Urban Forestry & Urban Greening 41 (2019) 313–322

Contents lists available at ScienceDirect

Urban Forestry & Urban Greening

journal homepage: www.elsevier.com/locate/ufug

Colonial history impacts urban tree species distribution in a tropical city☆

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ARTICLE INFO

Handling Editor: Cecil Konijnendijk van den Bosch

Keywords:
Biocultural diversity
Colonialism
Edible green infrastructure
Ethnicity
Guyana
Urban forests

ABSTRACT

Urban forests associated with green infrastructure for sustainable outcomes are particularly critical in the Global South, where some of the world's fastest-growing cities are located. However, compared to temperate cities, the drivers of urban tree species distribution in tropical cities remain understudied. In this study, we quantify the spatial distribution and abundance of urban forests in the tropical city of Georgetown, Guyana. British colonialism has shaped this city, including forced movement of peoples under slavery from Africa and indentured servants from the Indian Subcontinent. We studied how this multicultural context has influenced tree species distributions in the capital city of the only Anglophone country in South America. We quantified the abundance of tree species using a stratified sampling design to distribute transects across fifteen neighborhoods that vary in distance to the colonial center of the city and ethnic composition. We recorded a total of 57 unique species, the majority of which (73%) were cultivated for their edible fruits. We identify tree species that likely represent Guyana's unique multicultural heritage by comparing our species list to flora in nine cities in neighboring countries (Venezuela and Brazil) with different colonial histories. This international comparison identified a set of tree species that occurred only in Guyana. Relationships between ethnic composition and colonial history and tree species distribution were weak at the neighborhood scale, where proportion of East Indian residents had little explanatory power and distance to colonial center was correlated with abundance of only some species groups. This apparent discrepancy between neighborhood and national scales may relate to the establishment of Guyanese food as a unifying national identifier across ethnicities. The prominence of edible fruit trees in our study suggests a set of species that could be incorporated into urban planning to strengthen biocultural linkages, foster cultural integration, and promote food security.

1. Introduction

Trees in urban settings have quantifiable and intrinsic value to an increasingly urbanized global population (Elliott et al., 2018; Konijnendijk, 2018; Salbitano et al., 2016). Understanding why tree cover varies between and within cities can facilitate urban planning for green infrastructure (Martinuzzi et al., 2018). Tree species composition is a key component of urban forestry because different tree species provide different ecosystem services. Examples, where particular tree species outperform others include tree canopy remediation of air pollution (Beckett et al., 2000), perceived value to human residents (Gerstenberg and Hofmann, 2016), and food production (Lafontaine-Messier et al., 2016). Explanations for tree species distribution in cities could assist urban planners to increase tree cover and associated benefits by matching tree species to appropriate sites and resident needs.

Urban forestry is particularly critical in the global South, where some of the world's fastest-growing cities are located, including two-thirds of megacities (Konijnendijk et al., 2004; Kraas, 2007). Human well-being and ecological outcomes are tightly intertwined in these cities, where the urban environment may exacerbate risks associated with climate change, such as heat waves and torrential rainstorms (Carmin et al., 2012; Mycoo, 2014). Choosing appropriate tree species to alleviate risks of climate change and other threats will assist urban planning for green infrastructure. However, compared to temperate cities, the drivers of urban tree species distribution in tropical cities remain understudied (Meléndez-Ackerman et al., 2014). This research gap is problematic as different processes are likely to influence urban tree species cover in the global South, limiting the application of urban forestry studies from North America and Europe to tropical regions (Botzat et al., 2016; Fischer et al., 2016; Martinuzzi et al., 2018;

☆ Prepared for the special issue on "the role of cultural diversity and multicultural citizenship in urban forestry and urban greening" hosted by Cecil Konijnendijk, University of British Columbia in the journal 'Urban Forestry & Urban Greening'.

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https://doi.org/10.1016/j.ufug.2019.04.010
Received 31 December 2018; Received in revised form 20 April 2019; Accepted 20 April 2019
Available online 03 May 2019

