A city-scale assessment reveals that native forest types and overstory species dominate New York City forests

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Abstract. Cities are increasingly focused on expanding tree canopy cover as a means to improve the urban environment by, for example, reducing heat island effects, promoting better air quality, and protecting local habitat. The majority of efforts to expand canopy cover focus on planting street trees or on planting native tree species and removing nonnatives in natural areas through reforestation. Yet many urban canopy assessments conducted at the city-scale reveal co-dominance by nonnative trees, fueling debates about the value of urban forests and native-specific management targets. In contrast, assessments within cities at site or park scales find that some urban forest stands harbor predominantly native biodiversity. To resolve this apparent dichotomy in findings, about the extent to which urban forests are native dominated, between the city-scale canopy and site-level assessments, we measure forest structure and composition in 1,124 plots across 53 parks in New York City's 2,497 ha of natural area forest. That is, we assess urban forests at the city-scale and deliberately omit sampling trees existing outside of forest stands but which are enumerated in citywide canopy assessments. We find that on average forest stand canopy is comprised of 82% native species in New York City forests, suggesting that conclusions that the urban canopy is co-dominated by nonnatives likely results from predominantly sampling street trees in prior city-scale assessments. However, native tree species' proportion declines to 75% and 53% in the midstory and understory, respectively, suggesting potential threats to the future native dominance of urban forest canopies. Furthermore, we find that out of 57 unique forest types in New York City, the majority of stands (81%) are a native type. We find that stand structure in urban forest stands is more similar to rural forests in New York State than to stand structure reported for prior assessments of the urban canopy at the city scale. Our results suggest the need to measure urban forest stands apart from the entire urban canopy. Doing so will ensure that city-scale assessments return data that align with conservation policy and management strategies that focus on maintaining and growing native urban forests rather than individual trees.

Key words: *forest management; invasive species; native biodiversity; spatial scale; urban biodiversity; urban canopy; urban forest; urban natural areas; woodland.*

Introduction

Urban habitats are expanding, causing declines in biodiversity (Güneralp and Seto 2013) and driving decreases in forest stem density globally (Crowther et al. 2015). Increased prevalence of introduced species is a well-known consequence of urbanization (McKinney 2006) and this pattern is commonly supported in urban canopy and other vegetation assessments within and across cities (Nowak et al. 2011, Moro et al. 2014, Gaertner et al. 2017). A common expectation in forested biomes then is that urban forests are degraded, dominated by nonnative species and significantly different in both composition and structure to non-urban forests. Yet urban areas are also shown to support high biodiversity (Godefroid and Koedam 2003, Alvey 2006) and some assessments in cities reveal that native species dominate in at least some forest stands (Cornelis and Hermy 2004, Kühn et al. 2004). One potential reason for contradictory conclusions among

assessments is the difference in their spatial scale and criteria for what constitutes urban forest (He et al. 2016). For example, landscape, park, and site-specific assessments tend to focus only on selected forest stands, which can range from native to nonnative dominated (Zipperer 2002, Turner et al. 2005, Zipperer and Guntenspergen 2009, Golivets and Bihun 2016), but all stands across cities are not examined and so whether forest stands are primarily native vs. nonnative dominated is unknown. In contrast, city-scale assessments typically focus on species composition and structure for all trees, regardless of land cover type, meaning they capture trees growing individually in parks and on streets, as well as those within forest stands, which respectively require different management approaches. Given that city-scale assessments are not stratified by land use type or connected to forest type when reported at the city scale, it is not possible to determine the relative nativity and structure of the forest stands included in these assessments.

Natural areas occupy 84% of municipal parkland in the United States (Trust for Public Land 2017) and forested natural areas are common across some of the world's largest and densest cities (Hedblom and Söderström 2008, Stewart et al. 2009, Lawrence et al. 2013). For example, cities across

the world contain small and also large areas of natural forests, such as Richmond Park (955 ha) in London, UK and Tai Po Kau Nature Reserve (460 ha) in Hong Kong, China. Such forested areas are spatially less uniform and often lack inventory data in comparison to street trees (Hauer and Peterson 2016). This lack of inventory data for forest stands within urban areas means that there is a paucity of knowledge about patterns of urban forest structure and composition at the scale necessary to align management with goals for urban forests (Kendal et al. 2014, Cortinovis and Geneletti 2018). Further, it is common to inform goals for urban forest using generalizations of urban forests derived from city-scale assessments across multiple land uses (McPherson et al. 1994, Nowak et al. 2008, 2011, Rogers et al. 2015), which may then misrepresent the conditions of forested natural areas and hence their required management (Mexia et al. 2018). For example, in contrast to street trees, urban forested natural areas rely on natural regeneration to replace the canopy trees and are typically underlain by pervious surfaces such as natural soils and herbaceous species. Accurate data on the condition of urban natural area forests, and appropriate management, is needed because these areas are important for preserving native habitat and biodiversity (Alvey 2006, Aronson et al. 2017), and often contain the highest density of trees in cities leading to disproportionally high provision of ecosystem services per unit canopy cover (Vieira et al. 2018). Hence, for cities to achieve stated targets to increase canopy cover and biodiversity at citywide scales (Nowak and Greenfield 2010, McPherson et al. 2011, Aronson et al. 2017), requires quantitative knowledge of natural area forest condition independent of other canopy land use types (Cortinovis and Geneletti 2018).

