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Original Research Article

Analyzing the causal factors of carbon stores in a subtropical urban forest

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ABSTRACT

Studies of forests and urban forest ecosystems have documented the various biophysical and socioeconomic correlates of carbon storage. Tree cover in particular is often used as a determinant of carbon storage for local and national level urban forest assessments. However, the relationships among variables describing the biophysical and socioeconomic environment and carbon are not simple statistical ones. Instead, there are complex interactions that can have either a unidirectional causal effects, or produce indirect effects through interactions with other ecosystem structure and landscape characteristics. Thus, understanding the direct and indirect effects of structure, composition, and landscape characteristics is key to quantifying ecosystem services. This study used field data from plots across an urban watershed, site-specific biomass equations, and structural equation modeling of urban forest structure and landscape variables to quantify the causal influences of tree cover, land use, stand density, species composition and diversity on carbon stores. Our path analysis shows that the effect of tree cover on carbon stores is not only direct but also indirect and influential through basal area and composition. Findings suggest that species composition, species diversity and land use have much more complex relationships than previously reported in the urban forest literature. The use of path analysis in these types of studies also presents a novel method to better analyze and quantify these direct and indirect effects on urban forest carbon stores. Findings have implications for urban forest ecosystem assessments that use tree cover as the sole metric for inferring ecosystem functions and services.

1. Introduction

An increasing number of studies have documented the carbon storage and sequestration dynamics of forests and urban forest ecosystems (Escobedo et al., 2010; Hutyra et al., 2010; Schedlbauer et al., 2012; Strohbach and Haase, 2012). Recently, sequestering carbon in plant biomass has been proposed as a strategy to deal with rising atmospheric CO_2 concentrations (Millennium Ecosystem Assessment, 2003). Thus, there is increasing interest in integrating this ecosystem function as a means of mitigating climate change effects. Forest inventory and remote sensing data in particular are important for not only quantifying these functions but also for monitoring the effect of different forest management objectives on CO_2 concentrations.

Indeed, several climate change mitigation policies such as the United Nations program on Reduced Emissions from Degradation and Deforestation (REDD+) and voluntary carbon markets such as the Climate Action Reserve (http://www.climateactionreserve.org/) have been promoted as a means to offset and mitigate anthropogenic emissions and reduce land cover change and degradation in forests (Liverman, 2010). Furthermore, recent studies from temperate and subtropical urban forest ecosystems have indicated that trees are moderately effective at offsetting local-scale CO_2 emissions (Escobedo et al., 2010; Zhao et al., 2010b), and can also store more CO_2 per unit area than forested areas in the Amazon (Churkina et al., 2010). However, there is little research on the casual relations among the biophysical and socioeconomic characteristics of an urban forest ecosystem and their effect on climate regulation. More specifically, there are few quantitative analyses of casual influences or drivers of urban

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forest carbon storage in the coastal subtropics. This information is of importance since these urban and peri-urban forests are now home to 50% of the world's population and urban areas emit about 70% of all CO_2 emissions (UN-Habitat, 2011).

Rapid land use change in the form of urbanization in the subtropics has altered forest structure and diversity (Brandeis et al., 2009; Zhao et al., 2010a, 2013). Urbanization can decrease soil organic matter and carbon in the short term, but can in some instances increase it in the long-term (Hagan et al., 2012). Along with decreased forest cover, stand density and composition can also change as a result of urban morphology, choice of human management system, and policies (Tucker Lima et al., 2013; Zhao et al., 2010a). As such, land use is an important factor in driving carbon dynamics in urban and forest ecosystems (Davies et al., 2013; Raciti et al., 2012; Russo et al., 2014). In temperate areas of the eastern United States, land use change has been identified as a dominant factor contributing to the increased rate of carbon accumulation in the past several decades (Caspersen et al., 2000). Increases in forested area of ~250% in Costa Rica and Vietnam have resulted in increases in sequestered carbon ha^{-1} of 130% and 180%, respectively (Hall et al., 2012). Similarly, land use has a considerable influence on urban tree growth and mortality (Lawrence et al., 2012; Tucker Lima et al., 2013), which in turn affects carbon stores and sequestration. Climate change in particular is also expected to increase hurricane frequency and severity that can in turn affect urban forest structure (Allan and Soden, 2008; Zhao et al., 2010a).

