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Climate differentiates forest structure across a residential macrosystem

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Abstract

The extent of urban ecological homogenization depends on how humans build, inhabit, and manage cities. Morphological and socio-economic facets of neighborhoods can drive the homogenization of urban forest cover, thus affecting ecological and hydrological processes, and ecosystem services. Recent evidence, however, suggests that the same biophysical drivers differentiating composition and structure of natural forests can further counteract the homogenization of urban forests. We hypothesize that climate can differentiate forest structure across residential macrosystems at regional-to-continental spatial scales. To test this hypothesis, forest structure (tree and shrub cover and volume) was measured using LiDAR data and multispectral imagery across a residential macrosystem composed 1.4 million residential parcels contained in 9 cities and 1503 neighborhoods. Cities were selected along an evapotranspiration (ET) gradient in the conterminous United States, ranging from the colder continental climate of Fargo, North Dakota (ET = 464.43 mm) to the hotter subtropical climate of Tallahassee, Florida (ET = 1000.47 mm). The relative effects of climate, urban morphology, and socio-economic variables on residential forest structure were assessed by using generalized linear models. Climate differentiated forest structure of the residential macrosystem as hypothesized. Average forest cover doubled along the ET gradient ($0.39 - 0.78 \text{ m}^2 \text{ m}^{-2}$), whereas average forest volume had a threefold increase ($2.50 - 8.12 \text{ m}^3 \text{ m}^{-2}$). Forest volume across neighborhoods increased exponentially with forest cover. Urban morphology had a greater effect in homogenizing forest structure on residential parcels compared to socio-economics. Climate and urban morphology variables best predicted residential forest structure, whereas socio-economic variables had the lowest predictive power. Results indicate that climate can differentiate forest structure across residential macrosystems and may counteract the homogenizing effects of urban morphology and socio-economic drivers at city-wide scales. This resonates with recent empirical work suggesting the existence of complex multi-scalar mechanisms that regulate ecological homogenization and ecosystem convergence among cities. The study initiates high-resolution assessments of forest structure across entire urban macrosystems and breaks new ground for research on the ecological and hydrological significance of urban vegetation at subcontinental scale.

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Keywords

green infrastructure; socio-ecological systems; urban ecology; urban trees; urban ecosystem convergence theory

Introduction

Urbanization is a major cause of ecological homogenization whereby geographically separated urban ecosystems become more similar compared to the respective native ecosystems nearby (Groffman et al. 2014; McKinney 2006). In fact, despite being located in different climates and biomes, cities often host biological communities that are homogenous in their taxonomic, evolutionary, or functional composition (Epp Schmidt et al. 2017; Morelli et al. 2016; Wheeler et al. 2017). Ecological, hydrological, and biophysical characteristics and functions of urban ecosystems can further depart from those of native ecosystems to converge among distant cities (Hall et al. 2016; Pouyat et al. 2003, 2015; Steele et al. 2014). In this way, urban homogenization can affect numerous ecological and hydrological processes that underpin the provision of ecosystem services (Larson et al. 2016), such as heat mitigation from tree canopies or stormwater infiltration through urban soil. This seems particularly evident when investigating residential land at regional-to-continental spatial scales, across what have been recently defined as *residential macrosystems* (Groffman et al. 2016, 2017).

The degree of urban homogenization, however, is the product of environmental and social drivers that operate at multiple scales (Chowdhury et al. 2011; Jenerette et al. 2016; Yang et al. 2015). These drivers can regulate ecological homogenization as well as differentiation. Management practices of residential land are often remarkably similar in different cities (Groffman et al. 2016; Harris et al. 2012). Though homogenization of yard management likely depends on urban context and scale (Polsky et al. 2014), management can locally override the effects dictated by regional biophysical constraints, such as climate or soil type (Groffman et al. 2014). At city-wide scale, the homogenizing effects of residential land management upon forest cover have been related to the social composition of neighborhoods (Boone et al. 2010; Grove et al. 2006). In fact socio-economic variables, such as income and education level, often inform our understanding of urban forest cover and the theories related to social stratification, luxury effect, and the “*ecology of prestige*” (Grove et al. 2014). For instance, wealthier neighborhoods tend to have greater forest cover than less affluent ones, even across cities located in different climates and biomes (Grove et al. 2014; Jenerette et al. 2011; Luck et al. 2009; Shanahan et al. 2014).

Urban morphology, defined as the composition and spatial arrangement of urban development features such as buildings, land parcels and infrastructures, has long been recognized as a driver in the homogenization of urban forests (Sanders 1984). The amount physical space for urban trees and shrubs to grow declines with density of development (i.e., parcels, buildings, impervious surfaces), itself a function of human demographics (Grove et al. 2014). In this way, forest cover and plant species diversity tend to increase in neighborhoods with higher residential land cover (Bigsby et al. 2014), lower parcel and

housing density (Cook et al. 2012; Marco et al. 2008; Smith et al. 2005; Tratalos et al. 2007), and larger parcel size (Lowry et al. 2012; Robinson 2012). In the last century, the shift from compact development to urban sprawl has reshaped the morphology of most cities (Sanders 1984). This, together with the fact that trees and shrubs grow over time, explains why urban forest cover is often related to the age of neighborhoods in numerous cities located in different climates (Bigsby et al. 2014; Luck et al. 2009).

However, recent empirical evidence suggests that climate can differentiate urban forest characteristics, as observed for native forests (Bailey 2009; Zhang et al. 2016), and despite of urban morphology and socio-economic context. Climate can in fact affect the distribution of urban tree species across North America (Nowak and Greenfield 2012), as well as their biodiversity (Ramage et al. 2013; Yang et al. 2015; Blood et al. 2016). Climate determines the pool of native plant species that can survive within cities following urbanization. Similarly, exotic species can be lost from cities based on their tolerance to climatic factors, such as temperature extremes and water availability (Jenerette et al. 2016). The selection of plant species from nurseries and horticultural businesses available to residents for planting also likely depend on climatic factors (Ramage et al. 2013). Thus, because urban forest structure ultimately depends upon species identity and community composition (Threlfall et al. 2016), it is then reasonable to expect the structure of urban forests to be likewise affected by climatic factors at a macroscale level.

Comprehensive assessments of the distribution and structure of urban forests have usually focused on one or a few cities (Bigsby et al. 2014; Cook et al. 2012), and have placed little emphasis on the biophysical variables affecting urban forests at the macroscale. These studies found that urban morphology and socio-economic drivers can homogenize forest cover within cities. However, each of these studies provides little comprehensive evidence on the effects of climate variables in shaping the structure of urban forests. Thus, our knowledge on the role that climate might play in counterbalancing ecological homogenization of urban forests is limited. Further, our understanding on how the vertical structure of urban vegetation change (e.g., canopy height and volume, vegetation layers, etc.) across entire urban landscapes is still in its infancy (Mitchell et al. 2016; Ossola and Hopton 2018). Early attempts to evaluate forest vertical structure across cities have relied on categorical data (e.g., tree, shrub, lawn cover) derived from vegetation classification (Grove et al. 2006b), because field-based data on forest structure are rare over large spatial scales (Berland and Manson 2013). This a critical gap in our understanding of urban forests because their vertical structure, rather than their horizontal cover, is more likely to regulate important ecological and hydrological processes (e.g., Berland et al. 2017; Ossola et al. 2015a, 2016; Pataki et al. 2010), the provision of habitat for biodiversity (e.g., Beninde et al. 2015; Ossola et al. 2015b), and numerous other ecosystem services (e.g., Davis et al. 2016; Lehmann et al. 2014).

In this study, we examined the relationship of climate, urban morphology, and socio-economic variables on forest structure across a residential macrosystem in the conterminous United States (US) by asking: i) does climate affect the structure of residential forests over large spatial scales?, and ii) what is the relative importance of climate, urban morphology and socio-economics in structuring residential forests?. In answering these questions, we

further hypothesized that: i) climate can differentiate the structure of residential forests, with forest cover and volume predicted to increase along a large evapotranspiration (ET) gradient, and ii) urban morphological and socio-economic characteristics of neighborhoods homogenize forest structure across the residential macrosystem.

Methods

Study areas

The cities of Fargo-Moorhead, ND-MN (hereafter Fargo, ND), Milwaukee, WI, Boston, MA, Newark, NJ, Washington, DC (or DC), Norfolk, VA, Raleigh-Durham, NC, Birmingham, AL, and Tallahassee, FL were selected for the study based on their geographic location and data availability. Cities are distributed from the cold continental climate of Fargo to the hot subtropical climate of Tallahassee (Fig. 1) to ensure that the residential macrosystem investigated was subjected to the largest climatic gradient as possible. Evapotranspiration (ET) and maximum water pressure deficit (VPD_{max}) double along the climatic gradient, increasing from 464.43 to 1000.47 mm and from 8.8 to 17.6 hPa, respectively (Mu et al. 2013; PRISM Climate Group 2015). Mean annual temperature (MAT) ranges between 5.6 and 19.7 °C and mean annual precipitation (MAP) between 594 and 1447 mm (PRISM Climate Group 2015). Cities are located in ecological regions that change accordingly to climate. In fact, Fargo is located in the west-central semi-arid prairies in a cold continental climate (Kottek et al. 2006; Omernik and Griffith 2014). Milwaukee, also characterized by a cold continental climate, lies in the central plains of the eastern forest region. Boston and Newark are surrounded by mixed forests (Kottek et al. 2006; Omernik and Griffith 2014), as they have a cold climate but with hotter summers. Washington DC, Norfolk, Raleigh-Durham, and Birmingham are located along the warmer south-eastern forest region in a temperate rainy climate, which becomes sub-tropical around Tallahassee (Kottek et al. 2006; Omernik and Griffith 2014). Thus, the volume of rural forests around cities, averaged within a 50 km radius from urban centers, tends to increase with ET along the climatic gradient (Fig. 1).