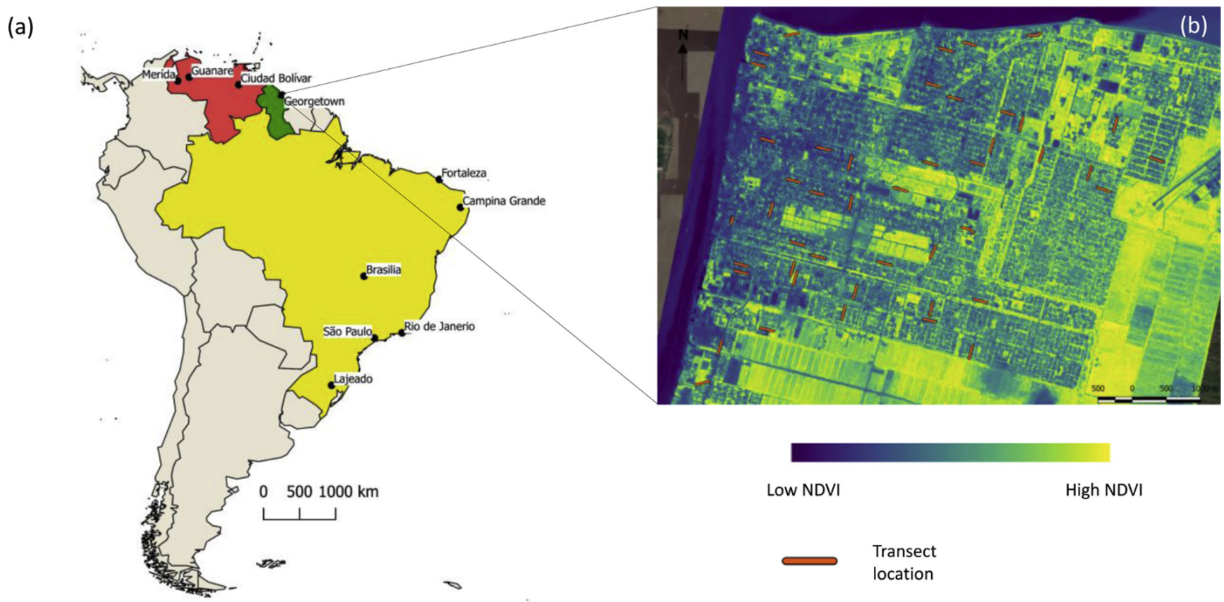

Fig. 1. Location of Georgetown, Guyana in relation to nine cities in neighboring countries of Venezuela and Brazil used to compare urban floristic composition (a). Venezuela is indicated by red shading, Brazil by yellow shading, and Guyana by green shading. Black dots indicate cities with urban tree species lists. Image to the right (b) shows the normalized difference vegetation index (NDVI) for Georgetown and location of tree transects. Darker colors indicate low vegetation presence and brighter green-yellow colors indicate higher levels of vegetation (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Mng'ong'o, 2005).

Compared to North America and Europe, tropical cities are characterized by high biocultural diversity, the variability within both human cultural and biological systems (Maffi et al., 2012). Tropical countries have higher tree species richness than their temperate counterparts (Elands et al., 2015), with this biological diversity also paralleled by cultural diversity, including greater richness of languages and ethnicities in tropical latitudes (Cashdan, 2001; Loh and Harmon, 2005; Maffi, 2005). Sacred trees provide one example of how these biocultural linkages may lead to tree species diversity in tropical cities. Public green spaces utilized for religious purposes are a common feature of cities throughout the tropics (Gopal et al., 2018; Ngulani and Shackleton, 2019). Sacred spaces in cities often contain particular tree species with cultural or religious significance, such as *Ficus benghalensis* (banyan) trees in India (Caughlin et al., 2012), potentially leading to higher tree species richness in sacred spaces relative to other urban green spaces (Jaganmohan et al., 2018). Trees with culinary uses in home gardens provide another example of biocultural diversity in tropical countries. For example, in the Cuban city of Trinidad, 182 species of plants were found in home gardens with high variability between gardens (Buchmann, 2009). Altogether, biocultural diversity is likely to promote tree species richness and increase spatial variability in tree species distributions in tropical cities.

Another major feature of many tropical cities is a history of colonial occupation. Across Latin America, Africa, and Asia, European colonizers established urban infrastructure, including green spaces, parks, and street trees. In some cases, colonialization has led to biotic homogenization, as experimental nurseries and extensive shipping operations distributed a suite of the same tree species across disparate regions (dos Santos et al., 2010; Fischer et al., 2016; Ignatieva and Stewart, 2009). Significant differences in urban tree species composition between older and newer parks demonstrate the continued legacy of colonial garden architecture (Abendroth et al., 2012; Nagendra and Gopal, 2011). In addition to colonial greening initiatives, forced and coerced movement of people associated with slavery has also resulted in the transference of tree species across the globe (Carney and Rosomoff, 2009). Differences in tree species preferences and planting regimes between the colonial and modern eras are likely to generate spatial patterns in urban tree cover in tropical cities.

The Guiana Shield region of northern South America provides an ideal arena for quantifying how colonial history and cultural context shape distribution of urban tree species. The Guiana Shield region contains high biodiversity, being part of the Amazon basin (Hammond, 2005) with countries in the region varying widely in culture and history, including the only English, Dutch, and French speaking countries in South America. In this study, we focus on the capital city of Georgetown, located on the northern Atlantic coast of Guyana. This multiethnic country is a result of Dutch (1580–1782; 1784–1803), French (1782–1784) and British (1803–1966) colonial rule (Edwards et al., 2005). Africans were the first translocated ethnic group, brought as slaves to work on sugar plantations in the 1700s after indigenous populations were decimated by colonial imperialism (Josiah, 1997). After the abolition of slavery in 1834, indentured laborers from India were brought to replace freed slaves on the sugar plantations, followed by European and Chinese emigrants (Delay, 1966). Today, in addition to these transplanted ethnic groups, Guyana has a strong and vibrant indigenous population. Each of these ethnic groups has cultural associations with particular plant species; over time, cross-cultural blending has also led to novel ethnobotanical knowledge and beliefs that transcend ethnic boundaries (Voeks, 2013). In this study, we quantify how ethnic diversity and colonial history have shaped urban tree species composition in the capital city, Georgetown. We begin with a regional perspective, comparing urban tree species composition in Georgetown to urban tree species from nine cities in the neighboring countries of Venezuela and Brazil. These countries were colonized by Spain and Portugal, respectively, leading to differences in ethno-cultural composition. By comparing urban tree species between these neighboring countries with similar biophysical conditions but different culture and history, we determine how Guyana's unique history has shaped tree species composition of urban trees in the national capital. We follow this regional perspective with an analysis of tree species distribution at the spatial scale of neighborhoods in Georgetown that vary in ethnic composition and colonial history. By relating the origin and use of tree species to neighborhood characteristics, we are able to quantify how two key features of tropical cities, ethnic diversity and colonial history, shape urban tree species distributions.

2. Materials and methods

2.1. Study area

We conducted our study in Georgetown (6.8044°, −58.1552°), the capital city of Guyana, which is located along the northern Atlantic coast of South America (Fig. 1). The area of the city is 70 square kilometers, and 0.9 m above sea level (Edwards et al., 2005). The local climate is tropical, with average daytime temperature of 26.0 °C and annual rainfall of 2400 mm per year. The city has a population of 191,810 persons, approximately 140.4 persons km^2 (Bureau of Statistics, 2014). Neighborhoods in Georgetown are defined by the boundaries of the city's 15 electoral consistencies. The main economic activities in this primate city include commerce and trade, finance and banking, telecommunication, tourism, and manufacturing services. Commercial activity in Georgetown is centered on the banks of the Demerara River, including a central business district that is several hundred years old around the historical landmark of Stabroek Market (Edwards et al., 2005).