Understanding these changes in urban forest structure and species composition – as a result of land use change – is important due to their effects on ecosystem function. For example, particular urban tree species or types (e.g. invasives) have been reported to comprise the majority of carbon stores in a subtropical urban ecosystem (Escobedo et al., 2010). But, despite the increasing number of urban forest carbon studies (Churkina et al., 2010; Escobedo et al., 2010; Hutyra et al., 2010; Strohbach and Haase, 2012; Timilsina et al., 2014; Zhao et al., 2010b) little is known on the overall causal factors behind these drivers of carbon stores in urban forest ecosystems. Therefore, a better understanding of the drivers behind carbon dynamics in highly altered ecosystems in the subtropics will allow land managers to better design management strategies which aim to sequester more carbon per unit area of land.

1.1. Drivers of carbon storage in urban forest ecosystems

The factors influencing carbon storage (i.e. drivers) are most often reported as the various biophysical and socioeconomic correlates of carbon stores. These drivers are defined as ecological or human factors that affect ecosystem structure and function, thus increasing or decreasing the provision of ecosystem services (Hanson et al., 2010; Millennium Ecosystem Assessment, 2003). Forest structural characteristics (e.g. overstory cover, basal area, species diversity), disturbances (e.g. urbanization, hurricanes), and socioeconomic variables (land use, management, demographics) both at the site and landscape scale will affect carbon storage. For example, structural characteristics that measure site competition, such as tree density have been shown to be correlated to aboveground tree carbon storage (Hoover and Heath, 2011; Woodall et al., 2011). Additionally, Hall et al. (2012) found that in Chile and Ecuador, increased area of forest plantations decreased both carbon storage and native floristic biodiversity.

In many national urban forest assessments, tree cover is assumed to be directly related to carbon storage (Nowak and Crane, 2002; Nowak et al., 2013). Also, urban soil quality and patterns of aboveground vegetation and forest structure have been found to be correlated with management regimes and the degree of urbanization (Dobbs et al., 2011). Similarly, land cover, tenure, and socioeconomics – among other factors – are also related to the spatial distribution of subtropical urban forests (Brandeis et al., 2009; Zhao et al., 2010a). But these relationships are complex as shown by Timilsina et al. (2014) who found that grass cover was related to tree biomass and Lawrence et al. (2012) who reported that the amount of grass and herbaceous cover was positively correlated with tree growth and that higher amounts of grass and herb cover were usually related to higher amounts of maintenance activities. However, forest soil properties interact with forest structure and organic matter to influence understory plant abundance and richness (Laughlin et al., 2007). Further, studies of forested ecosystems have also reported a relationship between plant species richness and biomass, and higher species richness is usually found at low to intermediate levels of biomass (Garcia et al., 1993; Huston, 1994). Similarly, increased urban forest maintenance activities can lead to higher soil moisture and increased nutrients, which can therefore influence species composition, growth (Lawrence et al., 2012) and subsequent carbon stores.

Despite these complex relationships, there are discernible patterns and quantifiable interactions that can be parsed out using ecological theory. According to the redundancy hypothesis, ecosystem function increases as more species are present up to a point, after which more species will not result in enhanced ecosystem function (Walker, 1992). The rivet hypothesis suggests that "just as a plane can fly even if it loses a few rivets", an ecosystem can lose a few species without fatal consequences; however, like a plane that loses many rivets, the loss of many species will lead to ecosystem collapse (Ehrlich and Ehrlich, 1981). In support of the rivet hypothesis, a controlled experiment demonstrated that carbon sequestration and plant productivity declined along with species richness (Lawton, 1994). On the other hand, the idiosyncratic response hypothesis indicates that ecosystem function changes according to diversity, but its magnitude and direction are unpredictable because individual species characteristics and their respective roles are complex and varied (Lawton, 1994). Several studies have additionally reported the positive influence of species diversity on overall ecosystem functions (Naeem et al., 1994; Schwartz et al., 2000; Zhao et al., 2010b). On the other hand, Woodall et al. (2011) found that aboveground carbon in forest stands of the eastern US with varying species mixtures, did not vary with tree species diversity, but maximum aboveground carbon did. Moreover, aboveground live tree carbon was the greatest in mixed species stands, with the exception of yellow poplar (*Liriodendron tulipifera*) dominated stands. While many studies have been conducted in natural forest stands, to our knowledge, these types of causal relationships have not been extensively explored in the urban forest literature.