Data sources

Airborne LiDAR data were collected during leaf off conditions by federal, state, and local governments between March 2013 and April 2015 (Appendix A). LiDAR data had mean point spacing ranging between 0.332 and 0.522 m and mean vertical accuracy between 0.053 and 0.100 m (Appendix A).

Visible and near-infrared 1 m resolution imagery (2013–2015) was obtained from the National Agricultural Imagery Program (NAIP, United States Department of Agriculture) and collected at the vegetation phenological peak (Appendix A). Despite being not spectrally calibrated, NAIP imagery is commonly used to discriminate accurately between woody, herbaceous vegetation and impervious surfaces over entire cities (e.g., Bigsby et al. 2014; Davies et al. 2016; Ossola and Hopton 2018).

Tax parcel and land use/zoning maps, acquired from city, county, and state governments were used to select residential land and exclude other urban land uses (Appendix A). A total

of 1.4 million residential parcels, covering an area of 1400 km² and a population of 5.8 million inhabitants, were considered in the study (Table 1). Socio-economic indicators for 1503 census tracts were obtained from *American FactFinder* for year 2010 (US Census Bureau 2010). These comprise a set of 35 variables related to population, income, education, employment, social inequality, and housing characteristics (Appendix B) and have been used in other studies of urban forest cover (e.g., Bigsby et al. 2014). To include recently developed neighborhoods in our analyses and set a common socio-economic baseline across cities, we used current census indicators rather than historical ones, despite the latter are suggested to predict better urban tree cover at small spatial scales (Boone et al. 2010).

Geospatial analyses and validation

Geospatial analyses were performed in ArcGIS Desktop 10.4.1 (ESRI, Redlands, CA). Digital terrain models (DTMs) and surface models (DSMs) for each city were interpolated from LiDAR ground and first returns, respectively, by using natural neighbor triangulation (Davis et al. 2016; Ossola and Hopton 2018). A raster cell size of 1.5 m was selected for interpolations (Chen et al. 2006). Normalized digital surface models (nDSMs), representing the height of physical features from the ground (e.g., man-made structures, trees, etc.), were calculated for each city by subtracting the DTM from the respective DSM.

NAIP imagery was used to calculate normalized difference vegetation indices (NDVIs) for each city. Supervised classification based on nDSM, NDVI, and NAIP visible and near-infrared bands for each city, implemented through a maximum likelihood (ML) classifier, was used to classify i) herbaceous vegetation, ii) wooded, and iii) non-vegetated areas. A minimum of 100,000 raster cells were manually attributed to each of three land cover classes in each city through NAIP photo interpretation to calculate the spectral signature of each land cover class (Singh et al. 2012; Ossola and Hopton 2018). Spectral signatures were then used to inform the ML classifier and extend the classification to entire cities. Supervised classification allowed the calculation of a canopy cover mask for each city (Appendix C), later used to crop the respective nDSM and derive canopy height models (CHMs). Forest volume was calculated by multiplying each CHM by the raster cell area (2.25 m²), assuming the entire volume to be occupied by vegetation (Davis et al. 2016).

In each city, randomly generated points (n=100) for each vegetation cover class were verified by inspecting NAIP imagery to calculate the performance of each classification (confusion matrix), and thus classification accuracy and reliability. Because the cities of Fargo, ND and Washington, DC are adjacent to state boundaries, separate classifications and validations were performed by using NAIP datasets available for adjacent states (Appendix A). Mean accuracy and reliability of classification of forest cover across cities was $96.50 \pm 0.77 \%$ and $94.55 \pm 1.08 \%$, respectively (Appendix D), which are comparable to those achieved in a recent study of Baltimore, MD and Raleigh, NC (Bigsby et al. 2014). Residential forest cover (m² m⁻²) and volume (m³ m⁻²) were first summarized within each residential parcel and then averaged at census tract level. Census tracts considered for statistical analyses had a minimum density of 100 residential parcels per km² with a minimum of 100 residential parcels per tract to exclude areas with marginal residential cover. Rural forest volume (m³ m⁻²) was calculated from a 1 km resolution global forest

canopy height dataset (Simard et al. 2011) by averaging all values within 50 km from urban centers.

Statistical analyses

Statistical analyses were performed in R 3.3.1 (R Core Team 2016) with the libraries *usdm* (Naimi 2015), *caret* (Kuhn et al. 2016), *devtools* (Wickham and Chang 2016), and *AICcmodavg* (Mazerolle 2015). A racial diversity index, computed as the Shannon-Weiner diversity index on the proportion of races living in each census tract, was calculated using the R library *vegan* (Oksanen et al. 2014). The age of maximum housing development of each census tract was calculated as the decade having the highest number of structures built.

Prior to statistical modeling, a stepwise selection based on variance inflation factors (VIF = 2) was performed by using the “vifstep” function in the R package “usdm” (Naimi et al. 2014) to exclude multicollinear variables at $R^2 > 0.5$ (Zuur et al. 2010). In particular, mean residential parcel size, percent high school graduate, percent bachelor’s degree graduate, median income, percent families below poverty level, and percent renter-occupied housing units were excluded due to multicollinearity. Generalized linear models (GLMs) were used to assess the effects of climate, urban morphology, socio-economics, and their interactions upon residential forest structure (response variables: forest cover and volume). VIF-selected variables were used to compose 7 model types based on climate, urban morphology, socio-economic variables, and their combinations (Table 2). Global models were fitted by using all VIF-selected variables. GLMs predicting forest volume were fitted by using linear regression. Logistic regression was used to predict forest cover as it has higher predictive power in modeling tree canopy cover compared to linear regression (Bigsby et al. 2014). Linear and quadratic terms were used for each GLM based on exploratory statistical analyses. An information-theoretic approach based on minimized Akaike Information Criterion (AIC) was used to select the best performing GLMs considering equally predictive models with $\Delta AIC < 3$ (Burnhan and Anderson 2002). Average values are reported with the respective standard errors (SE).

Results

Forest volume in residential parcels increased exponentially with forest cover (Fig. 2). Overall, residential forest structure increased with ET (Fig. 3). Mean residential forest cover doubled from Fargo, ND to Tallahassee, FL (0.39 ± 0.03 and $0.78 \pm 0.01 \text{ m}^2 \text{ m}^{-2}$, respectively), with a three-fold increase in mean forest volume (2.50 ± 0.25 and $8.12 \pm 0.26 \text{ m}^3 \text{ m}^{-2}$, respectively). The volumetric difference between residential and rural forests (averaged within 50 km from urban centers) was greater in Fargo-Moorhead and Tallahassee, at the extremities of the ET gradient (Table 3). As such, the residential forest in Tallahassee had about half volume compared to that of the surrounding rural forest, whereas the rural forest around DC had a volume six times greater than that of the residential forest (Table 3).

The GLM based on climate and urban morphology best predicted residential forest cover, whereas forest volume was best predicted by the global model (Table 4). Forest cover and volume decreased with residential parcel density and increased with residential land cover

(Fig. 4A, B, D, E). Mean forest cover and volume peaked in census tracts developed during the 1970s and 1980s, respectively (Fig. 4C, F). Residential parcel density was the best predictor of forest cover and volume, followed by residential land cover and ET (Appendix E). Residential forest volume decreased in census tracts with high unemployment rates (Appendix E), whereas forest volume increased with median monthly rent in some cities (i.e., Newark, Birmingham, and Tallahassee) but not in the others (Appendix F). Similarly, median annual income (excluded from GLM modeling being correlated with monthly rent) had either negative, positive, or no relationship with forest structure in the different cities (Fig. 5; Appendix F).

Residential parcel size was negatively correlated to residential parcel density (Pearson's $\rho = -0.594$, $p < 0.001$), and positively to residential land cover ($\rho = 0.299$, $p < 0.001$). Parcel size had a logarithmic relationship with residential forest cover (Fig. 6A), and increased with the decade of maximum housing development from the 1930s to the 1980s, to then decrease in more recently developed neighborhoods (Fig. 6B). Median annual income was negatively correlated with percent vacant housing units ($\rho = -0.5496$, $p < 0.001$) and unemployment rate ($\rho = -0.519$, $p < 0.001$), and positively correlated with median rent ($\rho = 0.701$, $p < 0.001$) and median population age ($\rho = 0.485$, $p < 0.001$).

Discussion

Residential forest structure and climate

As hypothesized, residential forest cover and volume increased with ET, leading to the differentiation of forest structure across the residential macrosystem. Compared to urban morphological characteristics, however, climate had a relatively smaller effect on residential forest structure. Luck et al. (2009) found climate to have little effect on urban forest cover in nine urban areas located across two climatic zones in south-east Australia (Kottek et al. 2006). The discrepancy between the study from Luck et al. (2009) and this study might be explained by the larger urban macrosystem considered here, where cities are distributed across three climatic zones (Kottek et al. 2006). Both residential forest cover and volume, however, had relatively smaller variations between Fargo and DC ($0.16 \text{ m}^2 \text{ m}^{-2}$ and $0.42 \text{ m}^3 \text{ m}^{-2}$, respectively), compared to those measured between DC and Tallahassee ($0.55 \text{ m}^2 \text{ m}^{-2}$ and $5.74 \text{ m}^3 \text{ m}^{-2}$, respectively). In this way, climatic signals in the structure of urban forests might be concealed when considering narrow residential macrosystems over relatively small spatial scales, or climatic or biophysical gradients. The use of leaf-off, rather than leaf-on, LiDAR data might have determined small differences in estimates of forest height ranging in the order of centimeters. However, these differences are negligible when considering that the variation in forest height and volume across the macrosystem is an order of magnitude greater (Table 3). In fact, evidence suggests that leaf-off LiDAR data can be reliably used to model forest structure, particularly in the eastern US forests (Parent 2014).