The current ethnic composition of the city is dominated by people of African (49.6%), mixed race (28.06%), and East Indian ancestry (19.47%; Bureau of Statistics, 2014). Nearly all of the remaining ˜3% of people in Georgetown identify as Portuguese, Amerindian, and Chinese. Racial tensions between Indo- and African-Guyanese, fomented by covert British and American intervention, have dominated political and social life since Guyana achieved independence in 1966 (Rabe, 2006). Neighborhoods in modern-day Georgetown are segregated along socio-economic and ethno-racial lines (Edwards et al., 2005).

2.2. Tree transects

To quantify the distribution of tree species in Georgetown, we developed a stratified sampling scheme based on electoral constituencies (hereafter "neighborhoods") and vegetation greenness. The goal of our stratified sampling scheme was to ensure that randomly-selected field transects represented the range of tree cover within neighborhoods. To stratify samples, we used remotely-sensed measurements of vegetation greenness, calculated with the normalized difference vegetation index (NDVI) using a cloud-free remotely sensed optical image (retrieved June 2017) from the European Space Agency Sentinel-2 program (Berger et al., 2012). We then extracted the NDVI values within each constituency as a grid of points and divided these points into the lower, middle, and upper quantiles (0–33%, 33–66%, 66–100%). We randomly selected one starting point within each of these categories, with the constraint that each point was > 150 m away from other points. Streets that were located nearest to each random point generated were used as the start of transects with dimensions of 200 m in length and 60 m in width (30 m on each side). This sampling design resulted in 45 transects within 15 neighborhoods for a total area sampled of 54 ha.

Along the transects, all trees with a diameter at breast height, defined as 1.3 m above the ground, of 7 cm were mapped with a SoftWell mobile GPS unit. We identified each tree to species level (Wheat, 1975), recorded their diameter (cm) and measured their crown radius (m) by taking two measurements perpendicular to the trunk of the tree based on a north-south and east-west direction of the tree canopy. We determined the primary use of tree species in our study based on local expertise, including interviews with Georgetown residents (Hunte, 2018).

2.3. Comparison with neighboring countries

To explore how Guyana's unique colonial history and ethnic diversity has influenced tree species composition, we compared tree species occurrence in nine cities of neighboring countries of Venezuela and Brazil. These neighboring countries share a similar tropical climate as Guyana, but had different colonial occupation, with Venezuela occupied by the Spanish and Brazil by the Portuguese. Similar to Guyana, both countries saw the forced migration of Africans slaves to the New World in addition to European settlers. However, these countries did not experience a second wave of laborers from the Indian sub-continent after the abolition of slavery.

To construct lists of species occurrence in urban Venezuela and Brazil, we searched Google Scholar for published papers on urban tree species composition in those countries. We identified ten papers with lists of tree species in urban environments, including six cities from Brazil – Brazilia (Kurihara et al., 2005); Cidade de Campina Grande (Coelho and De Souza, 2004); Fortaleza (Moro and Castro, 2015); Lajeado (Ruschel et al., 2002); Rio de Janeiro (dos Santos et al., 2010); and Sao Paulo (Dislich and Pivello, 2002) – and three cities from Venezuela – Ciudad Bolívar (Díaz P and Delascio-Chitty, 2007); Guanare (Giménez and Berrío, 2017); and Mérida (Aranguren and Gámez, 2010; Luján et al., 2011). From these papers, we constructed a dataset of tree species occurrence. Because the vegetation sampling methodology varied widely between the ten studies, the focus of our analysis was identifying tree species found only in Georgetown. For tree species that occurred in Georgetown but were completely absent from any of the ten tree species lists from Venezuela and Brazil, we assume there is a reasonable chance our species record represents a regionally unique occurrence, at least in the urban flora.

2.4. Neighborhood comparison of urban tree species composition within Georgetown

We evaluated the importance of ethnic diversity by extracting demographic data for each electoral constituency (Bureau of Statistics, 2014). As a metric of ethnic composition, we chose the percent of people that identified as East Indian (heritage from the Indian Subcontinent) in each neighborhood. We chose to analyze tree data using this metric for three reasons: (1) percent of East Indian residents was highly variable between neighborhoods, ranging from 2 to 48%, (2) many of the exotic tree species in Guyana have links to Indian religion and cuisine, and (3) while the descendants of African slaves in Guyana have largely lost their ancestral culture, Indo-Guyanese have retained many cultural practices from India (Richards-Greaves, 2013). As a proxy for the impact of colonial history, we calculated distance of each tree transect to an early colonial landmark: Stabroek market, a trading post in continuous use since original establishment by the Dutch c. 1793. The data on tree species abundance and neighborhood characteristics are available from the Dryad data repository (https://doi.org/10.5061/dryad.ps7jt5b).