1.2. Methods for determining the effects on carbon stores

Urban forest carbon dynamics are complex and influenced by several factors, which separately or collectively will impact aboveground carbon stores (Davies et al., 2013; Dobbs et al., 2011; Raciti et al., 2012). But, using more advanced statisticaplex relationships. Jonsson and Wardle (2009) for example, using structural equation modeling (SEM) found that aboveground carbon was *directly* affected by time since fire and *indirectly* affected through alteration of litter decomposition, species diversity and composition, and net primary productivity. The effects of biophysical and socioeconomic drivers are often multifaceted interaction between biotic and abiotic factors (Hall et al., 2012; Lawton, 1994). These relationships, therefore, are not simple but can have either a unidirectional causal effect on ecosystem function, or produce indirect effects through interactions with other drivers.

Methods such as SEM and path analysis (PA) have been used for causal analyses and have the distinct advantage of testing both direct and indirect influences as model effects (Shipley, 2000). By partitioning covariances into pathways, these methods describe direct effects, i.e. when variable A affects variable B directly ($A \to B$), and indirect effects, i.e. when variable A affects variable B through its effect on variable C ($A \to C \to B$). Therefore, SEM has been used to examine the importance of abiotic conditions, disturbance, and biomass on plant species richness in coastal marsh landscapes (Grace and Pugesek, 1997). Also, PA has been used to understand the relative importance of environmental, historical (e.g. land use changes), and spatial context variables on the distribution of tree species, and herb and shrub composition on agroforestry sites in Canada (de Blois et al., 2001). Furthermore, PA has been used to reveal the influence of spatial location (i.e. topography, aspect and slope) and stand-level variables (e.g. basal area of susceptible trees, age, and stand density) on tree mortality during disturbance events (e.g. fire and insect outbreaks; McIntire, 2004). Studies such as those of Laughlin et al. (2007) for example have also used SEM in describing the complex relationship among organic and mineral soil properties, forest structure, and understory plant abundance and richness. Therefore, these same statistical techniques could be useful for developing and testing different hypotheses that describe causal relationship that best fit measured data and to better understand the relative importance (i.e. effect size) of direct and indirect interactions among urban forest structure and function variables (Mitchell, 1992).

1.3. Objectives

The urban forest ecosystem literature has reported a relationship between structure, diversity, composition and carbon storage, and that tree cover and land use are directly related to carbon stores (Churkina et al., 2010; Escobedo et al., 2010; Hutyra et al., 2010; Nowak and Crane, 2002; Strohbach and Haase, 2012; Zhao et al., 2010b). However, in our literature review we found that there are no studies that analyze the direct and indirect casual effects on aboveground carbon storage in subtropical urban forest ecosystems using more advanced quantitative techniques such as PA and SEM. To address this lack of information, our aim was to gain insights into the relative importance and directionality of various plot and landscape-level variables for subtropical urban forest carbon stores. Specifically our objective was to use field data from plots across an urban watershed in San Juan, Puerto Rico to analyze the direct and indirect relationships and interactions among drivers of urban forest carbon storage such as land use, stand density, species composition, and diversity. Using this approach we analyze causality using PA models to test the influence of several commonly reported drivers of aboveground tree carbon storage. Specifically, PA was used to determine whether or not a set of multivariate data fit an a priori defined causal model based on the urban forest ecosystem literature and plot-level data. As such, we hypothesized that:

1. Percent herb-grass cover and tree cover will affect carbon stores directly or indirectly through their influence on tree basal area, species composition, and diversity.
2. Basal area, a measure of tree stand density, will affect carbon stores directly or indirectly through its influence on species composition and diversity.
3. Tree and shrub species composition and diversity will have a direct effect on aboveground carbon stores, and
4. Land use will affect aboveground carbon stores directly or through its effect on species composition, species diversity, and stand density.