Despite growing evidence on the homogenization of lawn florae (Wheeler et al. 2017), climate affects how plant species are filtered in urban environments based on their climatic tolerance and commercial availability (Jenerette et al. 2016, Ramage et al. 2013). People's perceptions, values, and management practices of urban trees and shrubs can be also affected by climate (Schroeder 2006). For instance, residents prefer shade trees in the hotter areas of

a climatic gradient in southern California - an effect likely to be amplified at larger spatial scales (Avolio et al. 2015). This suggests that in warmer climates larger tree species with higher leaf area could be preferred over smaller species with sparser canopies, further affecting the structure of residential forests.

Residential forest volume across Raleigh-Durham had higher variability ($SE = 0.222 \text{ m}^3 \text{ m}^{-2}$) compared to other cities (average $SE = 0.049 \text{ m}^3 \text{ m}^{-2}$). In this urban area, one of the ten most sprawled in the US (Resnik 2010), forests contained in residential parcels may have retained a significant proportion of the native species originally occurring in rural forests prior to urbanization, as similarly reported for other cities in southeastern US (Blood et al. 2016). Because rural forests around Raleigh-Durham are characterized by a mix of tall conifer species (McNab et al. 2007), this might explain the relatively high residential forest volume recorded in some census tracts and the overall higher variance in this urban area. Previous land use has been shown to impact important urban forest characteristics, such as forest productivity (Briber et al. 2015), and future investigations on forest structure across urban macrosystems could be refined to further investigate this factor.

Despite changing along the ET gradient, residential forest volume was 15–50 % of that measured in rural forests. This suggests that a decrease in the intensity of local homogenizing drivers could lead the structure of residential forests toward the structure of surrounding rural forests. Residential forests could be actively managed to enhance their structure, particularly in cities with lower forest structural complexity. The exponential relationship between forest cover and volume we found implies that increasing residential forest cover might determine increasingly larger gains in term of forest volume. In this way, the provision of ecosystem services related to the vertical structure of forest on residential parcels (e.g., stormwater canopy interception, heat mitigation, habitat for biodiversity, etc.) could be enhanced even through relatively small increments in forest cover. This is important because increasing tree canopy cover across cities is not always feasible due to lack of space, opportunity, and residents' personal preferences toward private vegetation with low structural complexity (Shakeel and Conway 2014; Visscher et al. 2016). Devising urban forestry practices that consider climate and the larger biophysical settings of urban macrosystems could help define more realistic targets for urban forestry and greening programs at the national level.

Homogenizing effects of urban morphology and socio-economics

Our second hypothesis, that urban morphological and socio-economic characteristics of neighborhoods would homogenize forest structure across the residential macrosystem, was partially supported. Variables representing urban morphology had, in fact, greater influence in homogenizing forest structure than socio-economic variables. In particular, neighborhoods with residential parcel density higher than 2000 parcels km^{-2} had less than a fourth of each parcel covered by woody vegetation, regardless of the city. In contrast, across the 9 cities, neighborhoods with an average residential forest cover exceeding $0.50 \text{ m}^2 \text{ m}^{-2}$ had parcels density lower than 1000 parcels km^{-2} . As parcel density is negatively related to yard area, this suggest that the available physical space for vegetation to grow is an important factor that can lead to the homogenization of residential forest structure across

cities. Socio-economic variables alone had the lowest power in predicting residential forest cover and volume, as also observed in a study of canopy cover in Salt Lake County, UT (Lowry et al. 2012). Forest volume was best predicted by the global GLM, but two significant socio-economic variables, median monthly rent and unemployment rate, had the lowest importance among all significant variables. This resonates with recent evidence that attributed tree cover homogenization in Baltimore, MD and Raleigh, NC to urban morphology rather than the socio-economic context of these cities (Bigsby et al. 2014). Similarly, weak effects of socio-economic variables upon urban tree cover and biodiversity have been found in other cities in North America (Berland et al. 2015; Jenerette et al. 2016). As pointed out in other macroecological work (Ramage et al. 2013, Jenerette et al. 2016), this study does not lessen the importance of socio-economic drivers in shaping urban forests. Instead, it reinforces that these factors might be locally-important sources of ecological homogenization, but their effects could be masked by more complex multiscale interactions with other homogenizing and differentiating drivers such as those dictated by urban form and climate. Further, only partial support for the luxury effect theory was found, as noticed in a study of urban tree cover in Los Angeles, CA (Clarke et al. 2013). A positive relationship between median annual income and residential forest structure was observed in Milwaukee, Newark, Boston, and DC, but this relationship was weak or negative in the other cities. This might be partially due to the resolution of census data used in the study (i.e., census tract vs census block level) or the development history of cities. Further, we predicted parameters of forest structure by using census data for the year 2010 to be able to include more recently developed neighborhoods. Stronger social effects could have been detected by using historical census data (Bigsby et al. 2014; Boone et al. 2010). In general, comparing forest characteristics among cities is a difficult task due to different urbanization trajectories, historical legacies, future development plans, and because most studies to date focused on a few cities (Cook et al. 2012). Synoptic analyses of urban macrosystems can improve our knowledge of urban forests and their structure while allowing more robust generalizations across spatial scales and environmental gradients.

Overall, residential parcel density was the most important driver leading to homogenization of forest structure across the residential macrosystem. This confirms findings from other cities where parcel density had a negative relationship with tree cover and above-ground biomass (Briber et al. 2015; Tratalos et al. 2007). Census tracts with greater residential cover had higher forest cover and volume, as observed for tree cover in Baltimore, MD and Raleigh, NC (Bigsby et al. 2014). The age of maximum housing development of neighborhoods had a small negative effect on the overall residential forest structure, though it was non-significant for forest cover. The effects of neighborhood age upon forest cover have been documented in numerous studies following the rationale that trees grow over time (Grove et al. 2006; Troy et al. 2007). However, as Bigsby et al. (2014) noticed in Raleigh, mean parcel size progressively increased until the 1980s to then decrease in the 2000s. The decade of maximum development of neighborhoods co-varied with the size of residential parcels across the residential macrosystem. Thus, residential forests could be structured by the availability of physical space for trees and shrubs to grow (Lowry et al. 2012; Robinson 2012), as well as the time allowed for them to grow (Berland et al. 2015).

Conclusion

Our study represents one of the first synoptic assessments of the three-dimensional structure of forests across urban residential macrosystems as affected by both homogenizing and differentiating drivers. More research is needed to understand to what extent differentiating and homogenizing effects of climate, urban form, and social context are consistent across other residential and urban macrosystems. This is particularly important when looking at interactions among these factors across large spatial scales and gradients in relation to mechanisms leading to ecological homogenization and differentiation. The use of big data, new GIS and remote sensing technologies, and increased computing capability offer promising venues for future research on forests across urban macrosystems, their emerging properties, and drivers of change. New investigations will provide a more complete understanding of how ecological and hydrological processes underpinning ecosystem services are generated by urban forests within and among cities.

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Appendix A.: Sources and specifications of LiDAR, multispectral imagery (NAIP), property and land use datasets used for the cities considered in the study.

City, State	Fargo, ND Moorhead, MN	Milwaukee, WI	Boston, MA	Newark, NJ	Washington, DC	Norfolk, VA	Raleigh- Durham, NC	Birmingham, AL	Tallahassee, FL
LiDAR dataset name	Fargo- Moorhead LiDAR 2014	Southeast WI Counties LiDAR 2015	LiDAR Point Cloud MA Sandy CMGP 2013	LiDAR Point Cloud NJ SdL5 2014	LiDAR Point Cloud MD-VA Sandy NCR 2014	LiDAR Point Cloud VA Norfolk 2013	North Carolina QL2 LiDAR 2015	LiDAR Point Cloud Jefferson County 2013	Leon County, FL LiDAR 2015
LiDAR provider	City of Fargo	Milwaukee County	USGS	USGS	USGS	USGS	NCDPS, NCDOT	USGS	Leon County
LiDAR collection period	10.05.2014 22.05.2014	24.03.2015 03.04.2015	16.11.2013 31.12.2014	21.03.2014 21.04.2014	10.04.2014 20.12.2014	21.03.2013 05.04.2013	10.01.2015 22.03.2015	13.04.2013 07.05.2013	15.01.2015 05.02.2015
Vertical accuracy (cm)	9.25	10	5.3	5.8	5.9	6.6	9.25	9.7	9.14
Horizontal accuracy (m)	0.67	0.27	0.36	0.5	0.5	1.0	NA	1.0	1.1
Nominal point spacing (m)	0.7 ^a	0.7 ^a	0.7	0.7	0.7	0.7	0.7 ^a	0.6 ^a	0.41 ^a
Minimum point	0.289	0.367	0.391	0.325	0.289	0.309	0.280	0.303	0.201

spacing (m)									
Mean point spacing (m)	0.375	0.457	0.508	0.522	0.410	0.418	0.403	0.403	0.332
Maximum point spacing (m)	0.463	1.349 ^b	1.231 ^b	1.088 ^b	0.946 ^b	1.162 ^b	0.484	0.583	0.640
Total LiDAR points	$3.023 \cdot 10^9$	$4.180 \cdot 10^9$	$2.689 \cdot 10^9$	$3.235 \cdot 10^9$	$3.579 \cdot 10^9$	$4.756 \cdot 10^9$	$5.998 \cdot 10^9$	$7.977 \cdot 10^9$	$16.38 \cdot 10^9$
Number of LiDAR tiles	151	88	295	379	253	338	405	544	722
USDA NAIP collection year	ND 2014 MN 2015	WI 2015	MA 2014	NJ 2015	MD 2015 VA 2014	VA 2014	NC 2014	AL 2013	FL 2015
Parcel, land use data provider	City of Fargo	Milwaukee County	City of Boston, Commonwealth of MA	NJ State	Arlington County and DC	Cities of Norfolk and Virginia Beach	Durham and Wake Counties	Jefferson County	Leon County

^a The original unit of measure of these LiDAR datasets is the US foot. These have been converted to meter using the equivalency 1 foot = 0.3048 meter.