We performed a vegetation assessment across all the designated forested natural area upland in New York City (NYC), New York, USA, accounting for 2,947 ha across 53 parks. Our aim was to use NYC as a case study to evaluate, by surveying natural area forest composition, structure, and community type across the entire city, competing conceptions of urban forest as co-dominated by nonnatives vs. harboring high native richness, that arise respectively from citywide vs. stand-level assessments. Specifically, NYC is particularly attractive as a case study given a rich published data set on the composition and structure of urban forests. For example, a citywide assessment of the aggregated urban canopy concluded that nonnative trees approximately co-dominate the overstory (55% native canopy vs. 45% nonnative; Nowak et al. 2007). Further, an analysis of urban land cover and vegetation patterns in the NYC region found that nonnative species richness increased by 60% as urban land cover increased, while native species richness decreased (Aronson et al. 2015). Lastly, analysis of historical and modern flora found that 42.6% of native species have been extirpated within protected NYC parkland, with native species extirpated at a greater rate than nonnatives (DeCandido et al. 2004). Such conclusions point toward nonnative species prevalence but are hard to reconcile in the context of site or park-level assessments, which show that the canopies of these forests are often primarily native (Loeb 2006). We therefore established 1,124 plots across NYC natural area forest to capture the full range of forest conditions and hence establish whether the structure and composition of the natural area forests fit with the contrasting conceptions yielded by broader- vs. finer-scale assessments. Using the data collected we asked (1) What is the range of species composition found across NYC's forests, and are they primarily native or nonnative dominated? (2) How do NYC's forests compare to rural forests in NY state, both in terms of stand structure and forest type. (3) Is overstory stand structure related to the understory species composition? We discuss potential applications of these data for natural resource management and conservation in light of the focus, both in the United States and internationally, on preserving and building native canopy and biodiversity in cities.

Methods

New York City (NYC, 40.7128° N, 74.0060° W) is situated on the edge of the Atlantic Ocean between the New England and Mid-Atlantic U.S. regions. NYC is the most populous city in the United States, but despite high population density, 40% of NYC's land cover is greenspace including 2,947 ha of forested natural area managed as municipal parkland. We sampled NYC parkland designated as upland Forever Wild natural area management zones, which is primarily forest but includes some grasslands and shrublands. Using ArcGIS (ESRI, Redlands, California, USA), a 2-ha grid was clipped to the Forever Wild Parkland boundary and then, within each grid cell, one random point was generated and designated as plot center. Each point was visited in the field in the 2013 or 2014 growing season. If >50% of the plot area was impermeable surface, landscaped, wetland, or was unsafe to access, we did not include it ($n = 200$). A total of 1,124 plots (10 m radius) across 53 parks were measured.

To estimate the species composition, tree density, and basal area in each plot, the diameter of each overstory tree was measured at 1.37 m from the ground (i.e., diameter at breast height; DBH). Overstory trees were defined as woody species >10 cm DBH and included both live and standing-dead individuals. All results are reported using live trees. Midstory abundance tallied all woody species between 2 and 10 cm DBH. Four 1-m^2 subplots were established 5 m from plot center in each cardinal direction. In these subplots, tree seedlings (<2 cm DBH) were counted and herbaceous plants were recorded by species; areal cover was estimated for each species to nearest 1%.

After sampling, all plots were assigned a vegetation association by ecologists in the New York State Natural Heritage Program, resulting in 57 unique vegetation types (Edinger et al. 2016). The 57 types were classified into five main vegetation groups for broader comparison of forest structure and composition. The five groups were mature hardwood, successional hardwood, forested wetland, maritime forest, and open upland. Any plots classified as emergent or estuarine marsh ($n = 9$) were excluded from analyses testing differences between vegetation groups. To compare NYC forests with rural NY forests, the 57 vegetation types were cross-referenced with data from the US Forest Service Inventory and Analysis in NY State (NYS; Woudenberg et al. 2010), collected between 2010 and 2015 for comparable forest types (NYC plots $n = 998$, NYS plots $n = 1,718$). Stand structure between NYC and NYS forest plots was compared using mean tree diameter (quadratic mean diameter, QMD) plotted

against tree density for each plot. QMD is a conventional metric in forestry that gives greater weight to larger trees and is better aligned with stand volume than the arithmetic mean (Curtis and Marshall 2000). When used in conjunction with density (trees/ha), QMD meaningfully describes stand structure. For example, stands with few very large trees have high QMD and low tree density (trees/ha), whereas stands with only small diameter trees will have low QMD and often high density. As forest stands establish and move through succession toward mature canopy forests, typically stem density will decrease, and average tree diameters increase, and hence QMD increases while stem density decreases.

The mean proportion of native species in each vegetation layer was estimated per plot based on relative abundance for canopy and midstory, and on relative percent cover of herbaceous vegetation. Plots that had no individuals in a specific layer (i.e., no canopy trees) were excluded from this analysis (canopy = 49, midstory = 27, understory = 0). Species richness was calculated by counting the individual species within a plot and across vegetation structural layer. Total species richness includes both native and nonnative species. Only 4.1% of our study area overlapped with tree planting efforts conducted in the prior 8 yr suggesting our findings are unlikely to be an artifact of current management. All statistical tests were run in JMP Version 12.1 (SAS Institute, Cary, North Carolina, USA). Differences in proportion native cover between forest groups, and stem density and QMD were tested for using ANOVA. To explore the relationship between different vegetation layers and composition, we used a linear mixed effects model with canopy basal area and invasive herbaceous cover as fixed effects and park as a random effect to predict native species richness. These analyses were performed using the R statistical program (version 3.3.1; R Core Team [2018]). Full species lists can be found in the supporting materials.

