Landscape and Urban Planning 120 (2013) 96–106

Contents lists available at ScienceDirect

Landscape and Urban Planning

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

Research paper

Temporal dynamics of a subtropical urban forest in San Juan, Puerto Rico, 2001–2010

Joanna M. Tucker Lima[a,*], Christina L. Staudhammer[b], Thomas J. Brandeis[c], Francisco J. Escobedo[a], Wayne Zipperer[d]

[a] School of Forest Resources and Conservation, University of Florida, PO Box 110410, Gainesville, FL, USA
[b] Department of Biological Sciences, University of Alabama, PO Box 870344, Tuscaloosa, AL, USA
[c] USDA Forest Service, Southern Research Station, Knoxville, TN, USA
[d] USDA Forest Service, PO Box 11086, Building 164 Mowry Road, Gainesville, FL, USA

HIGHLIGHTS

- We examined structural and compositional dynamics of subtropical urban forests.
- Tree mortality rates were higher in San Juan than in temperate urban forests.
- San Juan forests experienced greater in-growth than temperate urban forests.
- Average tree growth rates in San Juan were higher than in temperate urban forests.
- Mortality (death and removal) was higher for invasive than non-invasive species.

ARTICLE INFO

Article history:
Received 29 April 2013
Received in revised form 9 August 2013
Accepted 13 August 2013

Keywords:
Urban forest structure
Novel ecosystems
Caribbean
Permanent plots
Mangrove

ABSTRACT

Several studies report urban tree growth and mortality rates as well as species composition, structural dynamics, and other characteristics of urban forests in mostly temperate, inland urban areas. Temporal dynamics of urban forests in subtropical and tropical forest regions are, until now, little explored and represent a new and important direction for study and management of these ecosystems. This study used permanent plots and statistical models incorporating tree and plot-level covariates to analyze mortality, in-growth, diameter growth, and species composition, as well the socioeconomic and urban morphology factors driving change in San Juan, Puerto Rico's subtropical coastal island urban forests over a nine year period. A total of 87 plots contained 482 trees in 2001 and 749 trees in 2010. Between 2001 and 2010 average tree densities increased, and average annual mortality rates were nearly 30%. Mortality was lower for larger, open-grown, non-leguminous trees and in higher income neighborhoods, but higher for street trees and larger population areas. The most widespread tree was invasive *Spathodea campanulata*, but overall, average mortality was higher for invasive than non-invasive tree species. In-growth of invasive species increased with human population, while higher tree densities corresponded with increased in-growth of native species. Overall mean diameter growth rate was 0.98 cm/yr, but remnant forest patch growth rates were 0.35 cm/yr. Higher diameter growth rates were associated with larger human populations, amounts of duff/mulch cover, and open-grown conditions. This study adds new insights to broaden our understanding of these emergent ecosystems in the Caribbean region.

1. Introduction

Urban forest structure, composition and spatio-temporal dynamics are intricately linked to the provision of ecosystem services and quality of life (Escobedo, Kroeger, & Wagner, 2011; Roy, Byrne, & Pickering, 2012). In tropical and subtropical regions, trees regulate the urban climate, and in particular, tree shade can reduce interior temperatures of buildings and homes, increasing human comfort (Heisler, 1986; Pandit & Laband, 2010). Natural and planted trees in tropical, coastal areas can affect air quality, sequester carbon, and mitigate tropical windstorm effects (Escobedo, Varela, Zhao, Wagner, & Zipperer, 2010; Nowak & Crane, 2002; Zhao et al., 2013). Trees also convey important esthetic and psychological value in urbanized environments as people form strong emotional and spiritual associations with trees, and their

* Corresponding author at: School of Forest Resources and Conservation, University of Florida, PO Box 110410, Gainesville, FL 32611, USA. Tel.: +1 352 870 6028.
E-mail addresses: jmtucker@ufl.edu, lima.joanna@gmail.com (J.M. Tucker Lima), cstaudhammer@ua.edu (C.L. Staudhammer), tjbrandeis@fs.fed.us (T.J. Brandeis), fescobed@ufl.edu (F.J. Escobedo), wzipperer@fs.fed.us (W. Zipperer).

0169-2046/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.landurbplan.2013.08.007

presence helps reduce stress for urban dwellers and increases property values (Escobedo et al., 2011; Roy et al., 2012; Wolf, 1998).

Several studies report tree growth rates, mortality rates, species composition, structural dynamics, and other characteristics of urban forests in mostly temperate, inland urban areas (Broshot, 2011; Iakovoglou, Thompson, Burras, & Kipper, 2001; McPherson et al., 1997; Nowak et al., 2011; Nowak, Kuroda, & Crane, 2004). Little work has focused on growth and mortality of trees in non-temperate urban landscapes with the exception of recent U.S. studies on subtropical forests in Florida and Texas (Lawrence, Escobedo, Staudhammer, & Zipperer, 2012; Staudhammer et al., 2011; Zhao, Escobedo, & Staudhammer, 2010) and others in Asia and Brazil (Dislich & Pivello, 2002; Jim & Liu, 2001; Nagendra & Gopal, 2010; Zhao et al., 2013), making basic information relatively scarce for tropical and subtropical urban forests, and in particular, island urban forests.

The dynamics of tropical and subtropical urban forests certainly differ from those of temperate ones. Due to limited information, growth and mortality rates associated with inland temperate urban trees are often used to assess structural change and carbon dynamics of urban forests in tropical, subtropical, and coastal areas (Escobedo et al., 2010). To improve estimates of ecosystem services, benefits, and the value of these urban forests, a clear understanding of tree growth and mortality in tropical and subtropical urban ecosystems is critical (Brandeis, 2009; Escobedo et al., 2011; Roy et al., 2012), and identification of factors driving growth rates and dynamics in urban forests is imperative (Seguinot Barbosa, 1996). In urban settings, tree growth rates vary due to anthropogenic disturbance, soil properties (Hagan et al., 2010; Iakovoglou et al., 2001), site conditions (Vrecenak, Vodak, & Fleming, 1989), disease, insects, and mechanical injury (Iakovoglou et al., 2001), and climate conditions (Lawrence et al., 2012). Even within the same climate, growth rates vary significantly according to land use/land cover, species, and site characteristics (Brandeis, 2009; Iakovoglou et al., 2001). We cannot accurately apply results from long-term studies of inland, temperate urban forests to trees found in subtropical urban areas due to different climate and urban characteristics (Escobedo et al., 2010; Roy et al., 2012; Zhao et al., 2010).

Urban forest dynamics in subtropical and tropical forests regions are, until now, little explored and represent a new and important direction for study and management of these ecosystems (Roy et al., 2012). Although studies of street tree dynamics (Nagendra & Gopal, 2010; Sklar & Ames, 1985) and urban forest ecosystem structure using multiple inventories or permanent plots are increasing (Broshot, 2011; Cumming, Twardus, & Nowak, 2008; Jo & McPherson, 1995; Lawrence et al., 2012; Nowak et al., 2004; Staudhammer et al., 2011; Thompson, Escobedo, Staudhammer, Matyas, & Qiu, 2011; Zhao et al., 2013), to our knowledge, research on the temporal dynamics of subtropical island urban forests is lacking. The goal of this study was to examine how tree mortality, in-growth (i.e., recruitment by growth or planting), diameter growth, and species composition of island, subtropical forests across San Juan, Puerto Rico's urban and peri-urban areas varied across a set of permanent plots between 2001 and 2010. We examine temporal changes in tree densities, diameter, basal area, and species composition, and compare these patterns within and across San Juan's land use/land cover types, including remnant upland secondary forest, mangrove forest, residential, vacant, and commercial/industrial/institutional/transportation covers. We further analyze how species endemicity, invasiveness, and other socioeconomic factors and urban morphology affect forest dynamics in this subtropical, island urban forest.

We hypothesized that urban forests in San Juan, Puerto Rico will have greater mortality and in-growth rates than those in temperate cities, due to the city's dense urban morphology, and predicted higher tree diameter growth rates due to favorable year-round growth conditions. The long-term nature of our study (2001–2010), analysis of 21 tree, plot, landscape scale covariates, and geographic location are novel to the urban forestry literature and will add important new insights to broaden our understanding of these emergent ecosystems in the Caribbean region.