^b Some LiDAR tiles partially cover water bodies and consequently have relatively higher point spacing compared to tiles covering land.

Appendix B.: Details of the socio-economic indicators aggregated at census tract level (year 2010) obtained from the American FactFinder of the US Census Bureau (<https://factfinder.census.gov/>).

Socio-economic indicator	Description
DP0020001	Median age (both sexes)
DP0090001	White alone or in combination with one or more other races
DP0090002	Black or African American alone or in combination with one or more other races
DP0090003	American Indian and Alaska Native alone or in combination with one or more other races
DP0090004	Asian alone or in combination with one or more other races
DP0090005	Native Hawaiian and Other Pacific Islander alone or in combination with one or more other races
DP0090006	Some Other Race alone or in combination with one or more other races
DP0120002	Population in households
DP0120014	Population in group quarters
DP0130002	Family households
DP0130010	Nonfamily households
DP0160001	Average household size
DP0170001	Average family size
DP0180002	Occupied housing units

Socio-economic indicator	Description
DP0180003	Vacant housing units
DP0210002	Owner-occupied housing units
DP0210003	Renter-occupied housing units
HC01_EST_VC16	Percent high school graduate or higher (table S1501)
HC01_EST_VC17	Percent bachelor's degree or higher (table S1501)
HC01_EST_VC01	All families (table S1702)
HC02_EST_VC01	Percent families below poverty level (table S1702)
HD01_VD01	Gini Index (table B19083)
HC02_EST_VC02	Median income (dollars) per household (table S1903)
HC01_EST_VC24	Working-age population 20 to 64 years (table S2301)
HC02_EST_VC24	In labor population 20 to 64 years (table S2301)
HC03_EST_VC24	Employed population 20 to 64 years (table S2301)
HC04_EST_VC24	Unemployment rate 20 to 64 years (table S2301)
HD01_VD01	Median contract rent (table B25058)
HD01_VD02	Buildings built in 2005 or later (table B25034)
HD01_VD03	Buildings built 2000 to 2004
HD01_VD04	Buildings built 1990 to 1999
HD01_VD05	Buildings built 1980 to 1989
HD01_VD06	Buildings built 1970 to 1979
HD01_VD07	Buildings built 1960 to 1969
HD01_VD08	Buildings built 1950 to 1959
HD01_VD09	Buildings built 1940 to 1949
HD01_VD10	Buildings built 1939 or earlier

Appendix C.: Example of two neighborhoods in Boston, MA in false infrared imagery to highlight vegetation (in red, upper panel) and the canopy cover map (in green, lower panel) derived from supervised classification on NAIP and LiDAR data.



Appendix D.: Confusion matrices calculated to test accuracy, reliability, and Kappa statistic of the maximum likelihood supervised classification of urban vegetation in the urban areas investigated based on data fusion of the NAIP imagery, NDVI, and nDSM. Reliability represents type I errors (false positives), accuracy represents type II errors (false negatives), and Kappa evaluates the overall performance of classification. (*) Vegetation classification for Fargo-Moorhead, ND-MN, and Washington, DC was

modeled separately based on the two respective NAIP datasets available for bordering states (Appendix A).

Fargo, ND* (2014 NAIP North Dakota)		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	87	11	2	100	0.870	-
	Herbaceous vegetation	0	100	0	100	1.000	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	87	111	2	200	0.000	-
	Accuracy	1.000	0.901	0.000	0.000	0.935	-
	Kappa	-	-	-	-	-	0.871

Moorhead, MN* (2015 NAIP Minnesota)		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	94	3	3	100	0.940	-
	Herbaceous vegetation	1	99	0	100	0.990	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	95	102	3	200	0.000	-
	Accuracy	0.989	0.971	0.000	0.000	0.965	-
	Kappa	-	-	-	-	-	0.931

Milwaukee, WI		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	91	9	0	100	0.910	-
	Herbaceous vegetation	7	93	0	100	0.930	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	98	102	0	200	0.000	-
	Accuracy	0.929	0.912	0.000	0.000	0.920	-
	Kappa	-	-	-	-	-	0.840

Boston, MA		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	91	9	0	100	0.910	-
	Herbaceous vegetation	1	99	0	100	0.990	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	92	108	0	200	0.000	-
	Accuracy	0.989	0.917	0.000	0.000	0.950	-
	Kappa	-	-	-	-	-	0.900

Newark, NJ		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	95	5	0	100	0.950	-
	Herbaceous vegetation	4	95	1	100	0.950	-
	Non-vegetated	0	0	1	0	0.000	-
	Total	99	100	0	200	0.000	-
	Accuracy	0.960	0.950	0.000	0.000	0.950	-
	Kappa	-	-	-	-	-	0.900

Washington, DC* (2014 NAIP Virginia)		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	98	0	2	100	0.980	-
	Herbaceous vegetation	6	94	0	100	0.940	-
	Non-vegetated	0	0	2	0	0.000	-
	Total	104	94	0	200	0.000	-
	Accuracy	0.942	1.000	0.000	0.000	0.960	-
	Kappa	-	-	-	-	-	0.921

Washington, DC* (2015 NAIP Maryland)		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	99	1	0	100	0.990	-
	Herbaceous vegetation	9	92	0	100	0.920	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	107	93	0	200	0.000	-
	Accuracy	0.925	0.989	0.000	0.000	0.955	-
	Kappa	-	-	-	-	-	0.910

Norfolk, VA		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	94	2	4	100	0.940	-
	Herbaceous vegetation	1	99	0	100	0.940	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	95	101	4	200	0.000	-
	Accuracy	0.989	0.980	0.000	0.000	0.965	-
	Kappa	-	-	-	-	-	0.931

Raleigh-Durham, NC		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	97	1	2	100	0.970	-
	Herbaceous vegetation	6	93	1	100	0.930	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	103	94	3	200	0.000	-
	Accuracy	0.942	0.989	0.000	0.000	0.950	-
	Kappa	-	-	-	-	-	0.901

Birmingham, AL		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	99	1	0	100	0.990	-
	Herbaceous vegetation	3	97	0	100	0.970	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	102	98	0	200	0.000	-
	Accuracy	0.971	0.990	0.000	0.000	0.980	-
	Kappa	-	-	-	-	-	0.960

Tallahassee, FL		Classification					
		Woody vegetation	Herbaceous vegetation	Non-vegetated	Total	Reliability	Kappa
Ground truth	Woody vegetation	95	5	0	100	0.950	-
	Herbaceous vegetation	2	98	0	100	0.980	-
	Non-vegetated	0	0	0	0	0.000	-
	Total	97	103	0	200	0.000	-
	Accuracy	0.979	0.951	0.000	0.000	0.965	-
	Kappa	-	-	-	-	-	0.930

Appendix E.:

Summary statistics of the best fitting GLM (*climate – urban morphology model*) predicting residential forest vegetation cover ($\text{m}^2 \text{m}^{-2}$). Significant variables are in bold, marginally non-significant variables are indicated by an asterisk (*). Variables are ranked by importance.

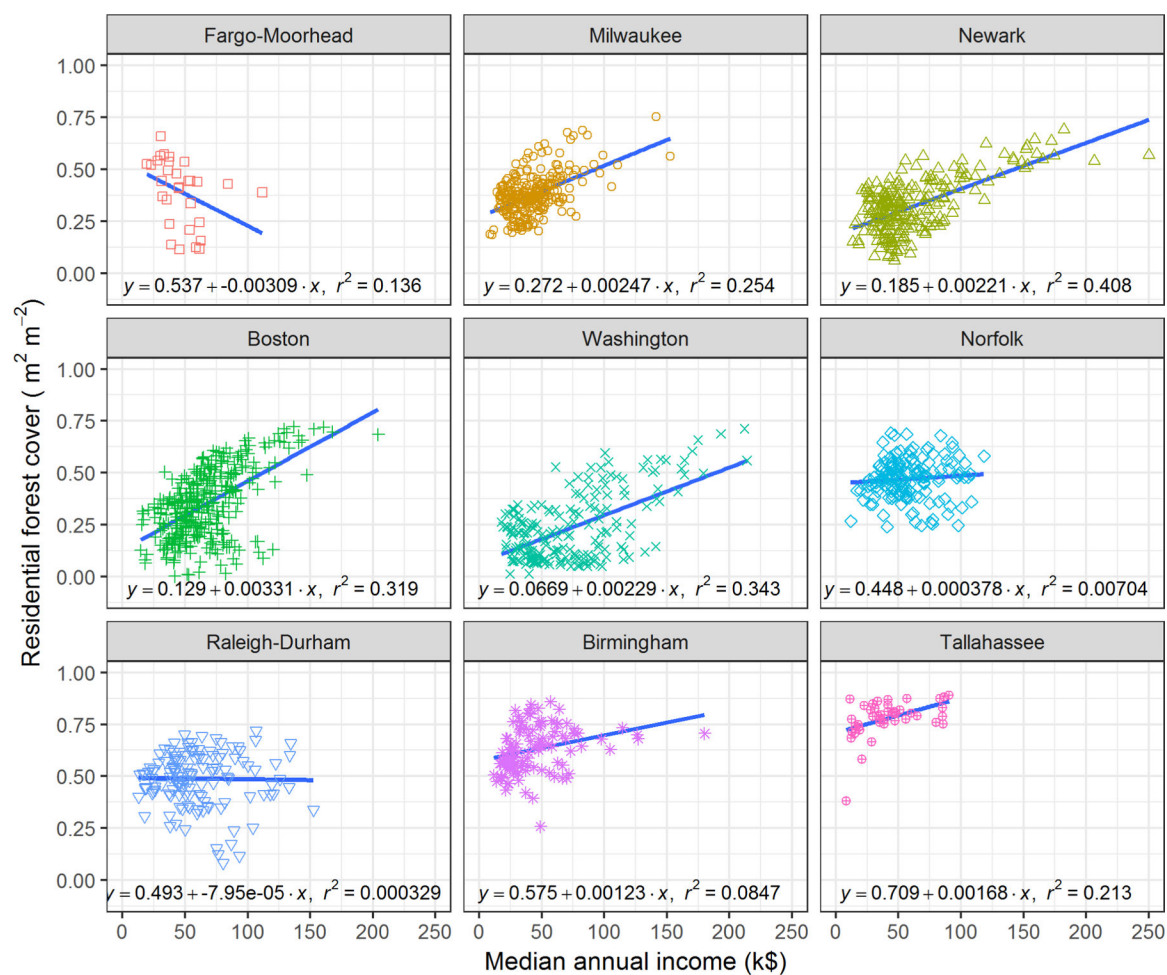
Response variable: forest cover						
Predictor variable	Term	Estimate	Standard error	Z value	Probability	Variable importance
	Intercept	12.764	6.834	1.868	0.062	
Residential parcel density	Linear	-18.331	3.269	-5.608	< 0.001	100.00
Residential land cover	Linear	13.099	2.508	5.223	< 0.001	90.859
ET	Quadratic	4.887	2.438	2.005	0.045	14.416
Maximum housing development	Linear	-0.007	0.003	-1.982	0.048	13.874
Residential parcel density	Quadratic	-4.241	2.479	-1.710	0.087*	7.423