Analyses using plot-level data and the PA technique are novel in the urban forest ecosystem literature and can be used to explore complex, casual relationships between biophysical and socioeconomic drivers of aboveground carbon storage by subtropical urban trees. Our carbon storage estimates were also based on site-specific biomass equations developed for Puerto Rican tree species. Results can be used to assess the use of tree cover as a measure of carbon storage and should contribute toward better understanding the complex socio-ecological interactions between an urban forest ecosystem and its functions.

2. Methods

2.1. Study area

The study area encompassed the 2288 ha San Juan Bay Estuary watershed, which lies along the northeast coast of the island of Puerto Rico at approximately 18° N, 66° W (Fig. 1). The watershed is surrounded by the highly dynamic and expanding San Juan metropolitan area, home to a population of 2,478,905 people and a population density ranging from 3215 to 8300 people per km^2 (US Census, 2010). The study area includes the densely populated metropolitan area, but also encompasses San Juan Bay, an ecologically important area with several large lagoons and channels, as well as extensive wetlands and forests. The study area is characterized by coastal plains of alluvial deposits and foothills comprised of sandstone, siltstone, volcanic and intrusive rock parent materials (Lugo et al., 2011). The watershed is within the Holdridge subtropical moist forest life zone (Ewel and Whitmore, 1973; Holdridge, 1967). Mean annual temperature is approximately 26 °C (Lugo et al., 2011). Mean annual rainfall is seasonal and varies with elevation, averaging around 1600 mm (Lugo et al., 2011), and characterized by hurricane activity primarily in the months of June through October.

Historically, forests covered much of the estuary's watershed. Mangrove forest composed of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* fringed the coastal water bodies, protecting the land from surf and wind. An extensive, protected mangrove forest area still exists on the eastern border of the urban area and along San Juan's many estuarine bodies of water. A diverse mix of woody and palm species (e.g. *Calophyllum calaba*, *Coccoloba uvifera*, *Manilkara bidentata*, *Sideroxylon foetidissium*, *Tabebuia heterophylla*) were found further inland in the upland moist coastal plain forests (Little and Wadsworth, 1989; Wadsworth, 1950). Previous island-wide forest inventories have shown a pattern of agricultural land abandonment followed by reversion to secondary forest (Rudel et al., 2000). Near the San Juan urban area, pasture and forest have been cleared for urban development (Ramos González et al., 2005). The current urban forest consists of small, scattered patches of subtropical moist secondary forest embedded in a highly urbanized matrix where a wide variety of native and non-native tree species are found (Tucker Lima et al., 2013).

2.2. Field data collection

The study area was systematically sampled using the USDA Forest Service Forest Inventory and Analysis sampling hexagons (Bechtold and Patterson, 2005; Brandeis et al., 2009). The base grid was intensified by decomposing it into smaller hexagons by a factor of 12, reducing the sampling grid size from approximately one sampling point every 2400 ha to one sampling point every 200 ha. Plots located on water (e.g. streams, sloughs, estuaries, canals, beaches, etc.) were removed leaving a total of 94, 0.06 ha plots within the study area. Most sampling points were measured