2. Methods

2.1. Study area

Research was carried out across the 216.6 km^2 San Juan Bay Estuary (SJBE) watershed, which lies along the northeast coast of Puerto Rico. The watershed is contained within the highly dynamic and expanding San Juan metropolitan area, which has a total population of ~2.5 million (U.S. Census Bureau, 2010). The SJBE falls in the subtropical moist forest life zone (sensu Holdridge, 1967) with average temperatures of 23–27 °C and 1500–2300 mm of precipitation annually (Lugo, Ramos Gonzáles, & Rodriguez Pedraza, 2011). Geologically, the watershed is covered in alluvial deposits of sand, gravel, and clay except in the southern portion, where soils are derived from volcanic rocks and areas with outcroppings of exposed limestone (Lugo et al., 2011).

Historically, the watershed's natural vegetation was mangrove forest in the low-lying areas protected from the surf and wind and subtropical moist forest in upland areas. The mangrove forest, while reduced in overall area, remains along bays and lagoons, particularly in the eastern portion of the watershed that falls within the Piñones Commonwealth Forest. Upland secondary forests have been heavily impacted by human activities and remain as scattered forest patches fragmented by urban development (Grau et al., 2003). The introduction and establishment of many non-native tree species has further altered these forests and continues today as ornamental tree and shrub species from around the world are brought into the San Juan area.

2.2. Urban forest inventory sampling design

The SJBE watershed was first systematically sampled from July 2001 to February 2002 (hereafter referred to as 2001), using an intensification of the island-wide forest inventory sampling grid already established by the USDA Forest Service's Forest Inventory and Analysis (FIA) program (see Brandeis, 2003; Brandeis, Helmer, & Oswalt, 2007 for details). We resampled these plots from May 2010 to March 2011 (hereafter referred to as 2010). Sampling intensity was approximately one plot per 200 ha. After excluding sampling points that fell onto water, a total of 108 sampling points remained within the watershed boundaries.

Two plot designs were used, both with the same total sample plot area of 0.067 ha. In areas that met the Caribbean FIA criteria for forested land (i.e., a contiguous area > 0.4 ha or > 30 m wide with > 10% tree canopy coverage), crews installed an FIA subplot cluster consisting of four 7.3 m radius circular subplots to sample trees with diameter at breast height (DBH) ≥ 12.5 cm and 2.1 m radius nested microplots to sample trees with DBH ≥ 2.5 cm (USDA Forest Service, 2011) (see Bechtold & Scott, 2005; USDA Forest Service, 2006, 2007 for details). In urban and agricultural lands that failed to meet minimum requirements for forest, crews installed single 14.6 m radius circular plots using the Urban Forest Effects (UFORE) urban forest inventory methods, sampling all trees with DBH ≥ 2.5 cm (Nowak, Crane, Stevens, & Hoehn, 2005). In the interest of time, two densely vegetated plots were measured using a 0.01 ha quarter-plot (northeast quarter of the UFORE plot), and data was adjusted accordingly; plot level density measures were calculated using plot-specific areas and tree-level data were weighted by their plot's area. Small patches (>0.4 ha) of tree-covered land that did not meet the minimum area requirements for forest were considered urbanized and usually categorized as vacant (V).

2.3. Tree information

The term "tree" applies to individual woody plants capable of growing to a minimum size of 12.5 cm DBH and 5 m height, including palms. We used the USDA National Resource Conservation Service's PLANTS database as our nomenclature and nativity reference (http://plants.usda.gov/). To categorize non-native species as invasive, we utilized a draft list produced by the Puerto Rico Department of Natural and Environmental Resources (E. Gonzalez, pers. comm., Puerto Rico Departamento de Recursos Naturales y Ambientales, 2009). For each tree, we recorded species, DBH, height, crown width, foliage density, and crown light exposure (CLE). Crown width entailed two measurements: one at the crown's widest diameter and the second at 90° to the widest diameter (Schomaker et al., 2007). Crown light exposure registered the number of sides of the tree crown receiving direct sunlight Schomaker et al., 2007

2.4. Land use, cover, and building information

Field crews noted the land use/land cover (LULC) classification for each plot. Developed land uses were commercial/industrial/institutional/transportation (CIT), residential (R), vacant (V) and water/wetlands/agriculture (WAG). The CIT land use was typified by the presence of buildings dedicated to business activities and included outdoor storage/staging areas, schools, manufacturing and medical complexes, and religious and government buildings, as well as parking lots, roads, median strips, railroad stations, tracks, shipyards, and airports and their related green spaces. Residential (R) land uses had buildings that were predominately single or multi-family houses and their related green spaces. Vacant (V) areas were those that had no apparent use, no vacant structures in the immediate vicinity, were not being actively used or developed, and had insufficient tree cover or area to be considered forest. Water, wetlands and agriculture were combined into the WAG classification, as sampling points that fell on agricultural lands were mostly seasonally flooded pasture in the eastern portion of the watershed and considered emergent wetlands. The two broadly defined forest covers encountered in the SJBE watershed were mangrove forest (MF) and upland secondary forest (UF).

At each plot, crews estimated ground cover as a percentage of the plot area covered by buildings, impervious surfaces (concrete, asphalt, etc.), permeable surfaces (gravel, bare soil, sand, mulch, leaf litter, etc.), herbaceous vegetation (agricultural crops, grass, woody vegetation < 30 cm tall), and water. The percentage of tree (woody stems ≥ 2.5 cm DBH) and shrub (<2.5 cm DBH and >30 cm tall) canopies were estimated as their projections onto the ground within a plot. Additionally, we estimated the percent of the plot area available for planting trees and recorded whether the tree was a street tree (i.e., planted in the space between the edge of the road and the sidewalk).

Ancillary data were obtained from the 2000 U.S. Census and georeferenced using plot centroids. Socioeconomic variables included total population, median income, and median value of owner occupied housing units, while urban morphology variables included total number of housing units and median year built (i.e., home age).

2.5. Data matching

We merged plot and tree data from the 2001 and 2010 inventories, and all trees in matched plots were categorized as survived, in-grown/planted, or dead/removed. Within urban environments, changes in vegetation occur naturally through tree recruitment and death, and through intentional planting and tree removal or land clearing. Mortality rates account for both losses from natural tree death and land clearing activities, while in-growth represents recruitment through natural growth and planting. Annualized mortality and in-growth in this study were considered a long-term average and not necessarily typical values for a single year. Some trees likely both in-grew and died between our two measurements and therefore were not recorded. Individual trees present in both samples were matched into a paired tree dataset for diameter growth analyses. For growth analyses we only included broadleaf trees, as palms experience no secondary growth, and thus their diameter growth in not comparable.

We matched a total of 87 plots from the two sampling periods, although not all plots had trees. Some plots were excluded because access was denied by landowners, or because the presence of multi-stemmed individuals made matching trees questionable. Estimates of overall tree density for our study may be biased low, because a majority of excluded plots contained trees rather than not; however, since omitted plots can be assumed a random sample of treed plots, no bias should be introduced to estimates of mortality, in-growth, or diameter growth. Of plots with trees in either 2001 or 2010, crews measured a total of 482 trees in 2001 ($n = 48$ plots), and 749 trees in 2010 ($n = 54$ plots). We were able to match 244 trees between the two periods but used only 170 trees to calculate and analyze diameter growth, after removing palm trees, multiple-stemmed trees, and trees whose diameter was not consistently measured at breast height (1.4 m). Growth assessment via increment cores or dendrometer bands is preferred in forested environments due to the potential for stem shrinkage, measurement error, and litter depth effects on diameter height; however, urban environments present additional challenges such as permission and vandalism (Lawrence et al., 2012), and thus matched DBH measurements were utilized. Most re-sampled plots with trees continued under the same LULC over the sampling interval. Only three plots changed LULC between 2001 and 2010, converting from CIT to V, R to V, and V to R.

2.6. Statistical analyses

Models were developed to characterize mortality, in-growth, and diameter growth. Variables considered for analyses included those collected in 2001 on each individual tree (DBH, height, crown width, foliage density, CLE), as well as 2001 plot-level census-derived data, LULC, plot-level density (trees per hectare; TPH), and basal area per hectare (m^2/ha; BAHA). As a preliminary analysis step, we calculated Pearson's correlation coefficient between all pairs of input variables by LULC. Because of high correlations which can lead to multicollinearity, not all variables could be included simultaneously in all models. For example, TPH and BAHA were very highly correlated ($p < 0.001$), and thus we never included both at the same time in the same model. Also, many of the cover variables (e.g., herby/ivy and shrub) were highly correlated in some LULCs and were excluded. The WAG plots were omitted from modeling analyses, since these plots contained no trees in either measurement year. Where enough data were available, tree level classifications of street tree, native range, invasive status, and legume category (leguminous vs. non-leguminous species) were included as covariates.