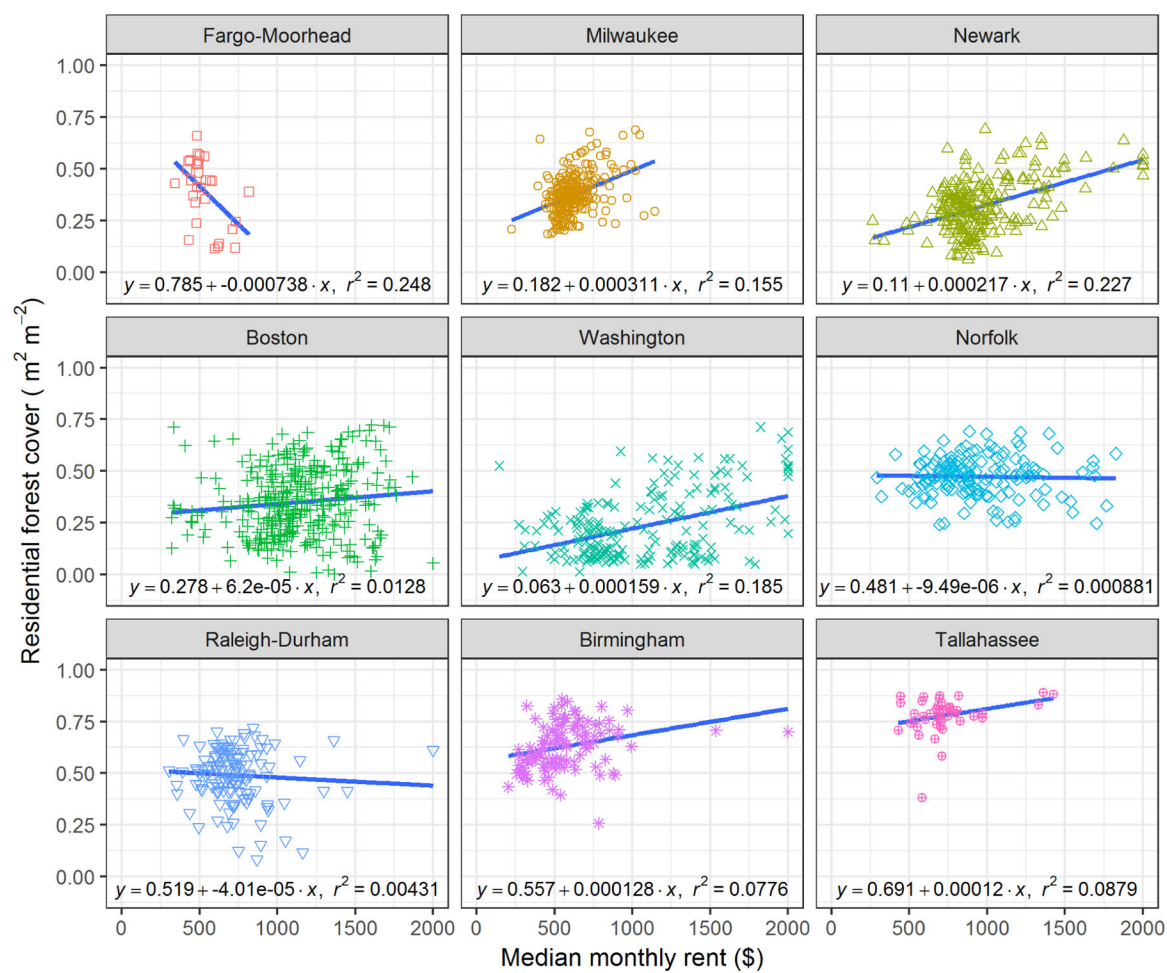
Response variable: forest cover						
Predictor variable	Term	Estimate	Standard error	Z value	Probability	Variable importance
Residential land cover	Quadratic	-3.770	2.302	-1.638	0.102	5.701
ET	Linear	3.305	2.365	1.398	0.162	0.000
Null deviance	123.038 on 1493 degree of freedom					
Residual deviance	42.143 on 1486 degree of freedom					
AIC	1217.4					

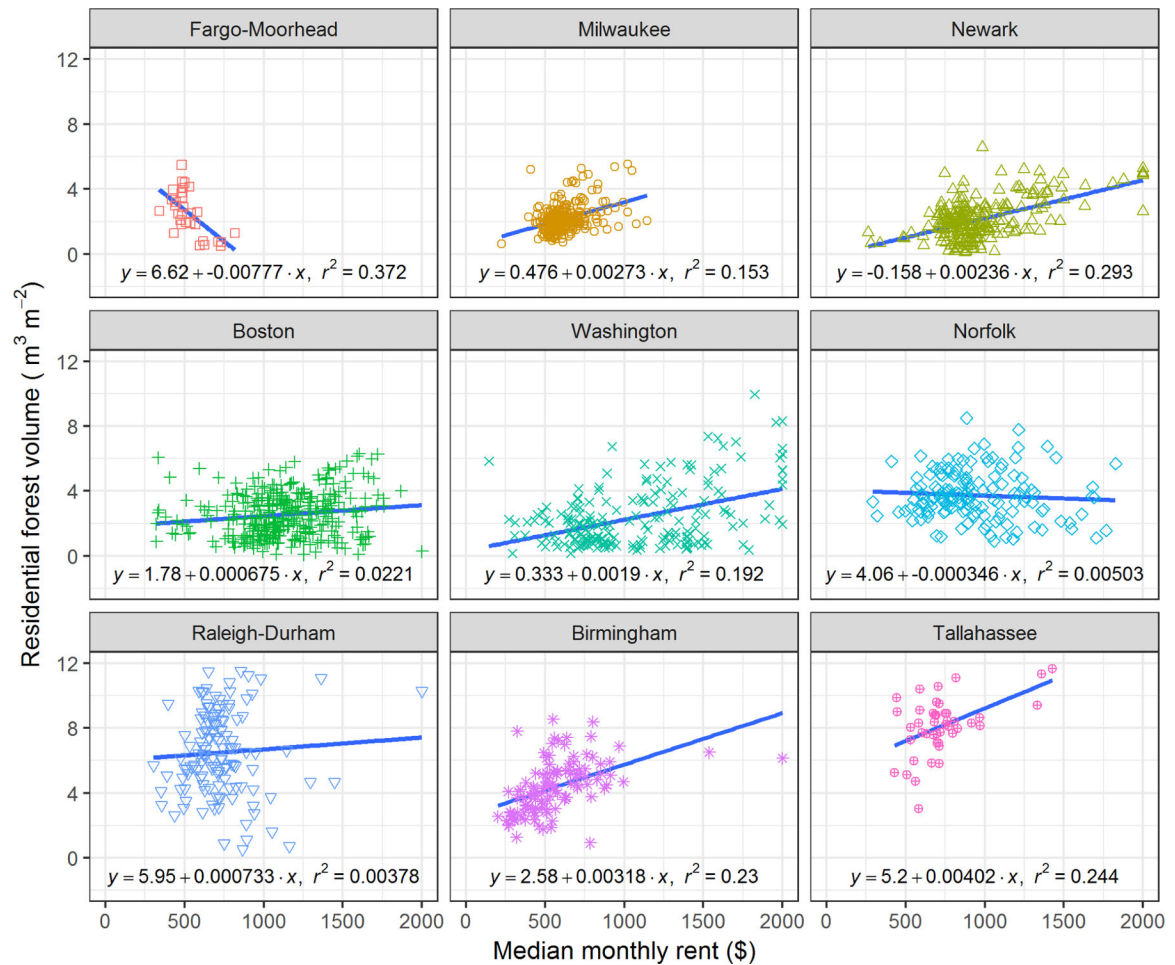
Summary statistics of the best fitting GLM (*global model*) predicting residential forest vegetation volume ($\text{m}^3 \text{m}^{-2}$). Significant variables are in bold.