We evaluated the importance of ethnic composition and colonial history using a generalized linear mixed model (GLMM). This approach enabled us to use counts of individual tree species in each transect as a response variable while accounting for shared variance between species, constituencies, and origin and use categories for species. Similar models have been widely applied to analyze tropical tree species composition due to their ability to account for skewed species rank abundance by leveraging data from common species to enable statistical inference on rare species (*e.g.* Caughlin et al., 2019; Condit et al., 2013). For our GLMMs, we used the count of each tree species within each transect as a negative binomial-distributed response variable fit with a log-link function. The negative binomial distribution is an appropriate distribution for overdispersed count data (Bolker, 2008). As predictor variables, we included species identity and constituency of each transect as random intercepts to account for non-independence between counts of the same species and transects in the same neighborhood. To represent the effects of distance to Stabroek market and proportion of East Indian residents in our model, we used a random slope for these continuous variables, enabling different effects for each origin and use category. Altogether, this model structure implies that each constituency and species identity generates a baseline abundance that can be altered by distance to Stabroek market and proportion of

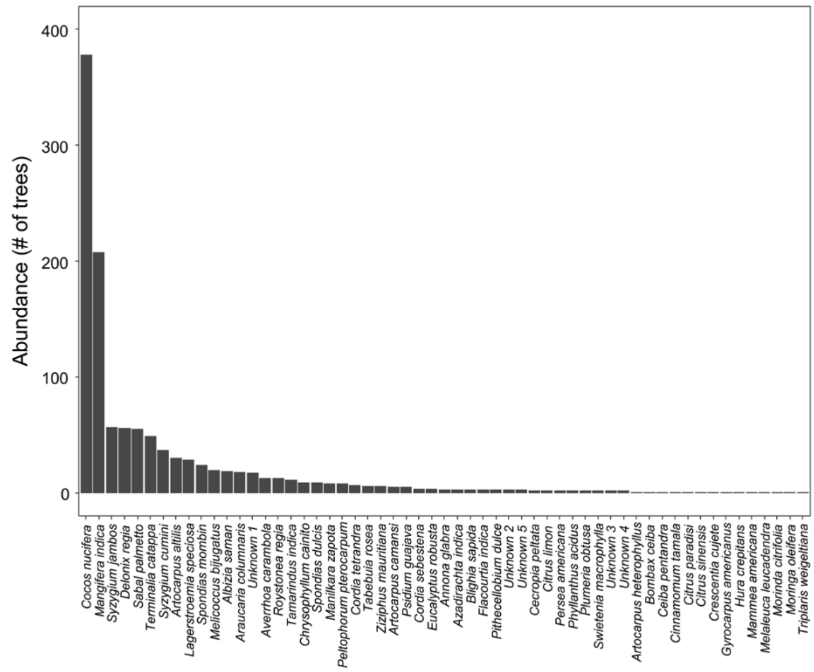

Fig. 2. Rank abundance of unique tree species identified across 45 transects in Georgetown, Guyana.

East Indian residents, with different effects depending on origin and use categories.

We fit our statistical model in a hierarchical Bayesian framework using the Hamiltonian Monte Carlo algorithm in the Stan programming language (Stan Development Team, 2016). The statistical model was implemented using the rstanarm package in the R programming language (Goodrich et al., 2018). We ran the model with four chains, each with 2000 total iterations, discarding the first 1000 as warm-up and assessed model diagnostics by visually inspecting output and by assessing the Gelman-Rubin statistic and number of divergent transitions (Betancourt, 2017).

3. Results

3.1. Tree transect data

We recorded a total of 1156 trees that included 57 unique species of which 5 species (33 trees) could not be resolved to the genus level across the 45 transects (Fig. 2; Table 1). The two most dominant species were *Cocos nucifera* (coconut; 378 trees) and *Mangifera indica* (mango; 208 trees), that accounted for 51% of all trees recorded. The 52 species identified to the genus level were from 29 families. The two most diverse families were Myrtaceae and Fabaceae, with five species each. We recorded a total of 28 exotic species from the Old World tropics and 24 species from the New World tropics (inclusive of pan-tropical species) in Georgetown. We present the average density, species richness, diversity and basal area of urban trees in Georgetown in Table 2.

The majority of the 52 species identified to the genus level have their origins in the Americas (21), followed by Asia (19), Oceania (5), and Africa (4), with 3 species, *Cocos nucifera* (coconut), *Gyrocarpus americanus* (helicopter tree) and *Ceiba pentandra* (silk cotton) classified as Pan-tropical. Species with origins from Asia were the most abundant accounting for 38% of all trees, followed by the two pan-tropical species (34%), the Americas (17%), Africa (6%) and Oceania (5%).

In terms of how residents of Georgetown, Guyana used urban trees, 25 species were classified as primarily cultivated for their fruits, 18 species classified as ornamental, 4 species as having medicinal or herbal use and 5 species as native wild plants. Trees cultivated for their fruits represented 73% of all recorded trees, 26% were classified as ornamentals, with the remaining 1% of stems either associated with herbal use or wild plant recruits that have edible fruits or cultural significance (Fig. 3).

3.2. Comparison with neighboring neotropical urban areas

There were a total of 14 species found in Georgetown, that were not found in inventories of tree species listed for neighboring neotropical urban areas in Brazil and Venezuela (Table 1). Fortaleza, Brazil, shared the most species with Georgetown, with a total of 27 species in common (Fig. 4). The most common species among the urban areas were *Mangifera indica* (mango), *Psidium guajava* (guava) *Terminalia catappa* (Indian almond), *Persea americana* (avocado) and *Delonix regia* (flamboyant), that were found in at least 6 of other urban areas in Brazil and Venezuela.

3.3. Statistical models for effects of ethnic composition and colonial history

Our statistical models revealed that distance to Stabroek market explained the distribution of some groups of species, while proportion of East Indian residents had weak and uncertain effects across all groups (Fig. 5). Several groups of species exhibited a strong positive effect of distance to Stabroek market, indicating that these groups tended to be more abundant further away from the city center. These groups included African Ornamentals, Pantropical Cultivated, New World Ornamentals, and Asian Cultivated. We note that both the African Ornamentals and Pantropical Cultivated groups each consist of only one species: *Delonix regia* and *Cocos nucifera*, respectively. In contrast, the effects of proportion of East Indian residents were highly variable between groups, including mean effect size centered near zero and 95% credible intervals (CI) that overlapped zero for all origin and use combinations (Fig. 5). We found qualitatively similar results when the effects of distance to Stabroek market and proportion of East Indian residents were allowed to vary by species, rather than by origin and use combination. We evaluated the fit of our model by using Mean Absolute Error (MAE) to compare predicted and observed values. MAE of our models had a median of 0.69 (95% CI: 0.60 − 0.84), indicating that, on average, our predictions were off by less than one tree per species per transect.