Mortality was modeled in a generalized linear mixed modeling framework. Using the SAS procedure PROC GLIMMIX (version 9.2), the response variable was modeled assuming a binary distribution (individual tree survival/mortality). The mean response was modeled as a function of year 2001 tree- and plot-level variables, utilizing a logit link. A random effect was included to account for the correlation among trees measured in the same plot. Because forested land covers did not include some input variables (e.g., plantable space), and to account for the varying degree of correlation between variables in different LULCs, mortality models were developed separately by LULC classification. Because all 2001 trees recorded in the vacant land use died/were removed, no model could be developed for this land use. Model fit was assessed via the Generalized Chi-square statistic.

In-growth was modeled at the plot level, using the number of trees per ha from the second measurement period that were not matched to those in the first period as the response variable. General linear models (GLMs) were estimated for plot-level in-growth, using plot-level variables as predictors via the procedure PROC MIXED. Because too few plots were available in any single LULC classification, we conducted one single analysis for all LULCs combined. We included LULC as a predictor variable and combined MF and UF data to create one classification (F) with $n = 7$ plots. The interaction of LULC with other covariates was included where possible. Since none of the categorical variables associated with invasiveness, leguminous species, or native range could be used in this plot-level analysis, additional analyses of in-growth were performed to further investigate comparative invasive/non-invasive and native/non-native in-growth. We first estimated logistic models to find the factors associated with the presence of invasive species in-growth and the presence of non-native species in-growth. Where in-growth occurred, we further modeled the comparative density of invasive vs. non-invasive trees, and the density of native vs. non-native trees using a GLM.

Tree growth was characterized as the annual change in tree DBH between the first and second measurements. Growth models were developed separately for CIT, R and F; however, no model could be developed for the V land use category, as no matching trees were found over the study interval in these plots. For growth, a mixed model was estimated via the SAS procedure PROC MIXED, and similar to the mortality model, we included a random effect to account for correlations among measurements taken on trees in the same plot. As with the mortality model, to account for the varying degree of correlation between variables and differing available variables by LULCs, growth models were developed separately by LULC classification.

For mortality, in-growth, and diameter growth models, we first estimated a "full model", including all appropriate predictor variables. A stepwise backwards elimination procedure was then used to eliminate variables until all variables in the model were significant ($p < 0.10$). We used a more conservative significance level (alpha = 0.10) than the usual arbitrary 0.05 level (Burnham & Anderson, 2002; Johnson, 1999) to allow all possible significant effects to remain for the purpose of building the best explanatory model (Bancroft, 1968). Growth and in-growth data were log-transformed in order to meet the assumptions of normality and homoscedasticity of the residual errors. Where significant interactive effects were indicated, the underlying simple effects were retained and least square means were estimated, with all other effects in the model at their average values, to further illuminate the nature of the interaction.

3. Results

3.1. Urban forest structure and composition

Across the SJBE between 2001 and 2010, average TPH and BAHA increased from 222 (±63.6 SE) to 328 trees/ha (±92.4 SE), and 3.66 (±0.79 SE) to 4.62 m^2/ha (±0.87 SE), respectively across all plots – WAG plots excluded (Table 1). Within and across LULC classes, TPH, BAHA, and DBH varied. Average tree diameter was highest

Table 1
Mean (±SE) basal area (m^2/ha), tree density (tree/ha), diameter at breast height (DBH) (cm), Shannon diversity index, and species richness (% native) in 2001 and 2010 from 87 matched, re-sampled plots (with and without trees) in the San Juan Bay Estuary watershed, Puerto Rico, by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove forest (MF), Upland secondary forest (UF), Water/Wetlands/Agriculture (WAG).

	Mean basal area per plot (m^2/ha)		Mean tree density (trees/ha)		Mean DBH (cm)		Shannon's diversity index		Species richness (% native)	
	2001	2010	2001	2010	2001	2010	2001	2010	2001	2010
CIT ($n = 25,24$)[a]	2.03 (1.13)	1.62 (0.85)	48 (18)	58 (28)	17.1 (3.3)	14.0 (3.4)	0.195 (0.098)	0.216 (0.092)	18 (56%)	19 (26%)
R ($n = 38,38$)[a]	4.47 (1.17)	3.66 (0.83)	112 (35)	80 (18)	21.9 (3.0)	19.1 (2.3)	0.602 (0.103)	0.623 (0.108)	44 (34%)	44 (36%)
V ($n = 10,11$)[a]	0.03 (0.03)	5.88 (3.37)	13 (13)	386 (196)	4.9 (–)	10.5 (1.9)	0.000 (0.000)	0.381 (0.193)	2 (0%)	16 (50%)
MF ($n = 3,3$)[a]	9.87 (2.22)	22.19 (0.84)	1966 (481)	3509 (975)	12.0 (0.8)	11.0 (0.8)	0.734 (0.102)	0.647 (0.039)	4 (100%)	5 (100%)
UF ($n = 4,4$)[a]	17.03 (8.22)	23.20 (4.87)	1958 (560)	2337 (376)	14.7 (2.4)	14.2 (1.8)	1.249 (0.167)	1.634 (0.196)	25 (84%)	32 (88%)
WAG ($n = 7,7$)[a]	0 (0)	0 (0)	0 (0)	0 (0)	–	–	–	–	–	–
ALL ($n = 87,87$)[a]	3.66 (0.79)	4.62 (0.87)	222 (63.6)	328 (92.4)	17.6 (2.8)	15.9 (1.7)	0.437 (0.067)	0.519 (0.073)	68 (50%)	85 (53%)

[a] Denotes number of matched sample plots in 2001, 2010.

Table 2
Ten most common tree species by average plot density (trees/ha) across the San Juan Bay Estuary watershed in 2001 and 2010 by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove forest (MF), Upland secondary forest (UF).

Species	Frequency	Density (trees/ha)					
	(# plots)	All LULC	CIT	R	V	MF	UF
2001							
Avicennia germinans[a]	2	25.66	0.00	0.00	0.00	744.16	0.00
Spathodea campanulata[b]	8	25.57	0.60	10.22	0.00	0.00	455.46
Rhizophora mangle[a]	2	18.37	0.00	0.00	0.00	532.61	0.00
Laguncularia racemosa[a]	3	16.99	0.00	0.00	0.00	492.79	0.00
Syzygium jambos[b]	2	13.39	0.00	0.00	0.00	0.00	291.19
Albizia lebbeck[b]	5	11.84	2.99	21.61	13.44	0.00	0.00
Calophyllum antillanum	3	12.62	0.00	1.97	0.00	0.00	255.73
Cocos nucifera	8	9.70	2.99	3.14	0.00	0.00	162.40
Conocarpus erectus	2	7.81	3.58	0.00	0.00	196.62	0.00
Erythroxylum rotundifolium	1	6.44	0.00	0.00	0.00	0.00	140.00
2010							
Rhizophora mangle[a]	2	63.77	0.00	0.00	0.00	1849.20	0.00
Spathodea campanulata[b]	7	38.28	2.49	1.18	162.91	0.00	358.39
Laguncularia racemosa[a]	3	29.78	0.00	0.00	0.00	863.63	0.00
Avicennia germinans[a]	2	19.48	0.00	0.00	0.00	564.96	0.00
Miconia prasina	1	12.87	0.00	0.00	0.00	0.00	279.99
Syzygium jambos[b]	2	11.76	0.00	0.00	0.00	0.00	255.73
Conocarpus erectus	3	9.53	6.22	0.00	0.00	226.48	0.00
Citharexylum spinosum	3	7.98	0.00	1.97	0.00	0.00	154.93
Calophyllum antillanum	4	6.69	1.24	0.79	0.00	0.00	130.66
Casearia guianensis	2	6.44	0.00	0.00	0.00	0.00	140.00

[a] Species only present in mangrove forest.
[b] Invasive species.

in R, while V had the lowest diameter values; however, average BAHA and TPH were greatest in UF, followed by MF. Between 2001 and 2010, BAHA in CIT and R declined 20% and 18%, respectively, whereas in V, MF, and UF, BAHA increased. Residential (R) plots showed the only drop in tree density (29%), and V had the greatest proportional increase in density from 13 to 386 TPH.

Over the entire study area, we encountered 68 tree species in 2001 and 85 in 2010, and approximately half of these were non-native (Table 1). Upland secondary forest (UF) plots displayed the highest species diversity of all LULC classes, while CIT had the lowest. Among non-forest classes, R had the highest tree diversity. Substantial variation in diversity within LULC classes was due to the frequency of plots where no trees were recorded in one or both years (Table 1). We found higher tree species diversity and richness in 2010 than in 2001. Seven species recorded in 2001 were absent in 2010, all of which were non-native species in R plots. Twenty-four new species appeared in the 2010 census, 46% of which were native and occurred predominantly within UF plots (7 of 11 species). Two new invasive species (*Delonix regia* (Bojer ex Hook.) Raf. and *Casuarina equisetifolia* L.) were recorded in 2010 within CIT, R, and V plots. No new non-native species were recorded in UF plots in 2010.