Results

The mean proportion of native canopy across all plots was 82% ± 0.8% (mean ± SE), with 53% of plots having 100% native canopy (Fig. 1a). Further, 84% of all overstory trees measured were classified as native (Data S1). Within the five vegetation groups, mean proportion native canopy varied and was highest in mature hardwood plots (92.3% ± 1.2%) followed by forested wetland (91.7% ± 1.3%) and maritime forest (89.9% ± 3.0%), and was significantly lower in successional forests (69.4% ± 1.6%) and open uplands (60.0% ± 8.5%; $P < 0.0001$, $F = 54.4$, df = 4, 1,069). Total species richness was, by contrast, less affected by vegetation grouping but varied markedly across species structural layer (Fig. 1b). For instance, the understory layer had the greatest floristic diversity (591 species across all plots; 79.4% of all recorded species) and also the greatest overall species richness ranging from 1 to 35 per plot, with an overall mean of 11.5 ± 0.14 species per plot with no significant differences between vegetation groups ($P = 0.06$, $F = 2.23$, df = 4, 1,114). Across all plots, the midstory and overstory had significantly less total species richness, with a range of 0–18 and mean species richness of 5.08 for the midstory, and a range of 0–10 with a mean of 3.46 species for the overstory layer. The mature hardwood forest had significantly greater species richness in the midstory ($P = <0.0001$,

$F = 49.2$, df = 4, 1,114) and overstory ($P < 0.0001$, $F = 79.95$, df = 4, 1,114) than other types. The 10 most common canopy species citywide (Fig. 2a) account for 69.7% of all overstory trees measured, and 75.4% of the canopy basal area. Sweetgum (*Liquidambar styraciflua*, 16.9%) recorded as the most common species across all plots, and northern red oak (*Quercus rubra*, 10.5%) recorded as the second most common species with the greatest overall basal area. Black locust (*Robinia pseudoacacia*, 5.3%), followed by Norway maple (*Acer platnoides*, 1.7%), were the most common nonnative species, but notably they were far less abundant than the dominant native overstory species (Fig. 2a, see Data S1 for full species lists).

The mean proportion of native midstory across all plots was 75% ± 9.0%, with 31.8% of plots having 100% native midstory (Fig. 1a), and 79.3% of all midstory species classifying as native (Data S1). Across all vegetation groups, the mean proportion native midstory was lower than the mean proportion native canopy. Still, similar to the canopy, native species dominated in mature hardwoods (82.8% ± 1.8%), forested wetlands (85.6% ± 1.9%), and in maritime forests (86.3% ± 2.4%). Successional forests (64.6% ± 1.6%) and open uplands (59.2% ± 7.1%) again had significantly lower proportion native species but still had a greater proportion than nonnative species ($P < 0.0001$, $F = 32.2$, df = 4, 1,092). The most abundant native midstory species included spicebush (*Lindera benzoin*; 12.5%) and black cherry (*Prunus serotina*; 7.5%); the most common nonnative species were apple (*Malus* spp.; 3%) and Norway maple (*Acer platanoides*; 2.3%; Data S1).