Table 1
Urban tree species found in Georgetown, Guyana, including place biological origin and primary use.

Scientific Name	Family	Common Name	Origin	Primary use
Albizia saman	Fabaceae	Saman	New World Tropics (Americas)	Ornamental
Annona glabra	Annonaceae	Monkey apple	New World Tropics (Americas)	Wild plants; edible fruit is often harvested
Araucaria columnaris	Araucariaceae	Christmas tree	Old World Tropics (Oceania)	Ornamental
Artocarpus altilis	Moraceae	Breadfruit	Old World Tropics (Oceania)	Cultivated for its edible fruits
Artocarpus camansi[a]	Moraceae	Katahar	Old World Tropics (Oceania)	Cultivated for its edible fruits
Artocarpus heterophyllus	Moraceae	Jackfruit	Old World Tropics (Asia)	Cultivated for its edible fruits
Averrhoa carambola	Oxalidaceae	Carambola	Old World Tropics (Asia)	Cultivated for its edible fruits
Azadirachta indica	Meliaceae	Neem	Old World Tropics (Asia)	Herbal/Medicinal
Blighia sapida[a]	Sapindaceae	Ackee	Old World Tropics (Africa)	Cultivated for its edible fruits
Bombax ceiba[a]	Malvaceae	Cotton tree	Old World Tropics (Asia)	Ornamental
Cecropia peltata	Urticaceae	Congo pump	New World Tropics (Americas)	Wild plants; often used as herbal medicines
Ceiba pentandra	Malvaceae	Silk cotton	Pan-tropical	Wild plants; cultural significance
Chrysophyllum cainito[a]	Sapotaceae	Star apple	New World Tropics (Americas)	Cultivated for its edible fruits
Cinnamomum tamala[a]	Lauraceae	Spice	Old World Tropics (Asia)	Herbal/Medicinal
Citrus limon	Rutaceae	Lemon/lime	Old World Tropics (Asia)	Cultivated for its edible fruits
Citrus paradisi	Rutaceae	Grapefruit	Old World Tropics (Asia)	Cultivated for its edible fruits
Citrus sinensis	Rutaceae	Orange	Old World Tropics (Asia)	Cultivated for its edible fruits
Cocos nucifera	Arecaceae	Coconut	Pan-tropical	Cultivated for its edible fruits
Cordia sebestena[a]	Boraginaceae	Spanish cordia	New World Tropics (Americas)	Ornamental
Cordia tetrandra	Boraginaceae	Gamma cherry	New World Tropics (Americas)	Ornamental
Crescentia cujete	Bignoniaceae	Calabash	New World Tropics (Americas)	Cultivated for its gourd fruits
Delonix regia	Fabaceae	Flamboyant	Old World Tropics (Africa)	Ornamental
Eucalyptus robusta[a]	Myrtaceae	Eucalyptus	Old World Tropics (Oceania)	Ornamental
Flacourtia indica[a]	Salicaceae	Psidum	Old World Tropics (Asia)	Cultivated for its edible fruits
Gyrocarpus americanus[a]	Hernandiaceae	Helicopter tree	Pan-tropical	Wild plants; often kept as ornamental
Hura crepitans	Euphorbiaceae	Sandbox tree	New World Tropics (Americas)	Ornamental
Lagerstroemia speciosa	Lythraceae	Queen of Flower	Old World Tropics (Asia)	Ornamental
Mammea americana[a]	Calophyllaceae	Mamey	New World Tropics (Americas)	Cultivated for its edible fruits
Mangifera indica	Anacardiaceae	Mango	Old World Tropics (Asia)	Cultivated for its edible fruits
Manilkara zapota	Sapotaceae	Sapodilla	New World Tropics (Americas)	Cultivated for its edible fruits
Melaleuca leucadendra[a]	Myrtaceae	Weeping paperbark	Old World Tropics (Oceania)	Ornamental
Melicoccus bijugatus	Sapindaceae	Genip	New World Tropics (Americas)	Cultivated for its edible fruits
Morinda citrifolia	Rubiaceae	Noni	Old World Tropics (Asia)	Herbal/Medicinal
Moringa oleifera	Moringaceae	Moringa	Old World Tropics (Asia)	Herbal/Medicinal
Peltophorum pterocarpum[a]	Fabaceae	Yellow flamboyant	Old World Tropics (Asia)	Ornamental
Persea Americana	Lauraceae	Avocado	New World Tropics (Americas)	Cultivated for its edible fruits
Phyllanthus acidus	Phyllanthaceae	Gooseberry	Old World Tropics (Africa)	Cultivated for its edible fruits
Pithecellobium dulce	Fabaceae	Bread and cheese	New World Tropics (Americas)	Cultivated for its edible fruits
Plumeria obtusa[a]	Apocynaceae	Frangipani	New World Tropics (Americas)	Ornamental
Psidium guajava	Myrtaceae	Guava	New World Tropics (Americas)	Cultivated for its edible fruits
Roystonea regia	Arecaceae	Royal Palm	New World Tropics (Americas)	Ornamental
Sabal palmetto[a]	Arecaceae	Cabbage palm	New World Tropics (Americas)	Ornamental
Spondias dulcis	Anacardiaceae	Golden apple	Old World Tropics (Asia)	Cultivated for its edible fruits
Spondias mombin	Anacardiaceae	Plum	New World Tropics (Americas)	Cultivated for its edible fruits
Swietenia macrophylla	Meliaceae	Mahogany	New World Tropics (Americas)	Ornamental
Syzygium cumini	Myrtaceae	Jamoon	Old World Tropics (Asia)	Cultivated for its edible fruits
Syzygium jambos	Myrtaceae	Plum rose	Old World Tropics (Asia)	Cultivated for its edible fruits
Tabebuia rosea	Bignoniaceae	Poui	New World Tropics (Americas)	Ornamental
Tamarindus indica	Fabaceae	Tamarind	Old World Tropics (Africa)	Cultivated for its edible fruits
Terminalia catappa	Combretaceae	Almond	Old World Tropics (Asia)	Ornamental
Triplaris weigeltiana	Polygonaceae	Long john	New World Tropics (Americas)	Wild plants; often kept as ornamental
Ziziphus mauritiana	Rhamnaceae	Dungs	Old World Tropics (Asia)	Cultivated for its edible fruits

[a] Species not found in neighboring urban centres in Venezuala and Brazil.