Approximately 22% of species were represented by a single individual (n = 15 in 2001 and 2010), and 65% of species had five or fewer individuals. The four most common species were identical during both survey years (although with different rankings) based on average TPH (Table 2). Many species were concentrated within one of the forest land cover types (UF or MF). In addition to *Casuarina equisetifolia* and *Delonix regia*, invasive species in the SJBE included *Albizia lebbeck* (L.) Benth., *Psidium guajava* L., *Spathodea campanulata* P. Beauv., *Syzygium jambos* (L.) Alston, *Terminalia catappa* L., and *Thespesia populnea* (L.) Sol. ex Corroa. Overall, *S. campanulata* had the widest distribution among plots and LULCs (CIT, R, UF and V) followed by *Cocos nucifera* (CIT, R, and UF).

3.2. Changes in San Juan's urban forest 2001–2010

Of trees present in 2001, an estimated 8992 TPH were lost by 2010, accounting for 109.2 m^2/ha of total basal area, or an average of 1012 TPH and 12.3 m^2/ha lost annually. Forty-nine percent of the trees inventoried in 2001 died or were removed by 2010. On the other hand, 64% of trees inventoried in 2010 were new since 2001. Overall, 18,403 new TPH were added between 2001 and 2010, equivalent to 153.0 m^2/ha basal area, or 17.2 m^2/ha annually, over the entire study area. Most trees were lost from UF (40%) and R (26%) land uses. Most new in-growth was recorded in MF (40%) and UF (27%).

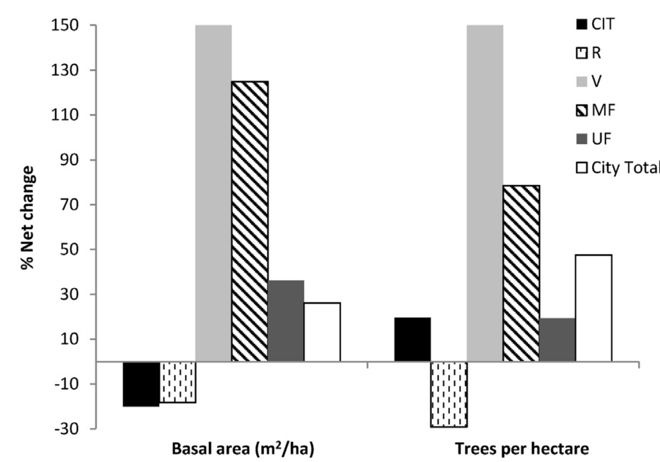

Fig. 1. Average net percent change in basal area (m^2/ha) and trees per hectare from 2001 to 2010 for 80 matched plots in the San Juan Bay Estuary watershed, Puerto Rico, by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove forest (MF), Upland secondary forest (UF). Note: vacant (V) land use plots were truncated at 150%.

Over the SJBE study area, average net change per plot for basal area (BAHA) and tree density (TPH) between 2001 and 2010 was 26% and 48%, respectively (Fig. 1). All net change was positive between 2001 and 2010, except in R plots where we found a negative trend and overall loss in TPH and BAHA, and in CIT with a net percent decline of 20% in basal area (but simultaneous 20% increase in TPH). The highest turnover occurred in V and MF land uses. Vacant plots showed very large increases in density and basal area between 2001 and 2010 (>2000%) as only one plot had trees

($n = 5$) in 2001, and otherwise substantial in-growth occurred over the sampling period.

3.3. Tree mortality 2001–2010

City-wide average plot-level annual mortality rates were nearly 30% for San Juan, with rates varying from 6% to 100% depending on LULC (Fig. 2). Forested plots (MF and UF) exhibited the lowest mortality rates (6–7%). No marked differences in mortality were found between street trees and non-street trees or native vs. non-native trees when considering all land uses together. Average annual mortality rates were higher for invasive (47%) than non-invasive trees (27%). Tree and plot-level variables included in models varied by LULC (see Supplementary Material). Street tree status could only be considered in the R mortality model. All mortality models except MF included invasive, legume, and native status tree variables.

Within CIT plots, mortality was lower for non-native trees, for those with greater heights, and in areas with greater grass cover, while mortality was higher for trees with higher CLE values (Table 3). In the R land use, mortality was lower for non-leguminous species, trees with greater DBH, greater CLE values, and in higher income neighborhoods, while mortality was higher for street trees and in neighborhoods with higher total population. Tree mortality in MF was positively correlated with higher plot BAHA but negatively correlated with shrub cover. Upland secondary forest (UF) tree mortality was higher for non-native species and positively correlated with increasing percent tree cover (Table 3).

3.4. Tree in-growth 2001–2010

Annual in-growth was highest in MF (89.7 TPH), followed by V (28.0 TPH), UF (14.2 TPH), CIT (2.8 TPH), and R (2.6 TPH). For in-growth, a model with some LULC interactions had the best fit statistics. Land use/land cover interacted with both TPH and total human population (Table 4). While in-growth in UF, MF and R plots was unaffected by TPH, in-growth in V and CIT increased with increasing TPH (Fig. 3). On the other hand, UF in-growth was most affected by population, with lower in-growth as population increased. In-growth in CIT land use was not affected by human population, whereas V and R in-growth increased slightly with population level (Fig. 3).

All MF plots contained only native, non-invasive species, and thus further comparative analyses of in-growth by invasive and native status were only conducted with other LULC plots.

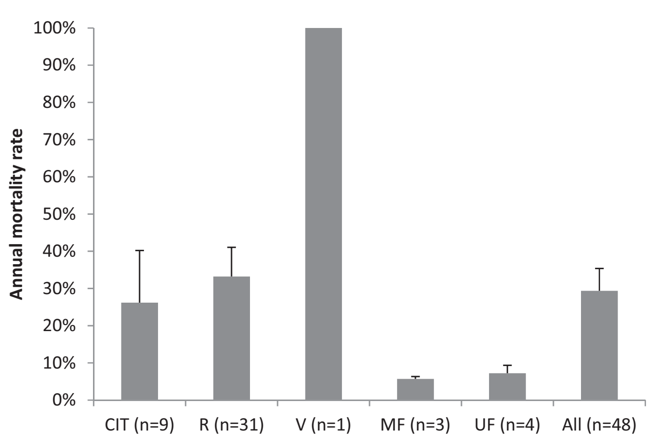

Fig. 2. Average annual plot-level tree mortality rates (±SE) in the San Juan Bay Estuary watershed, Puerto Rico, by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove forest (MF), Upland secondary forest (UF).

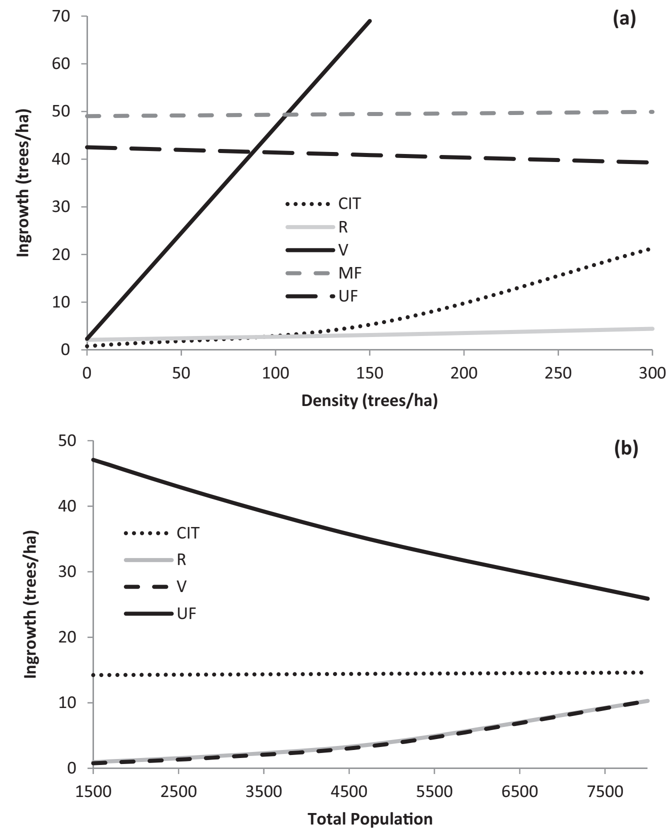

Fig. 3. Least square mean predicted values of in-growth over the study period vs. (a) trees per hectare and (b) total human population (# inhabitants), calculated with all other model variables at their average values. Land use/land cover (LULC) classes are: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove forest (MF), and Upland secondary forest (UF). Note: no predictions could be estimated for MF, since all plots had the same population value.