Response variable: forest volume						
Predictor variable	Term	Estimate	Standard error	Z value	Probability	Variable importance
	Intercept	4.682	0.749	6.250	< 0.001	
Residential parcel density	Linear	-9.801	0.380	-25.762	< 0.001	100.00
Residential land cover	Linear	5.885	0.291	20.230	< 0.001	78.287
ET	Linear	3.638	0.275	13.250	< 0.001	50.888
Residential land cover	Quadratic	-2.531	0.236	-10.733	< 0.001	41.008
Residential parcel density	Quadratic	-2.614	0.273	-9.590	< 0.001	36.524
Maximum housing development	Linear	-0.002	0.0003	-6.065	< 0.001	22.687
ET	Quadratic	0.935	0.247	3.775	< 0.001	13.699
Median monthly rent	Linear	0.714	0.306	2.330	< 0.05	8.029
Median monthly rent	Quadratic	-0.528	0.235	-2.250	0.025	8.291
Unemployment rate	Quadratic	0.492	0.233	-2.104	0.036	7.139
Race diversity index	Linear	-0.028	0.024	-1.191	0.234	3.556
Vacant residential units	Linear	-0.017	0.016	-1.020	0.308	2.886
Median age	Linear	0.001	0.001	0.573	0.566	1.133
Income inequality (Gini)	Linear	0.043	0.093	0.461	0.645	0.691
Unemployment rate	Linear	-0.084	0.296	-0.285	0.776	0.000
Null deviance	356.83 on 1493 degree of freedom					
Residual deviance	137.37 on 1478 degree of freedom					
AIC	708.26					

Appendix F.: Relationship between forest cover and median annual income summarized at census tract level in the nine cities investigated. Cities are ordered by increasing ET.







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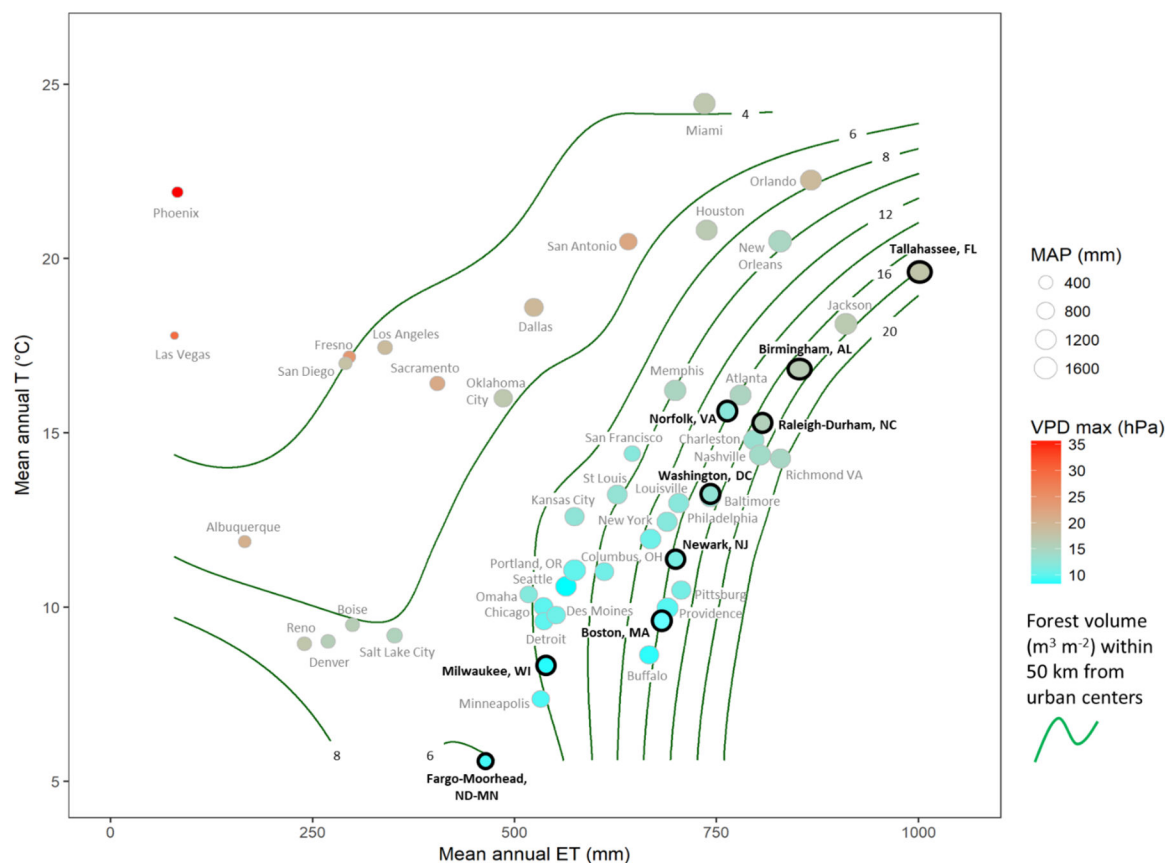
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**FIG. 1.**

Cities selected in the study (in bold) in relation to mean annual temperature (MAT), evapotranspiration (ET), maximum water vapor pressure deficit (VPD_{max}), precipitation (MAP), and rural forest volume (green lines) averaged within a 50 km radius from each urban center. MAT, MAP and VPD_{max} are calculated from 30-year normals at 800 m resolution (PRISM Climate Group 2015). ET is calculated from the 1 km resolution MODIS Global Evapotranspiration MOD16 Project (Mu et al. 2013). Rural forest volume (m³ m⁻²) is calculated from the 1 km resolution global forest canopy height dataset from Simard et al. (2011).