Nonnative species were more prevalent in the understory layer, with a mean proportion native species of 53% ± 0.90%. This pattern persisted across vegetation groups, with nonnative species dominant in open uplands (Fig. 1a). Mature hardwoods and forested wetland plots had the greatest proportion native cover with 65.7% ± 1.3% and 58.6% ± 2.7%, respectively. Significantly lower native understory was found in successional forests (46.0% ± 1.4%) and maritime forests (43.0% ± 3.6%), and the mean proportion of native species cover in open uplands was 24.0% ± 3.4%, significantly lower than all forest groups ($P < 0.0001$, $F = 40.4$, df = 4, 1,114). The most dominant occurring understory species (in both percent cover and frequency) were woody vines (lianas; Fig. 2b). These included natives such as poison ivy (*Toxicodendron radicans*) and Virginia creeper (*Parthenocissus quinquefolia*), as well as nonnatives such as Japanese honeysuckle (*Lonicera japonica*) and oriental bittersweet (*Celastrus orbiculatus*). Of the 10 most abundant species in terms of relative cover, one-half were nonnative (Fig. 2b). Notably, we found that 58% of our forest plots had nonnative vines climbing in canopy trees. Tree seedlings accounted for on average 39% of the understory cover, and when looked at separately had a mean proportion native species count of 72.4% ± 1.2%. Nine of the 10 most common tree seedlings were native and accounted for 70.1% of the total seedlings. Overall 81% of forest plots aligned with forest types found in the USDA forest FIA manual (Table 1), and those that did not were primarily native maritime coastal forests (12.5%) in addition to various other open upland and shrubland vegetation types making up the remaining 5.6% of vegetation types. Exotic hardwood is considered one forest type by USDA; however, we found nine different types of exotic hardwoods in NYC's forest that accounted for 15.5% of all forest plots in NYC.
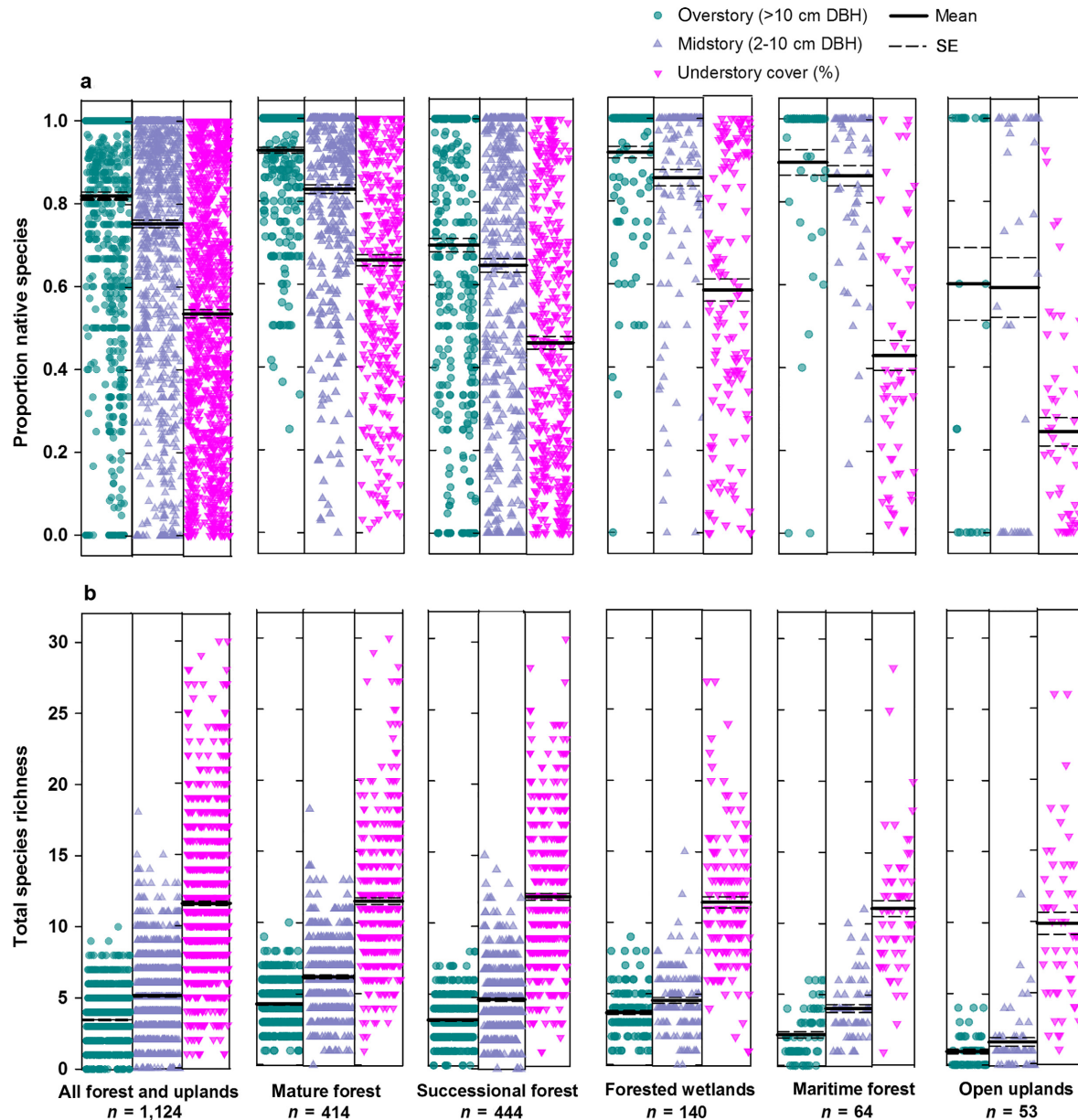
Fig. 1.   Mean (solid line) and standard error (dashed line) of individual plot (symbol) values of (a) proportion of native species in New York City natural area forests and (b) species richness across vegetation layers and vegetation groups. Data were collected in the growing seasons of 2013 and 2014. Forest groups are a subset of "all forest and uplands"; plots categorized as upland marsh ($n = 9$) were excluded from the vegetation group analysis.

Given that forest stand structure is an important metric for making management decisions, we also quantified stand structure for NYC forest types, and compared these structures to those for similar types in NYS. There was wide variation in tree density in NYC (95–7,066 trees/ha, >2 cm DBH, Fig. 3), with a mean of $1,180 \pm 22.5$ trees/ha. Mean tree density was significantly higher ($P < 0.001$, df = 1, 2,715, $F = 124.7$) in NYS forests (mean $1,605 \pm 25.9$ trees/ha). In contrast, mean tree diameter (QMD) was significantly but only slightly higher in NYC (18.3 ± 0.22) than in NYS (17.6 ± 0.17; $P = 0.014$, df = 1, 2,715, $F = 6.03$). In addition, variation in QMD in NYC's natural area forests extended beyond the range observed in NYS, with values

ranging from 2.3 to 70.9 in NYC vs. 2.1–64.8 in NYS (Fig. 2). A similar pattern was found when nonnative species were removed from the analysis suggesting that native tree species are driving these patterns in tree stand density.