Logistic models of the presence/absence of invasive and non-native in-growth each had only one significant predictor; as human population increased, so did the probability of in-growth of invasive species, and as tree density increased, the probability of native tree in-growth increased ($p = 0.028$ and $p = 0.0005$, respectively). Where in-growth occurred, the density of invasive vs. non-invasive in-growth was significantly related to LULC (Table 4). Vacant plots experienced significantly more and CIT plots had significantly less invasive in-growth (Fig. 4). Although we observed more in-growth of non-invasives in UF, the difference was not significant due to high variation among plots. No plot-level variables significantly predicted densities of native vs. non-native in-growth (data not shown).

3.5. Diameter growth 2001–2010

Tree diameter growth rates ranged from 0 to 3.78 cm/yr, with an overall average of 0.98 cm/yr (±0.17 SE). We recorded the highest rates of diameter growth in the R land use, and lowest in MF and UF plots (Fig. 5). The three fastest growing tree species across all LULCs (with $n \geq 5$) were: *Pithecellobium dulce* (Roxb.) Benth. (mean = 1.47 cm/yr ± 0.52 SE); *Schefflera morototonii* (Aubl.) Maguire (mean = 1.23 cm/yr ± 0.16 SE); and *Albizia lebbeck* (mean = 1.16 cm/yr ± 0.25 SE).

For CIT, non-native, non-invasive trees displayed the lowest diameter growth rates (0.12 cm/yr; Table 5), whereas non-native invasives and native trees had much higher rates (0.92 and 1.29 cm/yr, respectively). Higher growth rates were associated with

Table 3
Estimated parameters and their standard errors, degrees of freedom (DF), *t* values, and associated *p*-values for models of tree mortality by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove forest (MF), Upland secondary forest (UF).

Effect	Estimate	Standard error	DF	*t* value	Pr > |*t*|
CIT (*n* = 81 trees)					
Intercept	0.411	1.1529	34.37	0.360	0.723
Native range (native vs. non)	−1.716	0.8623	76	−1.990	0.050
Total height (m)	−0.550	0.183	76	−3.010	0.004
CLE[a]	1.320	0.5068	190	2.600	0.017
% Grass	−0.172	0.07947	76	−2.160	0.034
R (*n* = 220)					
Intercept	1.2973	1.0478	213	1.24	0.217
Legume (non-legume vs. legume)	−0.9082	0.54	213	−1.68	0.0941
Street tree status	1.1127	0.499	213	2.23	0.0268
DBH[b] (cm)	−0.0430	0.01242	213	−3.46	0.0007
CLE[a]	−0.2958	0.1312	213	−2.25	0.0252
Total population (# inhabitants)	0.00043	0.00013	213	3.34	0.001
Median income (US dollars)	−0.00003	1.4E−05	213	−2.53	0.0122
MF (*n* = 73)					
Intercept	−1.449	0.8249	70	−1.76	0.0834
Basal area (m^2/ha)	0.155	0.08947	70	1.73	0.0876
% Shrub	−0.0159	0.01257	70	−1.27	0.21
UF (*n* = 99 trees)					
Intercept	−7.3153	2.5575	96	−2.86	0.0052
Native range (native vs. non)	1.0958	0.4884	96	2.24	0.0272
% Tree	0.07803	0.03041	96	2.57	0.0118

[a] Crown light exposure.
[b] Diameter at breast height.

higher human populations, higher amounts of duff/mulch cover, and higher CLE. Growth was slower in plots with higher plot BAHA.

Within the forest covers, growth rates were lower for MF vs. UF trees (Table 5). In general, larger DBH trees grew more slowly, but taller trees grew more quickly. Unlike CIT, growth rates in forested plots were lower as human population increased (Table 5). They were also lower with more tree cover. Residential (R) plots exhibited lower growth rates with higher duff/mulch cover and for areas with newer homes, while growth rates rose with higher incomes. The relationship with plot BAHA differed for native trees vs. non-native species; non-native species had lower growth rates with higher plot BAHA, whereas natives were relatively unaffected.

Only two species had >20 observations: *Laguncularia racemosa* and *Spathodea campanulata*. No adequate species-level model could be estimated for *L. racemosa*, and *S. campanulata* growth rates were significantly affected by only one variable: higher plot BAHA was associated with lower growth.

4. Discussion

4.1. Urban forest mortality and in-growth

The SJBE experienced 30% average annual tree mortality and 5.3% average annual net change in TPH. In comparison, other studies of temperate and inland urban forests reported substantially lower mortality and negative net changes in tree densities. In Baltimore, U.S., Nowak et al. (2004) estimated 6.6% annual mortality and a −4.2% net change in TPH, and in Houston, U.S., Staudhammer et al. (2011) reported 4.7% annual mortality. For urban forests in

Table 4
Estimated parameters and their standard errors, degrees of freedom (DF), *t* values, and associated *p*-values for models of ingrowth density (trees/ha), and comparative invasive vs. non-invasive in-growth. LULC denotes land use/land cover classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove and upland secondary forest (F).

Effect	Estimate	Standard error	DF	*t* value	Pr > |*t*|
In-growth density (TPH)					
Intercept	−0.499	0.692	66	−0.72	0.4738
LULC (CIT vs. V)	0.643	0.816	66	0.79	0.4329
LULC (F vs. V)	4.139	1.134	66	3.65	0.0005
LULC (R vs. V)	0.161	0.854	66	0.19	0.8511
Trees per ha (TPH)	0.0196	0.0067	66	2.94	0.0045
TPH × LULC (CIT vs. V)	−0.0107	0.0069	66	−1.54	0.1289
TPH × LULC (F vs. V)	−0.0196	0.0067	66	−2.95	0.0045
TPH × LULC (R vs. V)	−0.0176	0.0067	66	−2.64	0.0104
Total population (# inhabitants)	0.00029	0.00014	66	2.08	0.0418
Total pop × LULC (CIT vs. V)	−0.00027	0.00016	66	−1.7	0.0947
Total pop × LULC (F vs. V)	−0.00038	0.00019	66	−1.97	0.0535
Total pop × LULC (R vs. V)	−0.00006	0.00017	66	−0.39	0.6993
Invasive vs. non-invasive in-growth					
Intercept	0.9551	0.3824	36.59	6.41	<0.0001
Invasive status	1.4974	0.5574	7.087	−2.69	0.0309
LULC (CIT vs. V)	−1.5777	0.5951	41.22	−2.65	0.0113
LULC (F vs. V)	−0.1615	0.6677	40.88	−0.24	0.81
LULC (R vs. V)	−1.1204	0.4835	41.99	−2.32	0.0254
Invasive × LULC (CIT vs. V)	−2.4324	0.7454	9.05	3.26	0.0097
Invasive × LULC (F vs. V)	−1.9125	0.7883	7.087	2.43	0.0453
Invasive × LULC(R vs. V)	−1.7755	0.6371	7.597	2.79	0.0249

Table 5
Estimated parameters and their standard errors, degrees of freedom (DF), *t* values, and associated *p*-values for models of tree growth by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Mangrove and upland secondary forest (F).

	Estimate	Standard error	DF	*t* value	Pr > |*t*|
CIT					
Intercept	−1.708	0.8222	21	−2.08	0.050
Native range (native vs. non)	−1.664	0.3693	21	−4.51	0.0002
Invasive status	−1.361	0.4361	21	−3.12	0.005
Total population (# inhabitants)	0.00044	0.000128	21	3.42	0.003
CLE[b]	0.132	0.07711	21	1.71	0.102
Basal area (m^2/ha)	−0.043	0.02232	21	−1.9	0.071
% Duff/Mulch	0.071	0.02271	21	3.11	0.005
R					
Intercept	108.3	43.2	37	2.51	0.0167
% Duff/Mulch	−0.05763	0.01661	37	−3.47	0.0013
Median income (US Dollars)	3.6E−05	0.00001	37	3.47	0.0013
Median year built	−0.05543	0.02196	37	−2.52	0.016
Native range (native vs. non)	0.9246	0.3278	37	2.82	0.0077
Basal area (m^2/ha)	0.0074	0.0106	37	0.7	0.4892
Basal area × native range	−0.0487	0.0147	37	−3.31	0.0021
F					
Intercept	0.374	0.868	92	0.43	0.668
Upland tree (vs. mangrove)	0.936	0.330	92	2.84	0.006
DBH[a] (cm)	−0.030	0.013	92	−2.32	0.023
Total height (m)	0.074	0.025	92	2.91	0.005
Total population (# inhabitants)	−0.00017	0.00006	92	−2.95	0.004
% Tree	−0.020	0.011	92	−1.83	0.070

[a] Diameter at breast height.
[b] Crown light exposure.