Table 2
Urban forest metrics calculated at the transect level (N = 45) for Georgetown Guyana.

Metric	Mean value (± standard deviation)
Shannon diversity	1.6 (± 0.54)
Simpson diversity	0.7 (± 0.15)
Stem density (trees ha^{-1})	21.4 (± 12.5)
Basal area ($m^2 ha^{-1}$)	1.3 (± 1.41)
Species richness	7.9 (± 3.77)

4. Discussion

Understanding how ethno-cultural differences shape urban tree cover will help achieve urban greening goals in an increasingly globalized world (Ordóñez-Barona, 2017). Our study fills a knowledge gap on how multiculturalism in cities of the Global South impacts urban tree species distribution. We studied urban tree species distribution in Georgetown, Guyana, a city shaped by colonial history and biocultural diversity, two key features of human-environment systems in the tropics. Guyana's unique position as the only Anglophone country in South America is reflected in the urban tree flora of its capital city, including a set of tree species absent from tree species lists in neighboring countries that lack a history of British colonialism. At the neighborhood scale, we found evidence that distance from Stabroek market, the colonial center of the city, impacted abundance of some tree species groups but not others. In contrast, proportion of East Indian residents had minimal effects on tree species distribution, despite the presence of many tree species characteristic of Indian culture and cuisine. These results demonstrate that while multiculturalism in Guyana has led to a diverse assemblage of trees from across the tropics in the capital city, spatial patterns of tree species abundance within the city are more challenging

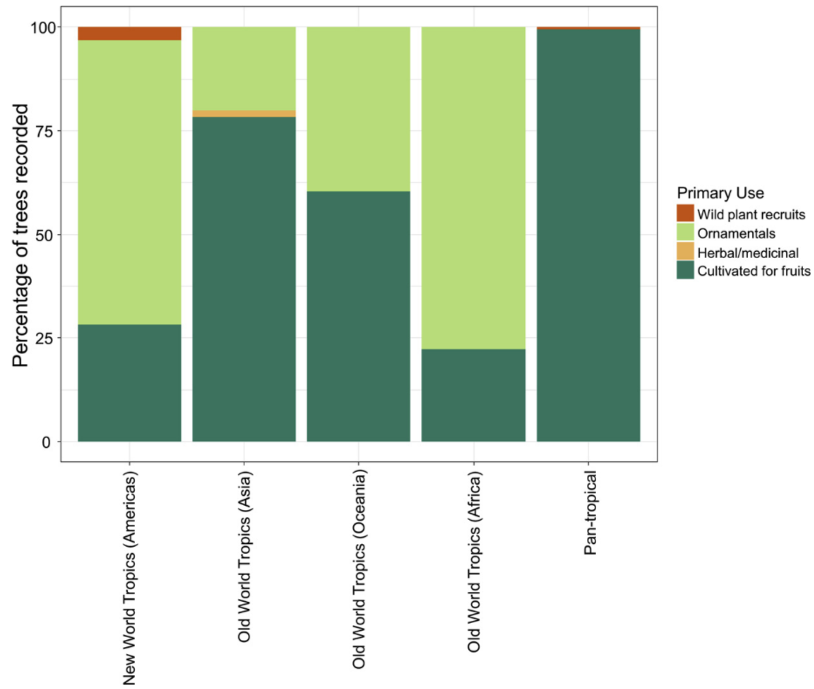

Fig. 3. Percentage of trees recorded in Georgetown, Guyana based on their primary uses (wild plant recruits with either edible fruits or cultural significance; ornamentals; herbal/medicinal; cultivated for fruits) and geographic origin.

to explain. Altogether, our work highlights the value of conducting tree species inventories in tropical cities for urban planning that acknowledges the biocultural context of the Global South.

We found that a substantial proportion (73%) of individual trees in Georgetown belonged to species that provided edible fruit. In addition to many other ecosystem services provided by urban trees (*e.g.*, shade, aesthetics, psychological benefits, air pollutant removal, stormwater attenuation), the livelihood benefits of fruit production in urban food forests are increasingly recognized (Clark and Nicholas, 2013). However, the majority of studies on edible green infrastructure have been conducted in developed countries (Russo et al., 2017). In Georgetown, the array of fruit trees that can be grown reflects the biocultural diversity of the tropics, including 14 different families found in our study. These cultivated trees were distributed throughout the city, with no apparent correlations between fruit tree species abundance and distance to city center or ethnic composition of neighborhoods. The