To visualize the variation in patterns between forest structure and composition between the overstory and understory layers we plotted the relationship between overstory native basal area (m^2/ha), native understory species richness and understory invasive cover across all plots (Fig. 4a), and by park (Fig. 4b). The r^2 of our linear model for all plots was only 0.21 suggesting that most of the variation in native species richness is explained by other factors not included in the model. Across all plots (Fig. 4a), native basal area has a positive relationship with
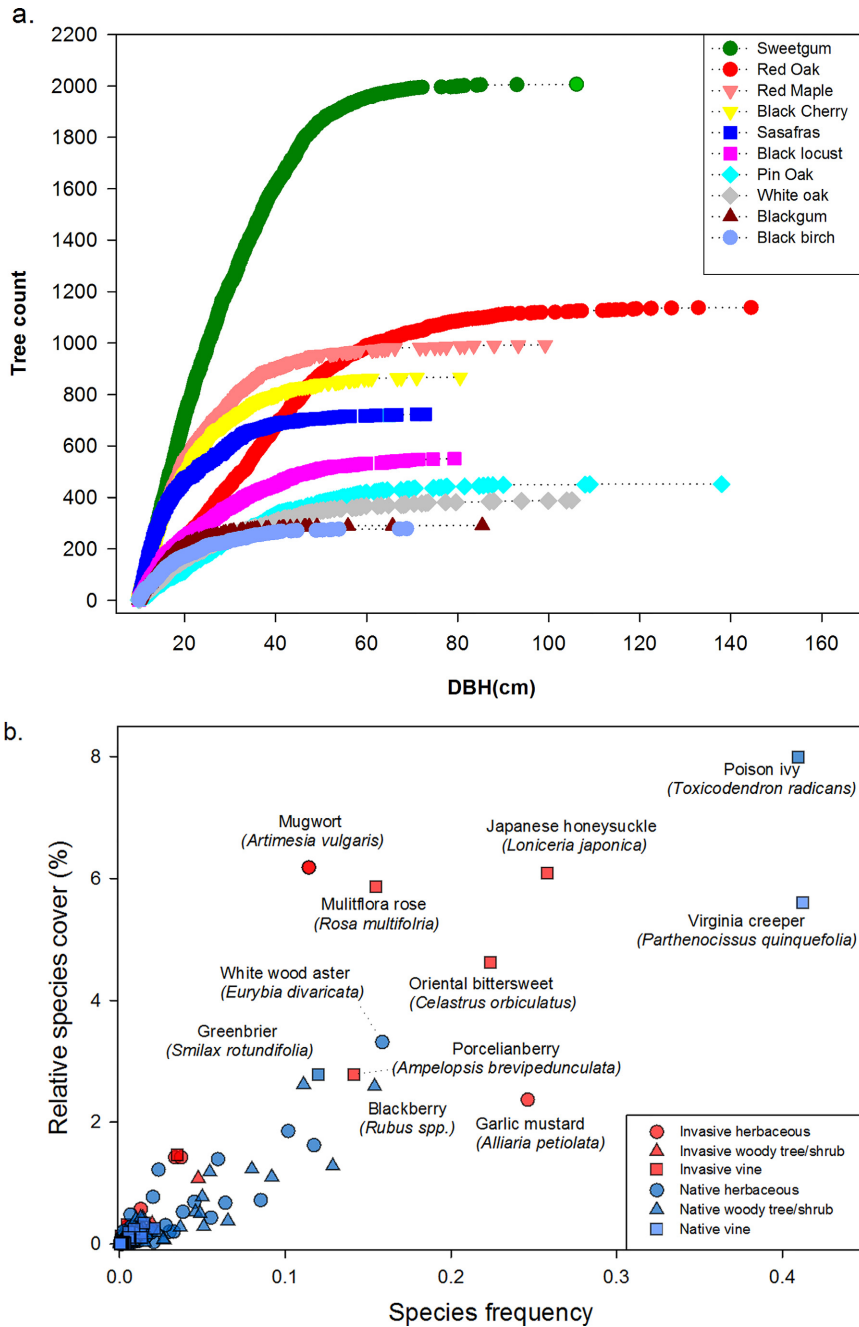
FIG. 2. (a) Top 10 most dominant canopy tree species by abundance and size (DBH) across natural areas in New York City, New York, USA. Each point represents a single tree measured. All 10 species are native to New York City. A total of 117 different tree species were found in the canopy. (b) Understory ground cover species by relative cover and frequency across all plots measured ($n = 4,496$). Each point represents an understory species.

understory native species richness (standardized coefficient = 0.58, SE = 0.20, $t = 2.97$), and a negative relationship with understory invasive species cover (standardized coefficient = -0.65, SE = 0.20, $t = -3.23$). At the park scale, average native basal area (m²/ha) can range from 0.09 to 39.27, average understory native species richness can range from 1.6 to 12, and average invasive understory cover range from 2.35 to 63.66. This variation in vegetation patterns can differ markedly at the park scale from the patterns seen citywide suggesting that different conclusions could be drawn if only some parks are measured.

DISCUSSION

Natural area forests provide recreation opportunities and biodiversity, in addition to a suite of other ecosystem services including storm-water mitigation, improved air quality, and reduced heat island. Notably, the origin (i.e., native or nonnative) of the canopy species figures prominently in estimating the social and ecological value of such urban forests (Kowarik 2011, Müller et al. 2013, Moro et al. 2014), and so dictates management of these systems. Yet many

TABLE 1.   The proportion of unique vegetation types in forested natural areas in New York City (NYC) and comparative rural forest types found in the United States Forest Service, Forest Inventory and Analysis (FIA) assessments. The native status of each forest type is based on the dominant vegetation of that forest type. The proportion of plots is out of all forest plots sampled in NYC forested natural areas ($n = 1,124$).