Gainesville, U.S., Lawrence et al. (2012) found an average annual mortality rate of 9.97%, and average −5% net change in TPH and BAHA over four years. Still, Sheil and May (1996) showed that mortality rate estimates are dependent on the time interval between inventories, so comparisons should be made with caution. Tree size, condition, and LULC contributed to mortality of Baltimore trees, with highest mortality rates along transportation corridors and on commercial–industrial LULC, and lowest rates were estimated for medium- to low-density residential land uses (Nowak et al., 2004). Grass and litter cover, and LULC contributed to hardwood mortality in Gainesville, with more mortality in residential plots; higher tree densities were associated with higher mortality in both softwoods and hardwoods (Lawrence et al., 2012). Similarly, Houston tree mortality increased with increasing TPH and for developed open land covers.

In the SJBE, we observed highest mortality rates in vacant areas and relatively similar mortality rates for R and CIT plots (25–35%), while average mortality was higher for invasive than non-invasive tree species. Additionally, tree variables such as DBH, crown light exposure (CLE), and native and street tree status, socioeconomic variables such as income and population, overall plot BAHA, and plot covers had significant effects on mortality rates in our study. The influence of these variables, however, varied by LULC classification. For example, greater CLE was associated with higher mortality in CIT, but lower mortality in R. Also, higher TPH meant more in-growth in CIT and V, but had no effect on F or R in-growth. In Houston, in-growth increased with TPH and was significantly higher on developed open space land uses (Staudhammer et al., 2011). This land classification closely resembles this study's V land use, showing rough agreement with our findings. The effects of these covariates in this and other studies could be attributed to the confounding influence of specific land use class definitions, variables used, and sample size and intensity. For instance, tree density in CIT plots was on average half the value of that in R plots (Table 1);

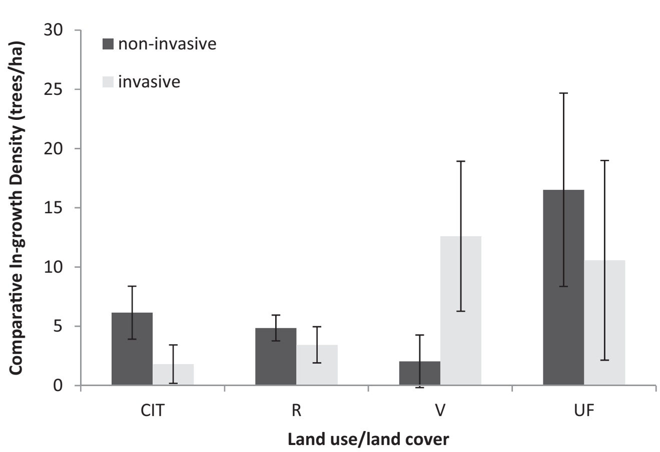

Fig. 4. Least square mean predicted values (±SE) of comparative in-growth (trees/ha) over the study period of invasive vs. non-invasive trees, estimated with all other model variables at their average values by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Upland secondary forest (UF). Note: Mangrove forest (MF) plots excluded.

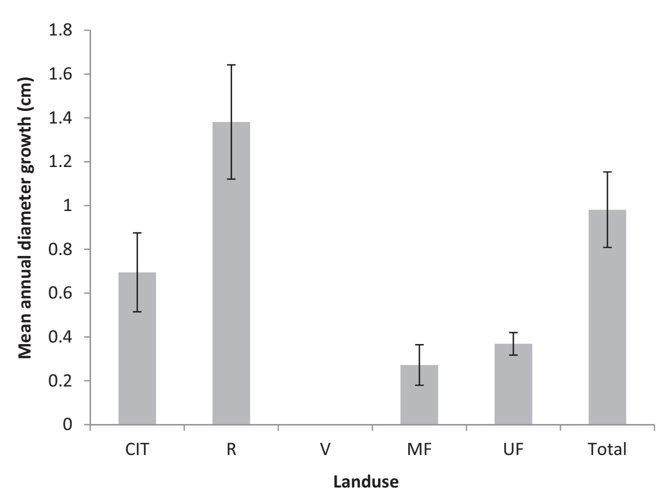

Fig. 5. Mean annual tree diameter growth (cm) (±SE) in San Juan Bay Estuary watershed, Puerto Rico, by land use/land cover (LULC) classes: Commercial/Industry/Institutional/Transportation (CIT), Residential (R), Vacant (V), Mangrove forest (MF), Upland secondary forest (UF).

the range of forest structure characteristics in each LULC was quite different (Iakovoglou et al., 2001; Lawrence et al., 2012).

In-growth was lowest in R and CIT land uses and highest in V and forested (UF and MF) areas, which implies that in-growth was more a result of natural regeneration than of human intervention (i.e., planting). Vacant areas, generally unmanaged and abandoned, experienced more invasive and non-native species in-growth than other LULCs, as expected, as introduced species move in from adjacent urban gardens (Lugo & Brandeis, 2005; Zhao et al., 2010). In general, remnant forests appeared to be relatively unaffected by invasive and non-native species, especially in mangrove forests where none was encountered in either sampling year. The lack of invasive and non-native trees in UF and MF may be related to shade tolerances and habitat conditions. Higher human population was associated with decreased in-growth in forested land covers, whereas the opposite was true in V and R land uses. This may result from a lack of maintenance activities allowing seeds to germinate or previously cleared trees to coppice in V land uses, whereas maintenance activities in R areas, including tree plantings and improved soil characteristics, are more conducive to tree growth and in-growth (Iakovoglou et al., 2001; Lawrence et al., 2012).

Overall net changes in TPH and BAHA and our review of the urban forest literature indicate that the SJBE is a very dynamic ecosystem. Nearly 50% of the trees originally sampled at the start of our study were removed or died during the course of the 9-year study period; however, in-growth of new trees in most cases surpassed these losses, as evidenced by the positive net change across the city overall (26% BAHA and 48% TPH). This positive change in the SJBE urban forest may be linked to an overall trend of reforestation seen on the island of Puerto Rico as a whole, where forest cover has been consistently increasing over the last 40 years (Grau et al., 2003). Annual increases in TPA and BAHA of 3% and 5%, respectively, for our study area differed from a 5% annual loss in TPA and BAHA in Gainesville, FL, where net losses occurred in all LULCs except institutional land uses (Lawrence et al., 2012).

Our results support the idea that urban forests in SJBE are much more dynamic (higher mortality and in-growth) than in temperate regions, following general observations made for subtropical vs. temperate urban forests (Brandeis, Helmer, Marcano, & Lugo, 2009; Lawrence et al., 2012; Nowak et al., 2004; Staudhammer et al., 2011). One major difference between this and many other urban studies is the quality and quantity of remnant forest plots. Twenty percent of sample plots in this study fell in forested areas. While this frequency was similar to that of subtropical Gainesville, FL (Lawrence et al., 2012), which is located in an area known for substantial forest operations, it was substantially less in Miami-Dade, FL (5%; Zhao et al., 2010).

4.2. Urban forest diameter growth rates

The mean diameter growth rate for the SJBE (0.98 cm/yr) included both open-grown urban trees as well as trees in dense forest stands, where resources are more limited due to competition. Trees growing in forest patches surrounded by the developed land matrix had a mean growth rate of 0.35 cm/yr, which is comparable to 0.37 cm/yr found for trees growing in subtropical moist forest on the island of Puerto Rico (Brandeis, 2009), while Weaver (1979) reported a 0.47 cm/yr growth rate for trees in thinned secondary forest stands in the San Juan area. Individual species growth rates for the most frequently encountered species were similar to those observed elsewhere in Puerto Rico's subtropical moist forest. In Brandeis (2009), *Spathodea campanulata* averaged 0.64 cm/yr, *Calophyllum antillanum* averaged 0.41 cm/yr, *Albizia procera*, a close relative to *Albizia lebbeck*, averaged 0.65 cm/yr, with a maximum observed growth rate of 2.22 cm/yr, and *Pithecellobium dulce* averaged 1.64 cm/yr. For the same species within the urban context of SJBE, we measured an average 0.49 cm/yr for *S. campanulata*, 0.52 cm/yr for *C. antillanum*, 1.16 cm/yr for *A. lebbeck*, and 1.47 cm/yr for *P. dulce*.