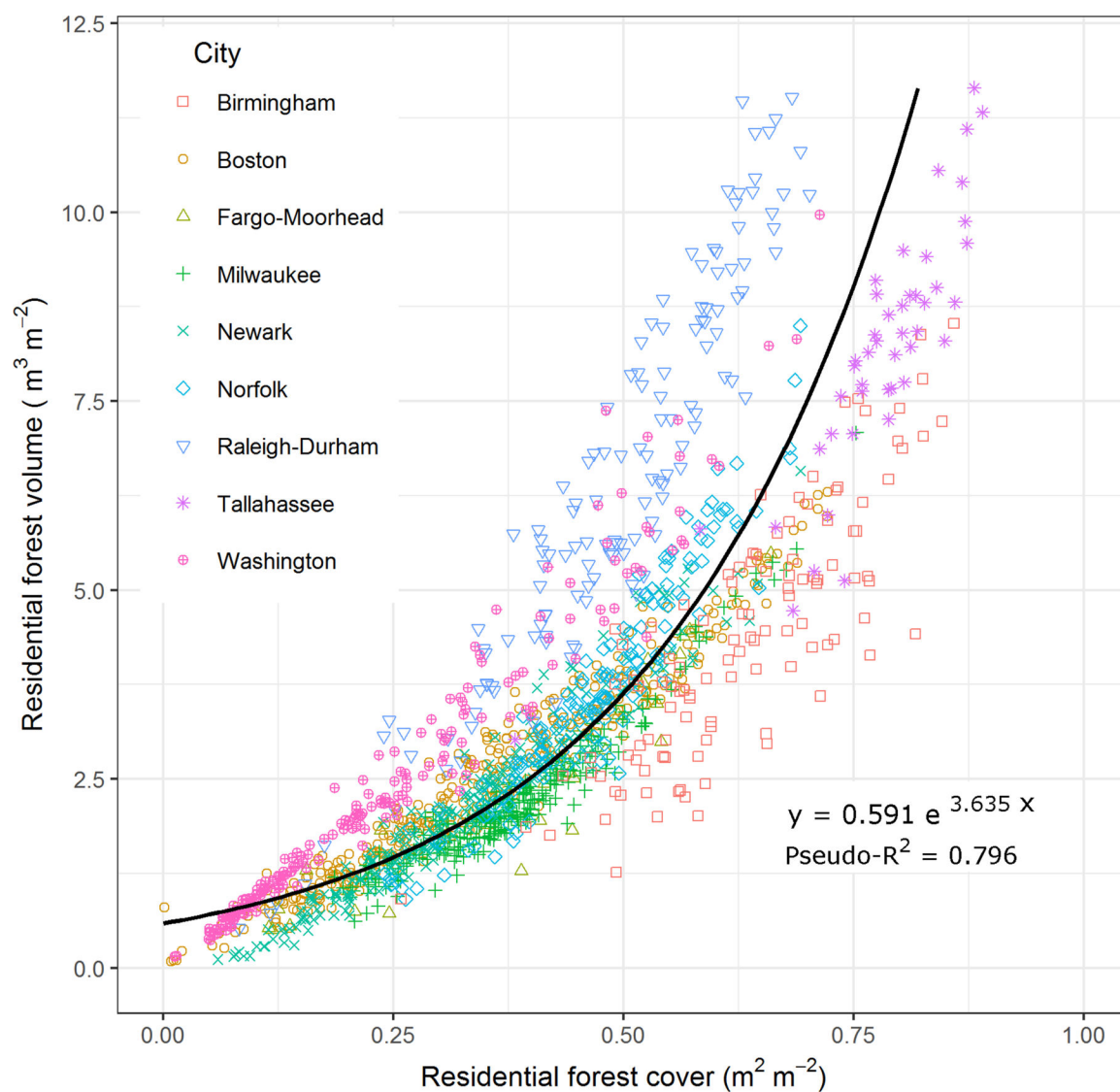
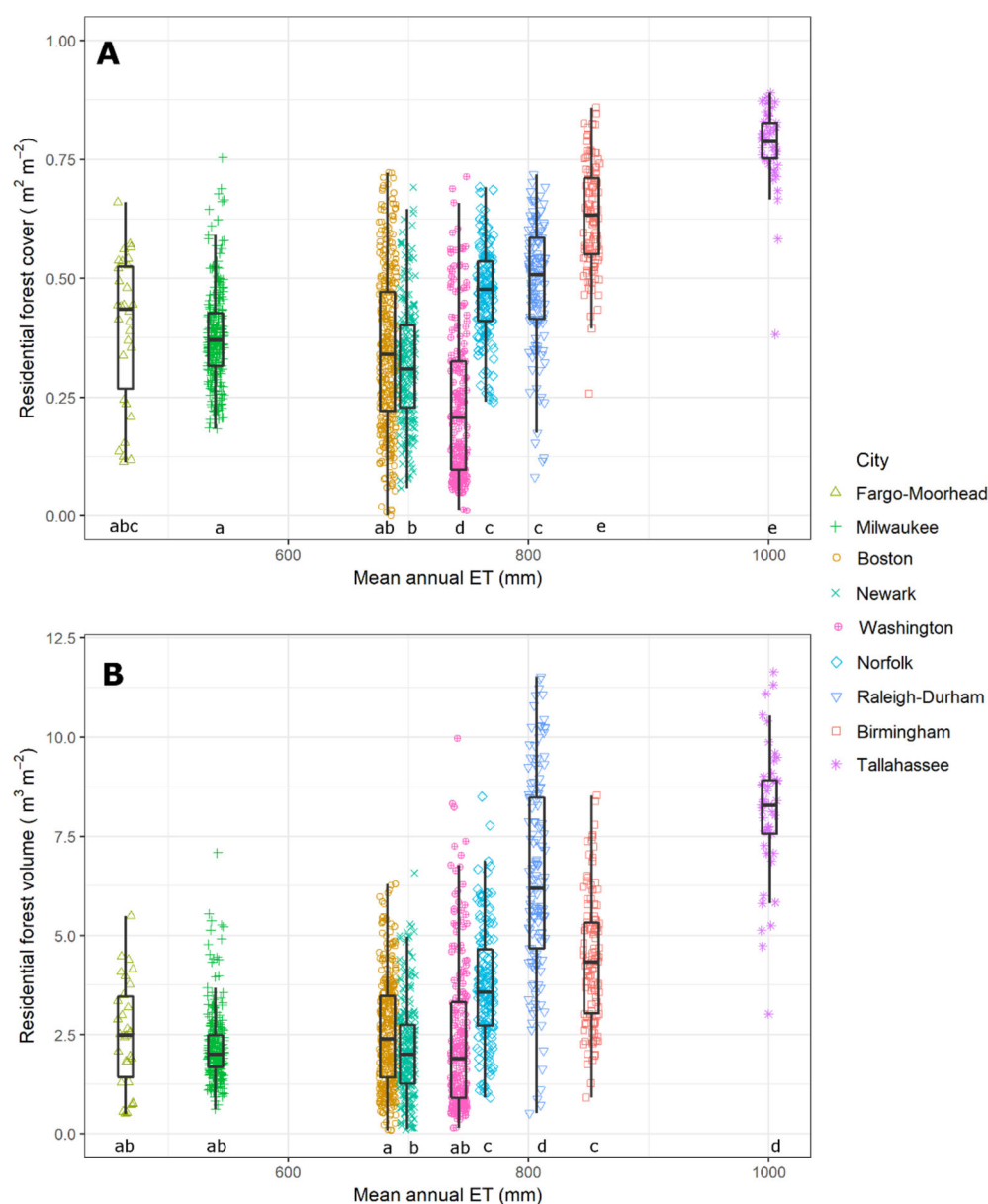
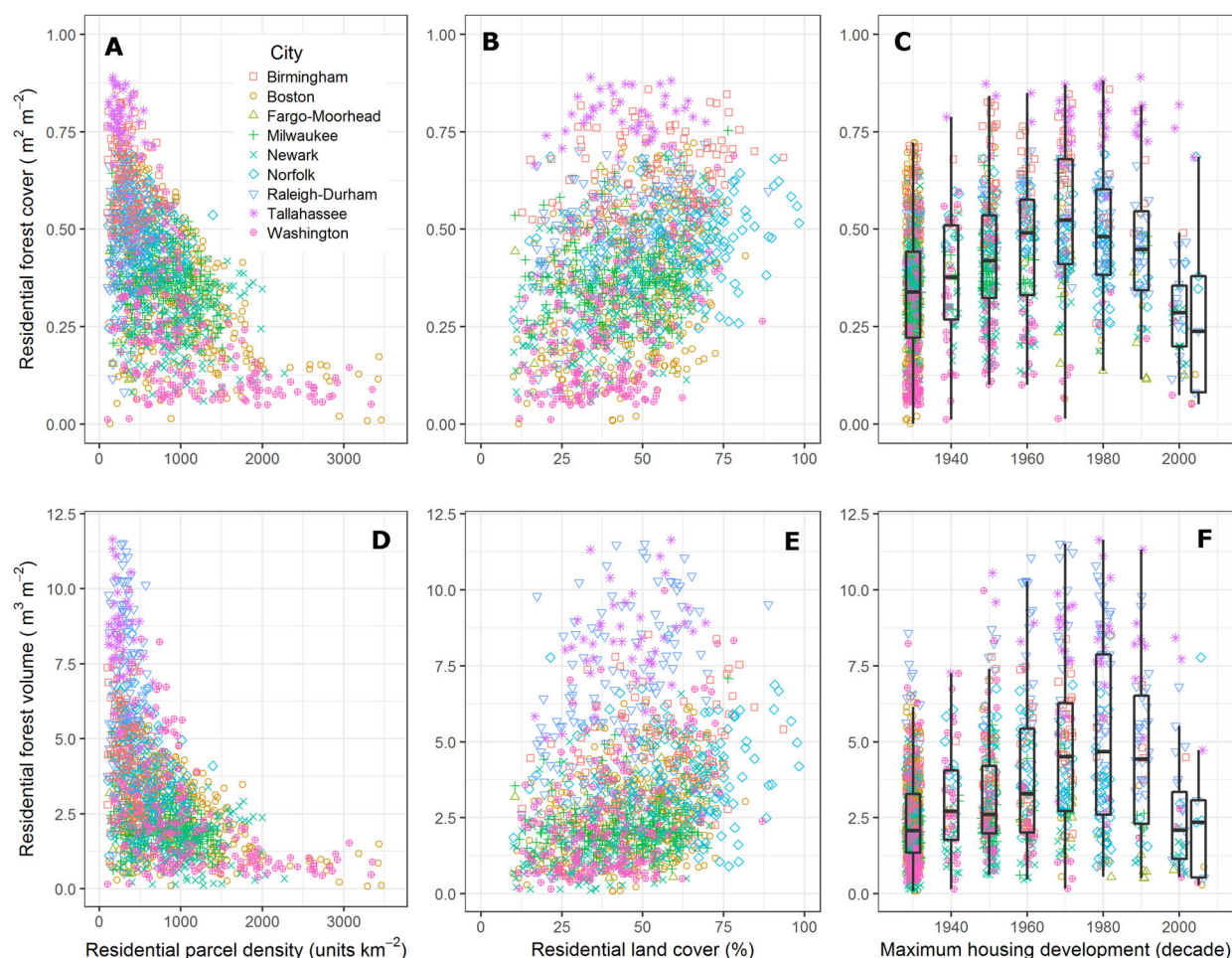


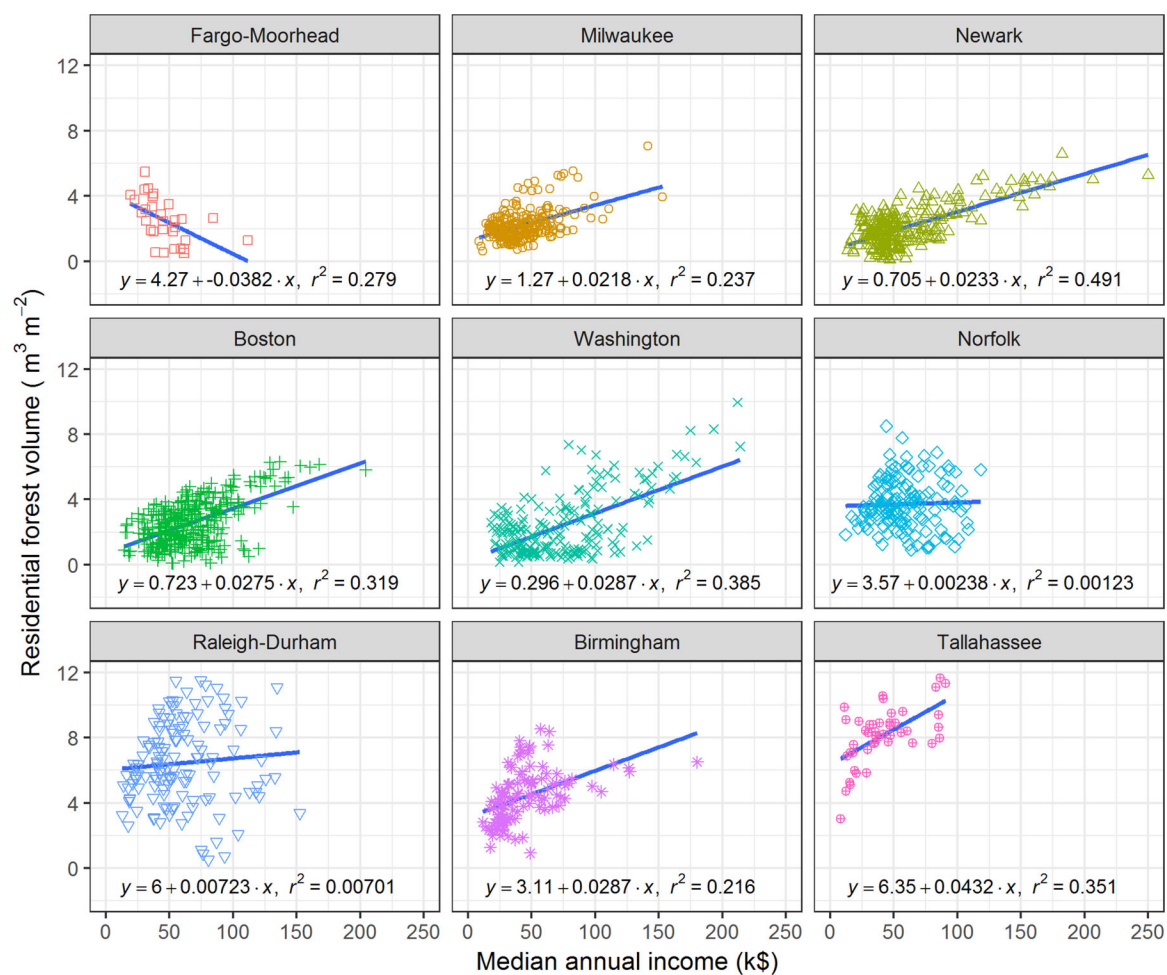
FIG. 2.
Relationship between residential forest cover and volume across the 9 cities investigated.
Points represent average values calculated at census tract level.