NYC vegetation type classification	Native status	N	Proportion of plots	USDA Forest Service forest types
Mature hardwood forest types		396	0.353	
Coastal oak–hickory forest	native	157	0.140	white oak/red oak/hickory
Oak–tulip tree forest	native	144	0.128	yellow poplar/white oak/northern red oak
Coastal oak–beech forest	native	56	0.050	white oak/red oak/hickory
Coastal oak–heath forest	native	29	0.026	scarlet oak
Beech–maple mesic forest (variant)	native	7	0.006	sugar maple/beech/yellow birch
Hemlock–northern hardwood forest	native	2	0.002	eastern white pine/hemlock
Chestnut oak forest	native	1	0.001	chestnut oak/black oak/scarlet oak
Successional hardwood types		387	0.345	
SSH, *Liquidambar styraciflua*	native	115	0.102	sweetgum/yellow poplar
SSH, *Robinia pseudoacacia*	nonnative	89	0.079	exotic hardwoods
SNH, *Acer platanoides*	nonnative	27	0.024	exotic hardwoods
SSH, *Ailanthus altissima*	nonnative	25	0.022	exotic hardwoods
SNH, *Populus/Betula*	native	23	0.020	gray birch
SNH, *Quercus/Acer rubrum/Betula*	native	13	0.012	red maple/oak
SSH, *Populus deltoides*	native	13	0.012	cottonwood
SSH, *Morus alba*	nonnative	13	0.012	exotic hardwoods
SSH, *Liriodendron tulipifera*	native	11	0.010	yellow poplar
SSH, *Quercus palustris*	native	11	0.010	white oak/red oak/hickory
SSH, *Acer pseudoplatanus*	nonnative	11	0.010	exotic hardwoods
SSH, *Pinus strobus*	native	9	0.008	eastern white pine
SSH, *Ulmus*	native	7	0.006	silver maple/American elm
SNH, *Betula lenta*	native	6	0.005	gray birch
SSH, *Alnus glutinosa*	nonnative	4	0.004	exotic hardwoods
SSH, *Fraxinus*	native	3	0.003	sweetgum/yellow poplar
SSH, *Malus*	nonnative	3	0.003	exotic hardwoods
SSH, *Aralia elata*	nonnative	2	0.002	exotic hardwoods
Pine Plantation	native	1	0.001	na
SSH, *Phellodendron*	nonnative	1	0.001	exotic hardwoods
Forested wetland types		137	0.122	
Red maple–sweetgum swamp	native	56	0.050	red maple lowland
Red maple–blackgum swamp	native	25	0.022	red maple lowland
Red maple–hardwood swamp	native	16	0.014	red maple lowland
FF, *Quercus palustris*	native	12	0.011	overcup oak/water hickory
FF, *Carya cordiformis*	native	9	0.008	yellow poplar/white oak/northern red oak
FF, *Juglans/Celtis*	native	8	0.007	black walnut
FF, *Acer negundo*	native	6	0.005	silver maple/American elm
FF, *Fraxinus Pennsylvanica*	native	2	0.002	sweetgum/yellow poplar
FF, terrace	native	2	0.002	silver maple/American elm
FF, *Acer/Ulmus*	native	1	0.001	black ash/American elm/red maple
Maritime coastal forest types		141	0.126	
Successional maritime forest	native	121	0.108	no similar type
Maritime shrubland (tall)	native	20	0.018	no similar type
Open upland types		63	0.056	
Other non-forested*	na	27	0.024	no similar type
Successional old field, *Artemisia vulgaris*	nonnative	18	0.016	no similar type
Successional shrubland	native	10	0.009	no similar type
Successional old field	native	8	0.007	no similar type

Notes: Forest types in NYC were cross referenced using the FIA field manual and confirmed by an FIA forester. SSH, successional southern hardwoods; SNH, successional northern hardwoods; FF, floodplain forest; na, no native status for that vegetation type could be determined.
  *MARSH plots.

conceptions of urban forest condition are based on citywide assessments of the urban canopy, which typically sample canopy trees across multiple land uses and not just in natural area forests. We took advantage of the rich data available for NYC to examine how our survey data compared to conclusions from a citywide assessment approach used commonly in the United States and internationally to assess the condition of urban canopy. Specifically, based on a city-scale urban canopy assessment, Nowak et al. (2007) concluded that nonnative trees approximately co-dominate the overstory (55% native canopy vs. 45% nonnative). In contrast, we found that 84% of the combined canopy was native
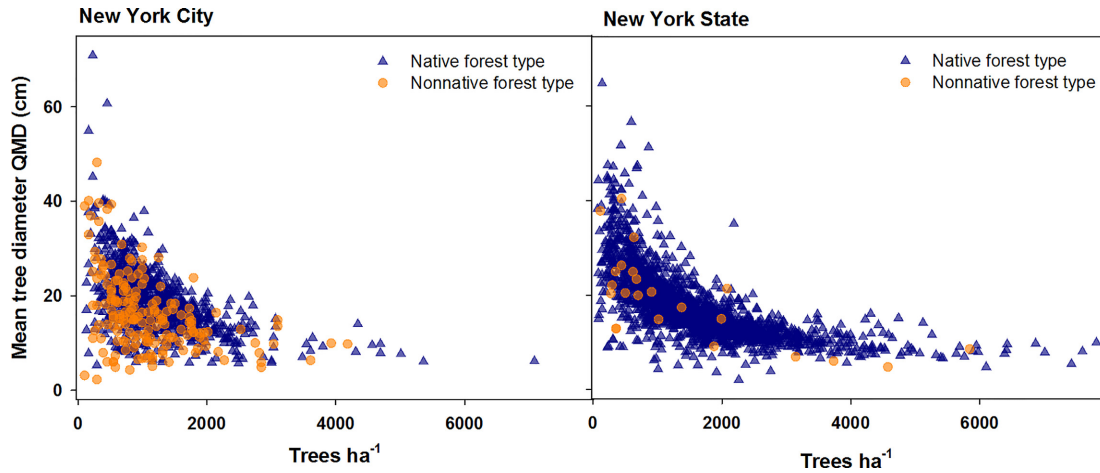
Fig. 3.   Variation in urban forest structure between similar forest types in (a) New York City, New York (NYC) and (b) New York State. Forest structure is represented by quadratic mean diameter (QMD) and density (trees/ha) between forest plots in NYC natural areas (a; $n = 998$, native = 822, nonnative = 176) and United States Forest Service Forest Inventory and Analysis forest plots across New York State (b; $n = 1,718$, native = 1,696, nonnative = 22). Forest plots classified as native forest types are represented by blue and nonnative forest types by orange. Average stem density is greater in New York State than in NYC, but overall forest structure spans a similar range and native forest types dominate in NYC.

with the mean proportion of native canopy per plot was 82%, and this proportion of nativity was even higher in mature forests (mean 92.3%; Fig. 1). Further, all 10 of the most common canopy species enumerated in our assessment were native, with sweetgum the most abundant and red oak having the greatest basal area (Fig. 2a). In contrast, based on the same prior city-scale urban canopy assessment, the invasive tree-of-heaven (*Ailanthus altimissa*) was the most abundant tree species in NYC, accounting for 9% of urban canopy (Nowak et al. 2007). We find it far less abundant in natural area forest, accounting for only 1.1% of the canopy. As such, our results show that native species dominate the overstory of NYC's natural area forests and that the majority of forests are a similar type to those found in rural parts of NY state. More generally, our data caution against using city-scale urban canopy assessments to understand species dominance or forest stand structure and hence question the basis of using them to develop management recommendations and policies for forested natural areas. Instead, our data highlight the need for land-cover-specific assessments to understand the species composition, structure, and forest type of natural area forests in cities across the world so that such assessments could be aligned with salient management and policy recommendations.