This study's mean 0.30 cm/yr growth rate for mangrove forest is somewhat comparable to the 0.46 cm/yr found for natural regeneration in cleared stands in the Piñones Commonwealth Forest from 1938 to 1975 (Weaver, 1979). Mean growth rate for mangrove species *Avicennia germinans* (0.57 cm/yr) was higher than the 0.22 cm/yr growth rate observed in Brandeis (2009) but similar to the 0.42–0.51 cm/yr measured by Weaver (1979). Growth rates in *Laguncularia racemosa* (0.16 cm/yr in this study) were comparable to those in Brandeis (2009) (0.13 cm/yr) but less than those reported in Weaver (1979) (0.47–0.54 cm/yr).

Compared to temperate urban tree growth rates, diameter growth ranged from 1.09 cm/yr for hardwood and 0.51 cm/yr for softwood trees measured along public right-of ways in Chicago, Illinois (Jo & McPherson, 1995). Nowak (1994) reported an average growth rate for Chicago's urban forests of 0.84 cm/yr, and estimated an average 0.63 cm/yr diameter growth in Baltimore's urban forests (Nowak et al., 2004). In a study comparing growth rates across land uses and city sizes in the Midwestern U.S., Iakovoglou et al. (2001) encountered higher tree growth rates in city parks followed by residential and commercial sites and found that site, land use, species, and age accounted for 49–77% of the variation in urban tree growth rates in the central U.S. Pavement and soil bulk density were other important factors found related to urban tree growth (Lawrence et al., 2012). Others have reported even higher tree growth rates in mainland U.S. subtropical cities: 1.69 cm/yr for *Quercus laurifolia* (Templeton & Putz, 2003), 0.90 cm/yr for *Pinus taeda*, and 1.2 cm/yr for *Quercus virginiana* (Staudhammer et al., 2011).

Urban tree carbon sequestration models commonly assume Smith and Shifley's (1984) 0.38 cm/yr growth rate for trees in remnant forests, which is then adjusted for site and growing conditions (Nowak & Crane, 2002). In the SJBE, we found a similar average growth rate of 0.33 cm/yr for UF and MF, but non-forested LULCs displayed much higher growth rates. Highest average diameter growth was recorded in R land uses (1.38 cm/yr), which also had the highest mean diameter. Lawrence et al. (2012) similarly found highest growth rates on residential plots (0.82 cm/yr). As previously stated, however, these studies' methods differed from ours in terms of land use/land cover classifications, covariates, and other tree measures, making true comparison difficult.

In general, non-native species had lower growth rates with higher plot BAHA, whereas natives were relatively unaffected by BAHA. Non-native species tend to be shade intolerant and could be responding to light competition in higher BAHA plots, exemplified by the significant negative effect of higher BAHA on the growth rate of invasive and shade-intolerant *Spathodea campanulata*. Similarly, non-native species growing in UF may have established when these patches were relatively open but are now succumbing to increased shade and competition as the forest grows (Lugo, 2004). Past hurricanes (Staudhammer et al., 2011; Zhao et al., 2010) and other anthropogenic disturbances (Brandeis et al., 2009; Carreiro & Zipperer, 2011) have also affected the SJBE's urban forest structure and composition.

4.3. Urban forest species composition

Between 2001 and 2010, we observed an overall increase in species diversity and species richness in the SJBE, but the more common species in 2001 continued to dominate the watershed in 2010. Species composition, richness and diversity of MF and UF were typical of that found in similar areas of the island (Brandeis et al., 2007), and these forested lands generally exhibited higher diversity than R, CIT, and V categories. Conversely, Zhao et al. (2013) found that species richness in a subtropical residential area was greater than in other land uses in peri-urban Shanghai, China. In our study, the high level of species richness observed in R relative to V and CIT was not surprising, even taking into account the greater number of R sample plots relative to other LULCs. During data collection we observed a wide variety of both native and non-native species being planted and naturally regenerating in residential areas.

Still, between 2001 and 2010 we observed a striking difference in species composition in the SJBE watershed's mangrove forest. Numbers of *Rhizophora mangle* increased considerably, and further examination of the data showed that a high concentration of new *R. mangle* saplings and seedlings established on a small island drove this increase. We speculate that channel and debris clearing activities during the study period are causing changes in seawater flow around this island such that the more saltwater tolerant *R. mangle* is now favored over *L. racemosa*, which makes up most of that plot's forest overstory. Zhao et al. (2010) also noted the effect of a single plot on the abundance of an invasive tree, *Melaleuca quinquinervia* in the overall species composition of Miami-Dade. These examples highlight data sensitivity to small sample sizes, stratification/definition of the LULCs, and other unidentified site and landscape scale drivers.

5. Conclusion

Climate change effects and LULC changes are likely to affect coastal subtropical urban forests in the future. In particular, increased hurricane and cyclone severity, urbanization, and sea level rise will likely affect the structure and composition of these urban forests. Of noteworthy importance are the tropical plant species from around the world that are increasingly being used as ornamentals in subtropical urban areas such as San Juan, often without consideration of their potential environmental impact (e.g., potential as invasive species, vectors for pests and diseases, etc.). Additionally, the dynamic nature of the urban tree species composition in these novel ecosystems illustrates how difficult it is to hypothesize about changes in species richness, species diversity, and persistence of non-native species, and assess the risk from potentially invasive trees and other ecological and anthropogenic disturbances.

Although Puerto Rico's forests are a highly diverse mix of native and non-native species that are novel, emerging assemblages, the approach used in this study and results showing that average mortality was higher for invasive than non-invasive tree species, has positive implications for land management efforts interested in the monitoring and control of invasive trees. Studies such as ours can also be used to promote the advancement of management of both anthropogenic and natural urban forest remnants. Although other studies in the subtropics have analyzed spatial patterns of urban forest structure, urban tree growth and mortality, and natural forest growth rates and ecology, our study provides new and unique descriptive information on growth and mortality of subtropical island urban forests. Additionally, this study provides one of the first assessments of the effects of tree and plot-level factors such as endemicity, invasiveness, socioeconomics, and urban morphology on the dynamics of Caribbean urban forests. Further monitoring and measurement of these permanent plots can also provide improved information for quantifying carbon sequestration, air pollution, mitigation of windstorm damage, shading effects on energy use, and other ecosystem services of interest to the community.

Acknowledgments

We thank Robin Morgan and Terry Hoffman of the USDA Forest Service's State and Private Forestry program and "Spatial distribution of invasive horticultural woody plants in urban landscapes" Tropical and Subtropical Agricultural Research (TSTAR-C FY2008) grant for funding; Olga Ramos and Eileen Helmer of the USDA Forest Service's International Institute of Tropical Forestry for compiling of GIS data sets; Jeffrey Glogiewicz of Consultores Ambiental and the Fundación Puertorriqueña de Conservación for collecting field data in 2001 and 2010; and Edgardo Gonzalez with Centro para la Conservación del Paisaje for data collection in 2010. We appreciate the cooperation of other public agencies and private landowners in providing access to measurement plots.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2013.08.007.

References

Bancroft, T. A. (1968). *Topics in intermediate statistical methods*. Ames, IA: Iowa State University Press.

Bechtold, W. A., & Scott, C. T. (2005). The forest inventory and analysis plot design. In W. A. Bechtold, & P. L. Patterson (Eds.), *The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures* (pp. 27–42). Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station (General Technical Report SRS-80)

Brandeis, T. J. (2003). Puerto Rico's forest inventory: Adapting the forest inventory and analysis program to a Caribbean island. *Journal of Forestry*, *101*, 8–13.

Brandeis, T. J. (2009). *Diameter growth of subtropical trees in Puerto Rico*. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station (Research Paper SRS-47).

Brandeis, T. J., Helmer, E. H., & Oswalt, S. N. (2007). *The Status of Puerto Rico's Forests, 2003*. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station (Resource Bulletin SRS-119).

Brandeis, T. J., Helmer, E. H., Marcano, H., & Lugo, A. E. (2009). Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the U.S. Virgin Islands. *Forest Ecology and Management*, *258*, 1704–1718.

Broshot, N. (2011). Mortality and recruitment in an urban forest (Forest Park in Portland, Oregon) between 1993 and 2003. *Urban Ecosystems*, *14*, 553–567.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach*. New York, NY: Springer-Verlag.

Carreiro, M. M., & Zipperer, W. (2011). Co-adapting societal and ecological interactions following large disturbances in urban park woodlands. *Austral Ecology*, *36*, 904–915.

