction) in these areas that could reduce diversity to relatively few tolerant species. The greater tree diversity of urban parks may result from a combination of factors such as better growing conditions (higher soil volumes), planting decisions and management practices (tree care) that may buffer trees from urban environmental stresses. Although the functional diversity of vacant plots was found to be relatively high with respect to other land use, including forest (Figure 3A), the rarefaction curve (Figure 3E, F) shows that diversity in vacant plots saturates quickly with increasing area or number of trees sampled. One possible interpretation of that result is that despite the relatively high density of stems, the species pool for vacant lots (that is, its potential diversity) is small because it is not enriched by tree planting, and/or tree species are excluded by competition with other vegetation. The opposite is found on institutional lands, which have enrichment planting as well as vegetation control during tree establishment, and thus a larger potential diversity. However, realized diversity is low because of a strong human influence on tree density by landscaping practices.

Compositional changes were evident in urban tree communities with introduced species comprising an important component (Figure 4A).

Although it is generally known that introduced tree species become more important in urban areas, we are not aware of other large-scale analyses that make this comparison with proximate forests as a benchmark. This approach also allowed us to determine that urban tree communities from the seven cities were less distinct from each other than their respective forest communities (Figure 4B, C), thus providing evidence for ongoing homogenization (through deliberate choices based on stress tolerance, aesthetics, and other characteristics making trees desirable for planting in the city) of tree species composition that is likely to increase with continued expansion of urban areas. Our results are consistent with previous comparisons documenting the importance of human introductions to the composition of the urban flora in Phoenix, Arizona and nearby desert plant communities (Walker and others 2009). Results of this study demonstrate for tree communities the importance of investigating the effects of scale on relationships between human influence and plant species diversity, for a study at the scale of a single metropolitan area would show a positive effect of urbanization on tree species diversity due to the somewhat distinct urban and extra-urban tree species pools (Walker and others 2009; Pautasso 2007; McKinney 2008).

Our results suggest that a diverse species and functional pool of tree species exists in urban environments—relative to nearby forests—but that tree density is often low and results in low diversity at local scales. A denser, functionally diverse and well-adapted community of urban trees could provide more ecosystem services that are more resilient to the increasing risks of biophysical disturbances induced by global changes. Although forest-like tree densities are not suited to all land uses, many opportunities for tree planting exist, even given the constraints of space for buildings and infrastructure. For example, designs for hybrids of traditional and green infrastructure have existed for some time. Tree density and diversity could be facilitated through the use of soils both conducive to root growth and load bearing for sidewalks (Grabosky and Bassuk 1996). Such changes to the growing environment of street trees could facilitate the planting of a broader array of species, including more native trees—these sort of efforts to preserve and promote native species are essentially slowing the loss of regional biotic uniqueness (McKinney 2006). Alternatively, changes to landscaping practices may allow for opportunities for natural regeneration (Nowak 2012). A significant challenge is that managing urban tree diversity will

require interdisciplinary co-operation by professionals in many disciplines, including: ecology, land-use planning, arboriculture, landscape architecture, and municipal engineering.

References to the importance of species diversity in the urban forest are often found in municipal management plans, but functional diversity is rarely included or discussed, despite the stronger links between functional diversity and ecosystem services and its rapidly increasing application in ecology (Díaz and Cabido 2001; Díaz and others 2004; Cadotte and others 2011). Although we did not find overall differences in the mean values for traits between urban and extra-urban samples (data not shown), traits for which data are not widely available may be important. Thus, research on traits likely related to urban tolerance (for example, root traits that may be important for tolerance of soil compaction) may help to identify new taxa suitable for urban areas. In particular, taxa should include those tolerant of high temperatures to cope with warming temperatures and the urban heat island. For example, recent research suggests that *Quercus rubra* L. (red oak) may benefit from the positive effects of the urban heat island on growth (Searle and others 2012).

In urbanizing regions across the globe, the goals of forest management shift from the tradition of commodity generation towards ecosystem services. Alternatively, one may view commodity generation as one service among a broad array of potential ecosystem services associated with forests, with an increased or even exclusive emphasis on non-commodity services in urbanizing regions. Developing a better understanding of interactions among urbanization and tree diversity will positively influence ecosystems in and beyond cities, and the health and well-being of billions of people.

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