We presume that urban canopy assessments, given the patchy distribution of natural area forests in cities, oversample street and other trees growing outside of forest stands. Our tree density data support this presumption. Specifically, tree density in the forest areas we sampled (a mean of 1,180 trees/ha) was only slightly less dense than the mean density in rural NY State forests (~1.3 times greater in NYS). However, they were almost 20 times greater than tree density estimates for NYC-wide canopy assessments (65.2 trees/ha), as well as 9 times greater than estimates for open space and vacant land (116–125 trees/ha; Nowak et al. 2007). Hence, land-cover specific assessments seem necessary for estimating both species composition and stand structure in natural area forests. Further, they provide the

basis for understanding differences in urban forest density by forest type (e.g., oak–hickory vs. maritime coastal forests), which can use baseline data such as ours to inform repeated sampling across time to follow population and successional dynamics of stands.

Our assessment also revealed differences between NYC and NYS forests. For example, whereas the majority of forest types that we identified overlapped with native forest types in rural forests (Table 1), NYC forests did have a higher proportion of high-QMD–low-density plots (Fig. 3). High-QMD–low-density values are indicative of stands with a few, old, large trees and relatively little recruitment of new canopy trees, a pattern likely explained by the historical preservation of canopy trees in private estates now converted to natural areas. Nevertheless, there is strong overlap in the structure and species composition of NYC and NYS forests. These stand characteristics are frequently used to create silvicultural prescriptions (e.g., thinning, shelterwoods) for rural forest management, and a similar approach could be employed to direct trajectories of urban forests toward specific diversity and tree size targets, natural regeneration, and/or varied vertical structure. For example, the forest type descriptions we report enable urban forest stands to be delineated by forest type and structure, permitting recommendations specific to the forest type, stem density, and species composition observed and that are aligned with overall goals for urban forests. Such adoption of established silvicultural practices in cities might augment current and expensive efforts such as nonnative species removal and tree planting projects common in national and international urban forest programs (e.g., million trees in Auckland, New Zealand; New York City, New York, USA; Los Angeles, California, USA; and London, UK) that might otherwise overlook silvicultural management of existing forest stands as an effective means to reach desired goals for biodiversity and tree abundance.

Our data suggest a need to test the efficacy and cost effectiveness of traditional silvicultural prescriptions in cites to
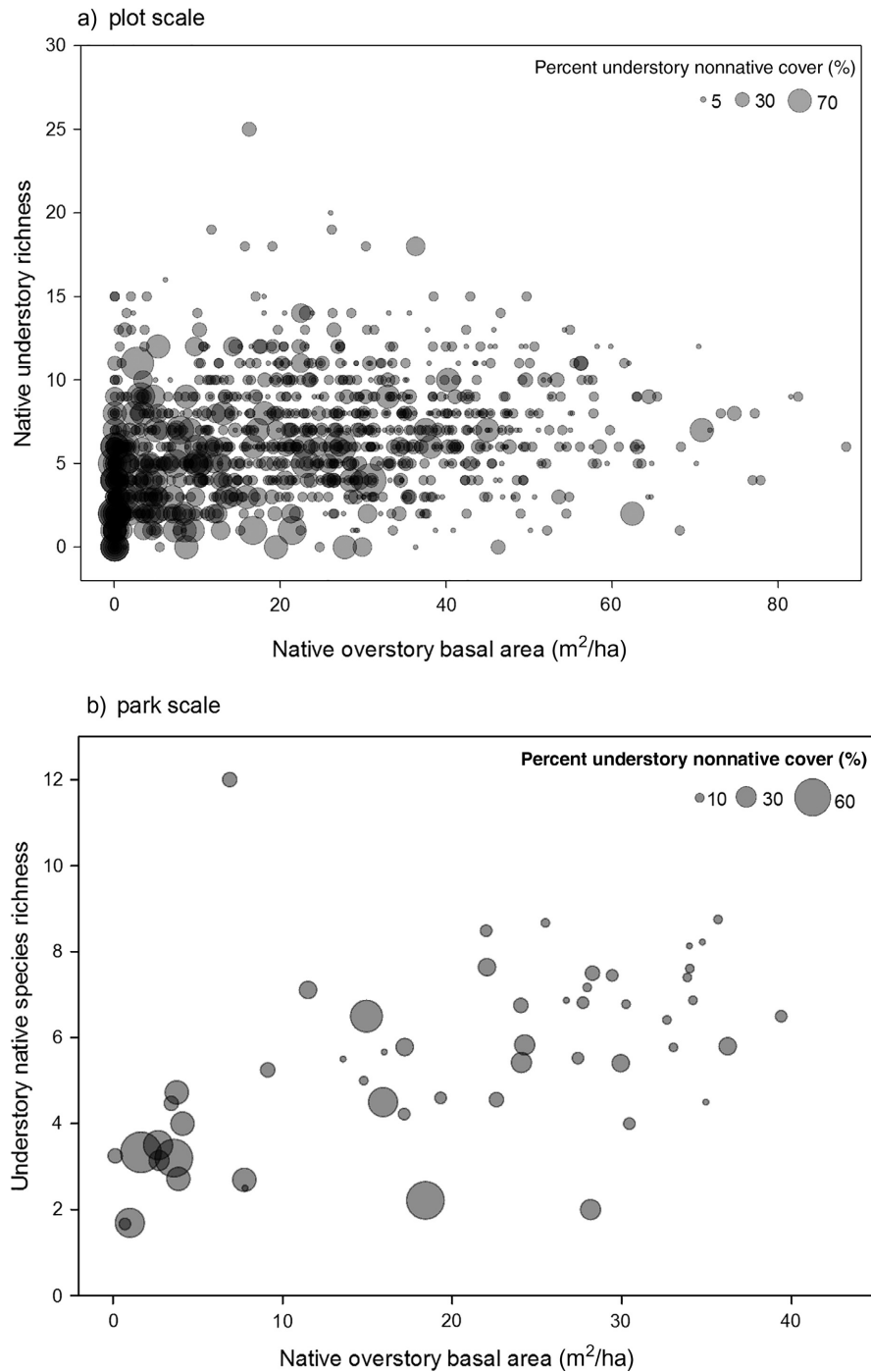
FIG. 4. Vegetation patterns across forest structural layers in New York City's forested natural areas for (a) individual plots and (b) parks. Overstory native basal area has a positive relationship (standard coefficient = 0.58) and understory invasive species cover has a negative relationship (standard coefficient = −0.65) on understory native species richness. The size of each point shows the relative proportion of average understory invasive species cover for that park or plot respectively. In panel a, each point represents one plot (n = 1,124). In general, as native basal area increases, native understory richness increases and understory invasive species cover declines but the r^2 for the linear mixed model is 0.21, suggesting that many other factors outside of invasive species and canopy closure explain variation in native understory species richness. In panel b, each point represents one park (n = 53). The average value of native species richness, native basal area and understory invasive cover vary markedly between parks in New York City.