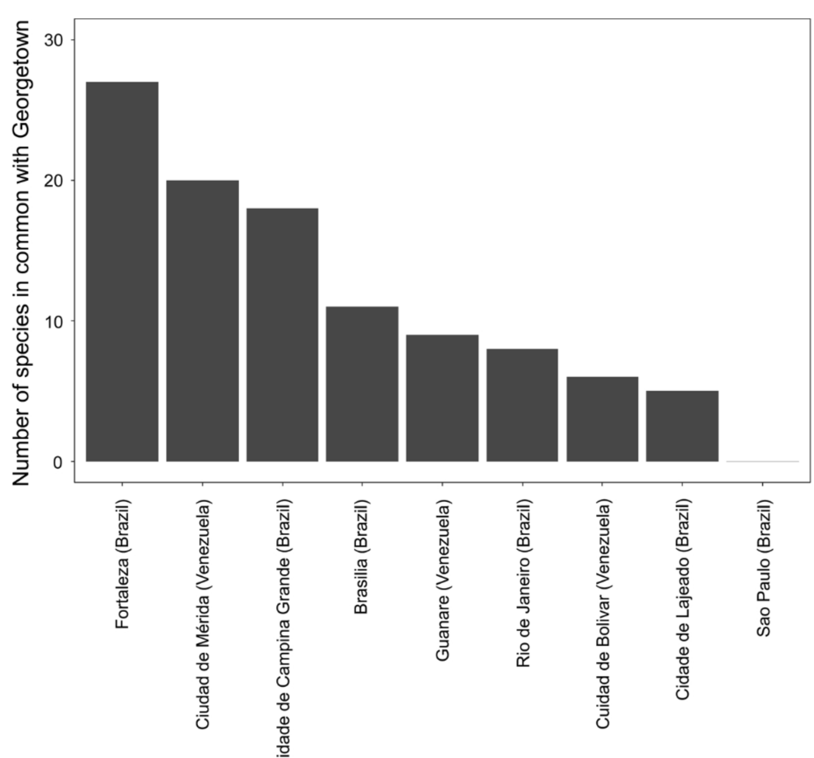

Fig. 4. Number of trees species found in Georgetown, Guyana that were also found in floristic inventories of cities in Venezeula and Brazil.

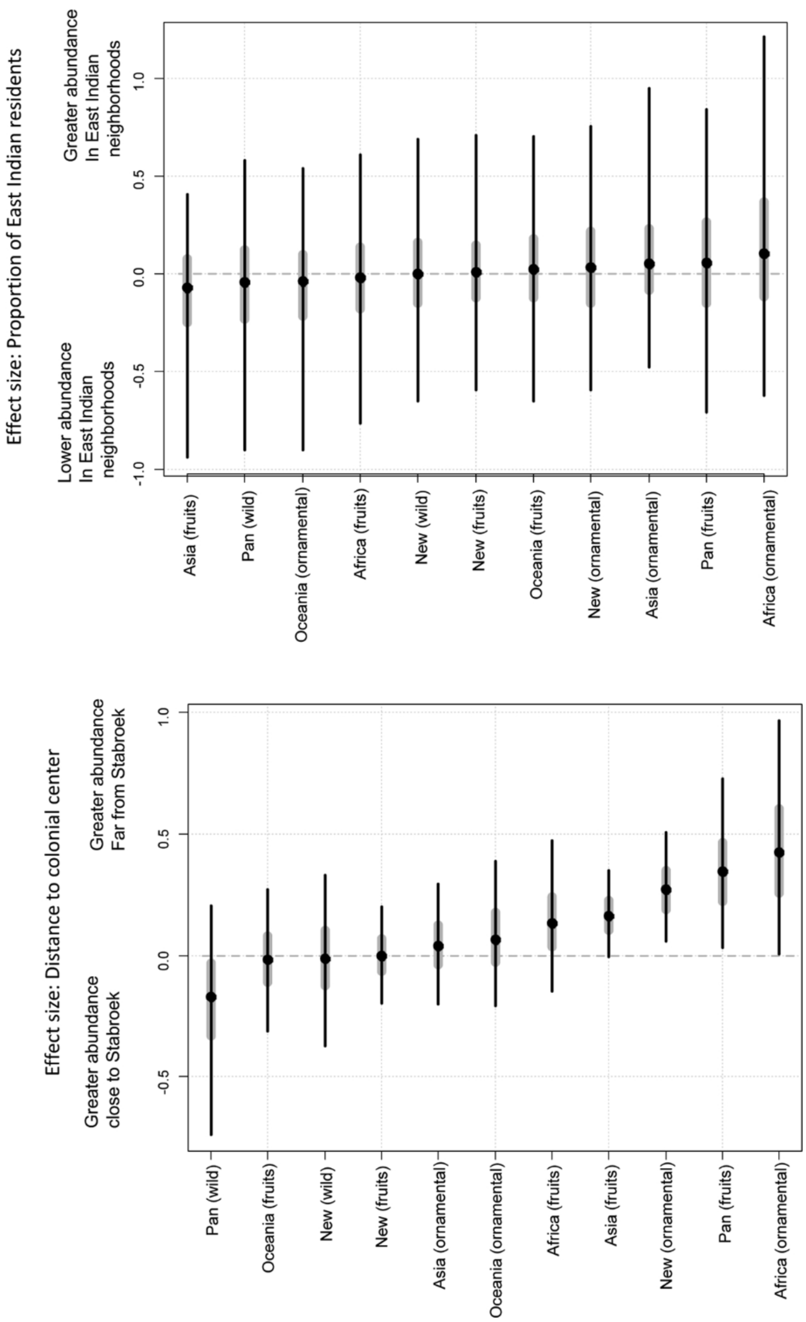

Fig. 5. Regression coefficients for effects of proportion of East Indian residents and distance to colonial center on tree species abundance in groups categorized by origin and use. This figure represents the output of the generalized linear mixed effect model, with effects of predictor variables estimated for each combination of tree species origin (New World, Asia, Africa, Oceania, and Pantropical) and use (cultivated for fruit, ornamental, and wild). The dashed horizontal line at y = 0 represents an effect size of zero. Points represent the median posterior estimate, thick gray lines represent the 50% credible intervals (CI), and thin black lines represent the 95% CI. Coefficients with 95% CI that do not cross zero can be considered statistically significant.