Cumming, A. B., Twardus, D. B., & Nowak, D. J. (2008). Urban forest health monitoring: Large-scale assessments in the United States. *Arboriculture & Urban Forestry*, *34*, 341–346.

Dislich, R., & Pivello, V. R. (2002). Tree structure and species composition changes in an urban tropical forest fragment (São Paulo, Brazil) during a five-year interval. *Boletim de Botânica da Universidade de São Paulo*, *20*, 1–11.

Escobedo, F. J., Kroeger, T., & Wagner, J. E. (2011). Urban forests and pollution mitigation: Analyzing ecosystem services and disservices. *Environmental Pollution*, *159*, 2078–2087.

Escobedo, F. J., Varela, S., Zhao, M., Wagner, J. E., & Zipperer, W. (2010). Analyzing the efficacy of subtropical urban forests in offsetting carbon emissions from cities. *Environmental Science and Policy*, *13*, 362–372.

Grau, H. R., Aide, T. M., Zimmerman, J. K., Thomlinson, J. R., Helmer, E., & Zou, X. (2003). The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *BioScience*, *53*, 1159–1168.

Hagan, D. L., Dobbs, C., Timilsina, N., Escobedo, F., Toor, G., & Andreu, M. (2010). Anthropogenic effects on the physical and chemical properties of subtropical coastal urban soils. *Soil Use and Management*, *28*, 78–88.

Heisler, G. M. (1986). Effects of individual trees on the solar radiation climate of small buildings. *Urban Ecology*, *9*, 337–359.

Holdridge, L. R. (1967). *Life zone ecology*. San José, Costa Rica: Tropical Science Center.

Iakovoglou, V., Thompson, J., Burras, L., & Kipper, R. (2001). Factors related to tree growth across urban–rural gradients in the Midwest, USA. *Urban Ecosystems*, *5*, 71–85.

Jim, C. Y., & Liu, H. T. (2001). Patterns and dynamics of urban forests in relation to land use and development history in Guangzhou City, China. *The Geographical Journal*, *167*, 358–375.

Jo, H., & McPherson, E. G. (1995). Carbon storage and flux in urban residential greenspace. *Journal of Environmental Management*, *45*, 109–133.

Johnson, D. H. (1999). The insignificance of statistical significance testing. *Journal of Wildlife Management*, *63*, 763–772.

Lawrence, A. B., Escobedo, F. J., Staudhammer, C. L., & Zipperer, W. (2012). Analyzing growth and mortality in a subtropical urban forest ecosystem. *Landscape and Urban Planning*, *104*, 85–94.

Lugo, A. E. (2004). The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and Environment*, *2*, 265–273.

Lugo, A. E., & Brandeis, T. J. (2005). A new mix of alien and native species coexists in Puerto Rico's landscapes. In D. F. R. P. Burslem, M. A. Pinard, & S. E. Hartley (Eds.), *Biotic interactions in the tropics: Their role in the maintenance of species diversity* (pp. 484–509). Cambridge: Cambridge University Press.

Lugo, A. E., Ramos Gonzáles, O. M., & Rodriguez Pedraza, C. (2011). *The Río Piedras watershed and its surrounding environment*. Rio Pedras, PR: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry (FS-980).

McPherson, E. G., Nowak, D., Heisler, G., Souch, C., Grant, R., & Rowntree, R. (1997). Quantifying urban forest structure, function, and value: The Chicago Urban Forest Climate Project. *Urban Ecosystems*, *1*, 49–61.

Nagendra, H., & Gopal, D. (2010). Street trees in Bangalore: Density, diversity, composition and distribution. *Urban Forestry and Urban Greening*, *9*, 129–137.

Nowak, D. J. (1994). Atmospheric carbon dioxide reduction by Chicago's urban forest. In E. G. McPherson, D. J. Nowak, & R. A. R. A. Rowntree (Eds.), *Chicago's Urban Forest Ecosystem: Results of the Chicago Urban Forest Climate Project*. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station (General Technical Report NE-186).

Nowak, D. J., & Crane, D. E. (2002). Carbon storage and sequestration by urban trees in the USA. *Environmental Pollution*, *116*, 381–389.

Nowak, D. J., Crane, D. E., Stevens, J. C., & Hoehn, R. E. (2005). *The Urban Forest Effects (UFORE) Model: Field Data Collection Manual*. Syracuse, NY: U.S. Department of Agriculture, Forest Service, Northern Research Station. Retrieved from http://www.fs.fed.us/ne/syracuse/Tools/downloads/UFORE_Manual.pdf

Nowak, D. J., Cumming, A. B., Twardus, D., Hoehn, R. E., Oswalt, C. M., & Brandeis, T. J. (2011). *Urban Forests of Tennessee, 2009*. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station (General Technical Report SRS-149).

Nowak, D. J., Kuroda, M., & Crane, D. E. (2004). Tree mortality rates and tree population projections in Baltimore, Maryland, USA. *Urban Forestry and Urban Greening*, *2*, 139–147.

Pandit, R., & Laband, D. N. (2010). Energy savings from tree shade. *Ecological Economics*, *69*, 1324–1329.

Roy, S., Byrne, J., & Pickering, C. (2012). A systematic quantitative review of urban tree benefits, costs, and assessment methods across cities in different climatic zones. *Urban Forestry & Urban Greening*, *11*, 351–363.

Schomaker, M. E., Zarnoch, S. J., Bechtold, W. A., Latelle, D. J., Burkman, W. G., & Cox, S. M. (2007). *Crown-condition classification: A guide to data collection and analysis*. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station (General Technical Report SRS-102).

Seguinot Barbosa, J. (1996). La ecología urbana de San Juan (una interpretación geográfico social) [The urban ecology of San Juan (a socio-geographic interpretation)]. *Anales de Geografía de la Universidad Complutense*, *16*, 161–184.

Sheil, D., & May, R. M. (1996). Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology*, *84*, 91–100.

Sklar, F., & Ames, R. G. (1985). Staying alive: Street tree survival in the inner-city. *Journal of Urban Affairs*, *7*, 55–65.

Smith, W. B., & Shifley, S. R. (1984). *Diameter growth, survival, and volume estimates for trees in Indiana and Illinois*. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station (Research Paper NC-257).

Staudhammer, C., Escobedo, F., Lawrence, A., Duryea, M., Smith, P., & Merritt, M. (2011). Rapid assessment of change and hurricane impacts to Houston's urban forest structure. *Arboriculture and Urban Forestry*, *37*, 60–66.

Templeton, M., & Putz, F. (2003). Crown encroachment on southern live oaks in suburban settings: Tree status and homeowners concerns. *Journal of Arboriculture*, *29*, 337–340.

Thompson, B. K., Escobedo, F. J., Staudhammer, C. L., Matyas, C. J., & Qiu, Y. (2011). Modeling hurricane-caused urban forest debris in Houston, Texas. *Landscape and Urban Planning*, *101*, 286–297.

U.S. Department of Agriculture Forest Service. (2006). *Forest Inventory and Analysis National Field Manual. Urban Inventory Pilot Supplement. Section 15. Urban Measurements and Sampling*. Knoxville, TN: U.S. Department of Agriculture Forest Service, Forest Inventory and Analysis Program. Retrieved from http://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/core_ver_4-0_10_2007_p2.pdf

U.S. Department of Agriculture Forest Service. (2007). *Forest inventory and analysis national core field guide. Volume I: field data collection procedures for phase 2 plots, version 4.0*. Arlington, VA: U.S. Department of Agriculture Forest Service, Forest Inventory and Analysis Program. Retrieved from http://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/core_ver_4-0_10_2007_p2.pdf

Vrecenak, A. J., Vodak, M. C., & Fleming, L. E. (1989). The influence of site factors on the growth of urban trees. *Journal of Arboriculture*, *15*, 206–209.

Weaver, P. L. (1979). *Tree growth in several tropical forests of Puerto Rico*. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station (Research Paper SO-152).

Wolf, K. (1998). Urban Nature Benefits: Psycho-social dimensions of people and plants. In *Human Dimensions of the Urban Forest, Fact Sheet #1*. Center for Urban Horticulture, University of Washington, College of Forest Resources.

Zhao, M., Escobedo, F. J., & Staudhammer, C. (2010). Spatial patterns of a subtropical, coastal urban forest: Implications for land tenure, hurricanes, and invasives. *Urban Forestry and Urban Greening*, *9*, 205–214.

Zhao, M., Escobedo, F., Wang, R., Zhou, Q., Lin, W., & Gao, J. (2013). Woody vegetation composition and structure in peri-urban Chongming Island, China. *Environmental Management*, *51*, 999–1011.