**FIG. 3.**

Relationship between evapotranspiration (ET) and forest cover (A) and volume (B) in residential parcels averaged at census tract level. Jittering of data points from the same city has been introduced to avoid overplotting, thus differences in ET do not reflect real values (provided in Table 3). Boxplots represent median (central bar), first and third quartiles (hinges), and 1.5 times the inter-quartile range (whiskers). Letters at the bottom of each boxplot represent statistically similar mean values following a Kruskal-Wallis test and a post-hoc Dunn test.

**FIG. 4.**

Relationship between residential forest cover, volume and i) residential parcel density (A, D), ii) residential land cover (B, E) and iii) decade of maximum housing development (C, F). Point shape and color refer census tracts from each city as represented in the legend in panel A. Urban morphology variables represented are significant predictors of forest volume in the best fitting GLMs predicting forest cover and volume (Table 4, Appendix E). Boxplots represent median (central bar), first and third quartiles (hinges), and 1.5 times the inter-quartile range (whiskers). Jittering of data points has been introduced to avoid overplotting of tracts developed in the same decade in panels C and F.

**FIG. 5.**

Relationship between forest volume and median annual income summarized at census tract level in the nine cities investigated. Cities are ordered by increasing ET. The relationships between forest cover and median annual income are presented in Appendix F.

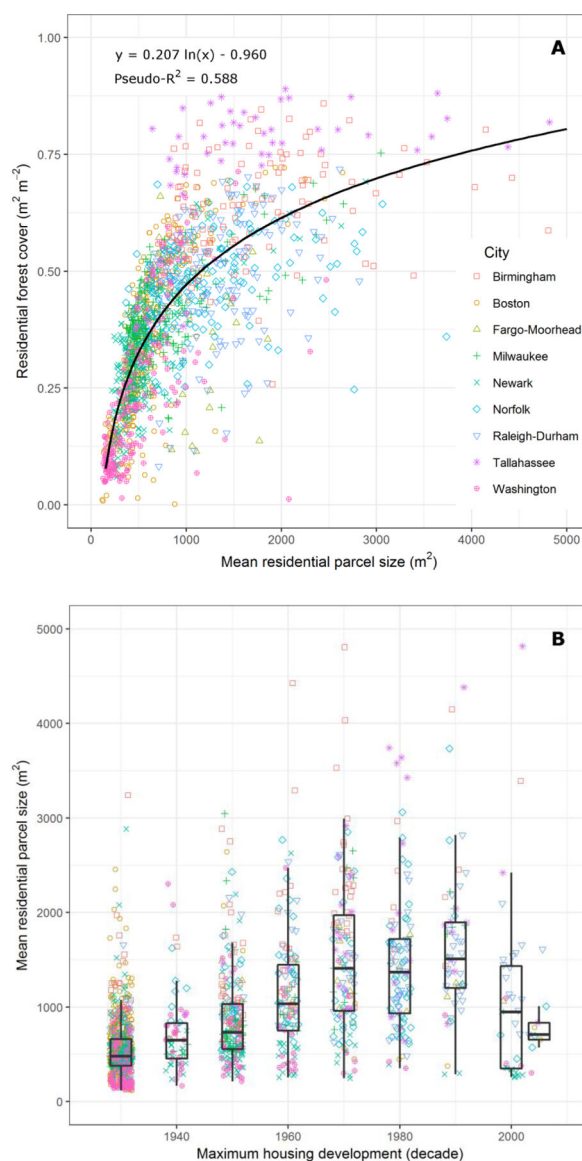


FIG. 6. Relationship between mean residential parcel size and A) residential forest cover and B) decade of maximum housing development across the 9 cities investigated. Points represent average values calculated at census tract level. Boxplots represent median (central bar), first and third quartiles (hinges), and 1.5 times the inter-quartile range (whiskers). Jittering of data points has been introduced to avoid overplotting of tracts developed in the same decade in panel B.

TABLE 1.

Summary statistics of tract, parcel, and population characteristics of the cities investigated.

City, State	Number of census tracts	Number of residential parcels	Total residential parcel area (km ²)	Residential land cover (% tract land)	Population (individuals)	Population density (individuals * km ⁻²)	City founding (year/s)
Fargo, ND	30	34,355	39.15	42.34	130,895	1626.71	1871–1871
Moorhead, MN							
Milwaukee, WI	258	205,860	157.90	43.56	811,519	3371.23	1846
Boston, MA	339	265,122	189.54	47.33	1,421,898	6841.74	1630
Newark, NJ	234	186,561	123.42	43.56	944,142	5840.69	1666
Washington, DC	199	146,164	72.41	39.56	693,042	6080.68	1791
Norfolk, VA	150	170,084	218.22	59.57	592,752	2082.45	1682
Raleigh-Durham, NC	134	174,300	241.37	42.11	599,689	1212.18	1792–1869
Birmingham, AL	114	164,249	278.13	51.71	419,859	960.85	1871
Tallahassee, FL	45	44,957	90.66	44.03	180,477	1275.08	1824
TOTAL	1503	1,391,652	1410.80	45.96	5,799,273	4295.69	-

TABLE 2.

Variables (and units) used for generalized linear models (GLMs) predicting forest cover and volume in residential parcels. Variables have been selected through stepwise selection based on variance inflation factors (VIF) to avoid multicollinearity at $R^2=0.50$ (Zuur et al. 2010). *Global models* are fitted by using all variables. Hybrid models are fitted by using each variable of each of two categories (e.g., *climate-urban morphology model*).

Category	Selected variables
<i>Climate</i>	Evapotranspiration, ET (mm yr ⁻¹)
<i>Urban morphology</i>	Residential parcel density (units km ⁻²) Residential land cover (%) Maximum housing development (decade)
<i>Socio-economic</i>	Vacant residential units (%) Median population age (y) Race diversity index Income inequality - Gini index Unemployment rate 20 to 64 years (%) Median monthly rent (\$)

TABLE 3.

Cities investigated in the study ranked by increasing potential evapotranspiration (ET) in relation to rural forest volume, residential forest volume, and their ratio. ET is calculated from the MODIS Global Evapotranspiration MOD16 Project (Mu et al. 2013) and rural forest volume from Simard et al. (2011) by averaging values within 50 km from urban centers.

City	ET (mm yr ⁻¹)	Mean rural forest volume (m ³ m ⁻²)	Mean residential forest volume (m ³ m ⁻²)	Residential to rural forest volume ratio (%)
Fargo, ND	464.43	5.72	2.50	43.63
Moorhead, MN				
Milwaukee, WI	539.56	7.85	2.20	27.99
Boston, MA	682.63	15.78	2.55	16.16
Newark, NJ	698.99	12.92	2.13	16.48
Washington, DC	741.82	15.91	2.38	14.97
Norfolk, VA	763.83	15.88	3.71	23.35
Raleigh-Durham, NC	806.78	18.02	6.49	36.00
Birmingham, AL	852.23	17.80	4.40	24.70
Tallahassee, FL	1000.47	15.69	8.12	51.76

TABLE 4.

Generalized linear models (GLMs) predicting residential forest cover ($\text{m}^2 \text{m}^{-2}$) and volume ($\text{m}^3 \text{m}^{-2}$) ranked by decreasing Akaike information criterion (AIC). Models were composed by using the respective climate, urban morphology, and socio-economic variables reported in Table 2.

Response variable: residential forest cover				
Model	N. parameters	AIC	ΔAIC	AIC weights
<i>Climate – urban morphology</i>	8	1217.41	0.00	1.00
<i>Global</i>	15	1230.86	13.45	0.00
<i>Climate</i>	3	1233.26	15.85	0.00
<i>Climate – socio-economics</i>	10	1243.20	25.79	0.00
<i>Urban morphology</i>	6	1254.10	36.69	0.00
<i>Urban morphology – socio-economics</i>	13	1259.91	42.50	0.00
<i>Socio-economics</i>	8	1356.38	138.97	0.00
Response variable: residential forest volume				
Model	N. parameters	AIC	ΔAIC	AIC weights
<i>Global</i>	17	708.26	0.00	0.99
<i>Climate – urban morphology</i>	9	718.10	9.84	0.01
<i>Urban morphology – socio-economics</i>	15	904.67	196.41	0.00
<i>Urban morphology</i>	7	917.35	222.45	0.00
<i>Climate – socio-economics</i>	12	1448.79	740.54	0.00
<i>Climate</i>	4	1642.94	934.68	0.00
<i>Socio-economics</i>	10	1972.88	1281.17	0.00