existing species diversity and broad spatial distribution of fruit trees in Georgetown reveal opportunities to improve nutrition and alleviate poverty by promoting urban food forests. Compared to other tropical urban areas, where the proportion of tree species that bear fruit is often < 50% (Akinnifesi et al., 2010; Jaganmohan et al., 2012), we found a relatively high proportion of fruit trees in Georgetown. One potential explanation is that fruit trees were planted in response to post-independence government policies during the 70′s and 80′s that sought to promote domestic agricultural production by restricting imported food items including fruits (Ford, 1992). Further research on the relationship between edible green infrastructure and food scarcity will be necessary to test this explanation. In temperate cities, including Seattle, Washington and municipalities in the Canadian provinces of British Columbia and Ontario, food forests are increasingly a component of urban forest policy (Kowalski and Conway, 2018; McLain et al., 2012). While work remains to be done to assess the risk of contaminants from urban pollutants in tropical fruit trees (*e.g.* Li et al., 2006), we suggest that formally incorporating fruit trees into urban planning has potential as a sustainability intervention in the Global South.

Although we found strong evidence that Guyana's ethnic composition has shaped species composition of urban forests, including many tree species with cultural significance in India and West Africa, ethnic composition within neighborhoods did not explain within-city differences in tree species distribution. This result was surprising, considering the wide range of ethnic differences between neighborhoods (*e.g.*, a range of 2–48% East Indian) and Guyana's long history of racial tensions associated with political power (Bulkan, 2014). One hypothesis is that social and cultural integration between the two dominant ethnic groups, especially around food, has forged a common Caribbean ethnic identity (Garth, 2013; Reynolds, 2006), diluting the associations trees previously had with a specific ethnic group. Testing this hypothesis will require a combination of household-scale data to assess individual motivation for tree species selection and historical data on the entities responsible for planting trees across the city.

Fig. 6. Two tree species unique to Georgetown. *Artocarpus camansi* (Katahar - a) a fruit tree with origins associated with the Old-World Tropics in Asia and *Blighia sapida* (Akee - b) native to Old-World tropics of Africa have clear association with the main ethnic groups of Indian and Africans. Both of these tree species were recorded in Georgetown but absent from tree species lists in Venezuelan and Brazilian cities.

At a city scale, several tree species that were recorded in our study in Georgetown were not found in cities in neighboring countries of Venezuela and Brazil (Table 1; Fig. 4). At least some of these unique tree species are likely to reflect Guyana's status as the only Anglophone country in South America, including the importance of colonial history in shaping tree species distributions. As an example, the Ackee tree (*Blighia sapida;* Fig. 6) is an African species that was brought to Jamaica in slave ships in the 18th century; its fruit has since become integral to Jamaican food culture (Rashford, 2001). The presence of this tree species in Georgetown may reflect close ties between Guyana and other English-speaking Caribbean countries impacted by the slave trade and British colonial rule. An example of a species not found in neighboring countries that is associated with people of Indian origin is Katahar (*Artocarpus camansi*; Fig. 6), a tree with origins in Papua New Guinea that most likely made its way to Guyana via India through indentured servants, perhaps representing historical trade linkages that preceded colonialism.

At a neighborhood scale, distance from the colonial center had an impact on several groups of tree species, with predictions of increased abundance for these species groups further away from Stabroek market. However, these species groups included a mix of tree species from both the Old and New World that include edible and ornamental species, without a clear trend across multiple groups (*e.g.*, edible fruit tree species, in general, were not more abundant away from the city center). These results complement recent studies from Indonesia (Abendroth et al., 2012) and India (Nagendra and Gopal, 2011) by providing a Neotropical example of how colonial history can have long-lasting legacy effects on tree species diversity. Other studies on urban forests in South America have raised the alarm about the high proportion of exotic species in urban flora (dos Santos et al., 2010; Fischer et al., 2016). In Georgetown, we caution that this simple dichotomy is unlikely to reflect the cultural value of trees that provide a sense of ethnic identity for African and Asian populations displaced by colonialism (*e.g.* Nelson, 2009).

Our study on urban forests in Georgetown also provides a nuisance perspective of the relationship of ethno-cultural backgrounds and interaction with urban tree species. Several studies that have been conducted in temperate cities have concluded that non-white ethnic groups may have a passive relationship with urban forests (reviewed in Ordonez-Barona, 2017). A deficiency in this conclusion is that recent emigrant ethnic groups from the tropics face a climate barrier when transferring culturally-important tree species to their adopted homes in temperate regions. Our results suggest that people in multicultural cities in the tropics may maintain the strong cultural connections with trees from their geographical origin centuries after arrival.

We anticipate that our study, along with other tree species inventories in urban forests of the Global South (Abendroth et al., 2012; Fischer et al., 2016; Nagendra and Gopal, 2010; Ruschel et al., 2002), will provide valuable information for urban planning in regions facing the greatest climate-induced threats. In our case, while Georgetown was once known as the "Garden City" of the Caribbean, there is now a widespread perception that urban tree cover in Georgetown is declining (Edwards et al., 2005). Our work provides baseline data that can be applied to monitor changes in urban forests over time. Overall, interpreting tree species distributions in an ethno-cultural context will contribute to achieving urban greening goals, with potential to integrate citizens into management of urban forests based on their tangible values.

Funding

This project was funded through a grant from the Norwegian Agency for Development Cooperation (Norad) in collaboration with the WWF-Guianas program titled "Building human capacity for natural resource management in Guyana". TTC was supported by National Science Foundation (SBE-1415297).

Acknowledgements

We would like to thank the Guyana Jesuit Society, the Guyana Forestry Commission (GFC), the University of Guyana Biology Club, the Guyana National Museum, the Guyana Elections Commission (GECOM) and the Guyana National Archive who assisted in tree data collection including tree species identification and compilation of neighborhood demographics.

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