retain the native dominance of the overstory. Specifically, nonnative species were much more common in the midstory and understory, and particularly dominant in herbaceous cover (Figs. 1, 2). High cover of nonnative herbaceous

species can decrease success of native seedlings (Stinson et al. 2006) and alter numerous other community and ecosystem properties (Vilà et al. 2011). Notably, invasive woody vines (lianas) were among the most common ground

cover and can climb standing trees, repress growth, and shorten life spans (Matthews et al. 2016). Our data appear consistent with such an expectation, with greater canopy basal area being associated with lower understory nonnative species cover and higher understory native species richness (Fig. 4; Wallace et al. 2017). Although our data are observational and so cannot be used to unambiguously tease out cause–effect relationships, it seems reasonable to assume that management strategies to remove encroaching midstory nonnative species and nonnative lianas will be required to maintain the native composition and health of the urban forest overstory (Stanley et al. 2015). Longer-term monitoring will be essential, however, to understand stand-level dynamics and whether the nonnative encroachment we see in the mid and understory layers will transition to the overstory, and to assess which managements are effective at combating such a transition.

Given the mean tree density that we determined and the areal extent of natural area forest across all of NYC (4,281 ha; Natural Areas Conservancy, *public communication*), we estimate there to be over 5 million overstory trees citywide in just this land cover type, which represents 5.4% of NYC by area. This estimation of ~5 million trees is equal to a prior estimate for the total number of canopy trees contained in NYC (Nowak et al. 2007), suggesting natural area forest is poorly represented in citywide assessments that aggregate canopy trees across many land use types. Yet such aggregated assessments of urban canopy are currently the foundation for estimates in most cities of urban forest structure, composition, ecosystem services, and change over time (Nowak et al. 2008, Steenberg et al. 2017). These estimates inform conceptions of the value of urban forests and consequently the policies enacted to maintain and manage them at global scales (Endreny et al. 2017). Our data highlight the importance of incorporating land use and forest types into estimates of urban forest conditions and challenge conclusions that vegetation in cities are degraded and dominated by nonnatives (McKinney 2006, Cameron et al. 2015). We find instead that urban forest stands harbor high proportions of native species and have similar structure and species combinations to forests in non-urban environments. Our data then suggest the potential adoption of rural silvicultural practices (for developing forest stand exams) that facilitate stand-level prescriptions for natural area forests that can help meet goals for urban forests of increasing tree abundance and native biodiversity. Importantly, these traditional silvicultural approaches emphasize management interventions that vary widely based on site context. Such nuanced management is important given that our data reveal a wide range of forest types, stem density, and invasive species proportions at both the plot level and the park level.

Our data also reveal the threat of nonnative species to the native-dominated overstory, highlighting the need for accurate data on forest species composition and structure across multiple vegetation layers. The dynamics of urban forests is just starting to be realized (Johnson and Handel 2016, Doroski et al. 2018) and combined data on the range of forest types, stand structures and species composition serves as a basis for establishing research into how forests could respond to urban stressors and be managed to achieve target forest conditions. Notably, broad-scale forest survey datasets (e.g., the U.S. Forest Inventory and Analysis and the international network of ForestGEO plots) have proven a critical resource for understanding rural forest dynamics over spatial and temporal scales (Iverson et al. 2008, Zhu et al. 2015). A similar network of plots focused on monitoring the condition of natural area forests in cities could provide a similarly critical resource for understanding urban forests. Such a network will be essential if we are to establish management prescriptions that maintain and enhance the value and complexity of natural area forests in an increasingly urban world.

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