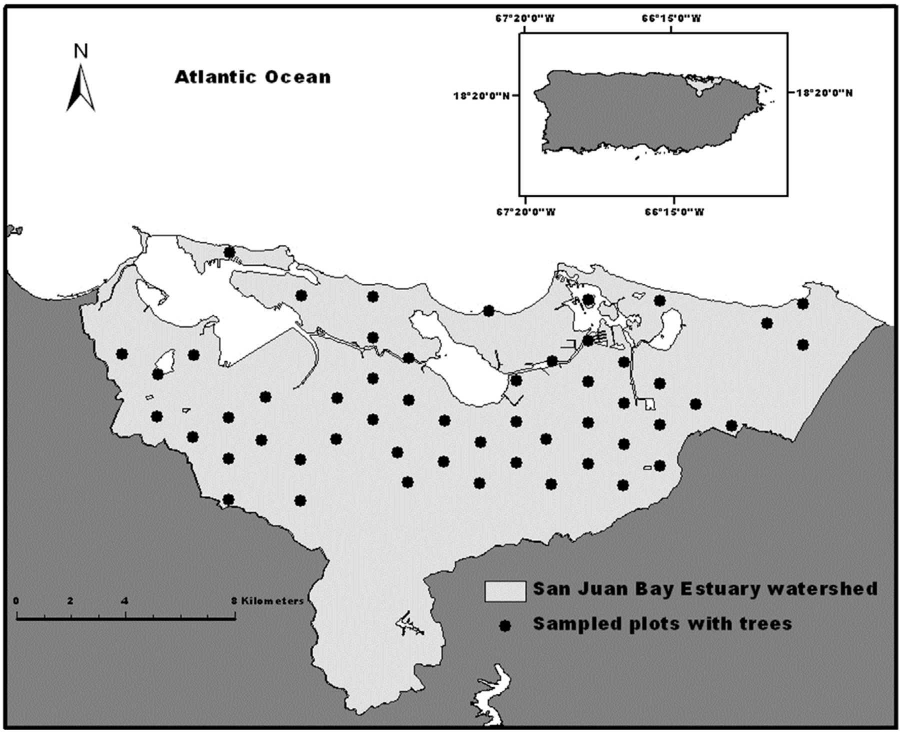

Fig. 1. The San Juan Bay Estuary watershed study area and tree sample plots in Puerto Rico.

using a single, circular plot with a radius of 14.6 m (USDA Forest Service, 2011). A subset of standard Forest Inventory and Analysis (FIA) subplot clusters ($n = 9$ plots) were installed in areas that met the Caribbean FIA criteria for forested land because this plot design was found to be more efficient in fully forested areas (see USDA Forest Service, 2011). The total sampled area was the same for both plot designs, 0.06 ha each.

Land use was classified according to a combination of plot location relative to National Land cover Database land covers (http://www.mrlc.gov/nlcd01_data.php) and FIA land use definitions (USDA Forest Service, 2011). Small patches of tree-covered land that did not meet the minimum area requirements were considered urbanized and usually categorized as vacant or barren land uses. Three plots in densely forested areas (i.e. mangroves forested and remnant forests) were measured using 0.01 ha quarter or 0.02 half plots (i.e. the northeast quarter or northern half of the 0.06 ha plot, respectively) in the interest of time. The total sampled area was 6.3 ha.

From June to October 2010, plots were measured in the study area in the urbanized portion of the San Juan Bay's Estuary watershed (Fig. 1), where permission could be obtained from landowners. Plot center was recorded and data were collected for each tree and palm on the plot with a minimum diameter at breast height (DBH) of 2.5 cm. Trees in this study included all woody perennials with a DBH $\geq$ 2.5 cm regardless of tree growth form. Tree measurements included: species identification, number of stems, DBH and total height. On a plot-level, ocular estimates of overstory tree, palm and shrub cover were made, as well as estimates of surface cover categories (e.g. maintained grass, herbaceous, pervious, impervious, buildings, and water) using field methods from USDA Forest Service (2011). Species were named based on the USDA PLANTS database (http://plants.usda.gov/).

Since the goals of this study included analyzing direct and indirect relationships between urban forest aboveground carbon stores and tree and shrub diversity, we used only 53 plots, discarding the 40 plots where no tree species were recorded. As such, analyses and results are only applicable to areas with existing trees. Plots located on agriculture, industrial and commercial land uses were classified as Commercial ($n = 8$ plots), while plots on parks, institutional, transportation networks, utility corridors, and public rights of way were classified as Institutional ($n = 4$). Other plots in forested areas were classified as Forests ($n = 15$) and the remaining plots ($n = 26$) were classified as residential. Plots in densely forested areas ($n = 3$ mangroves and remnant forests) were measured using quarter or half plots and weighted according to area sampled, and tree densities were adjusted in subsequent analyses following methods outlined in Zhao et al. (2010a). Plots ($n = 5$) that included more than one land use were classified based on the most dominant land use present on that plot.

2.3. Aboveground carbon storage estimates

We calculated aboveground tree biomass in metric tons per hectare (Mg/ha) for each plot by summing aboveground biomass values for individual trees based on allometric biomass equations for Puerto Rican forest species (Table 1). Since San Juan's tree species diversity is very high (>175 species) and few species-specific biomass equations exist, biomass for most individual trees was calculated using a grouped species equation (Table 1). Species-specific equations were used only for *Bucida buceras*, *Prestoea Montana*, and three mangrove species. For all other species, we applied the subtropical moist and dry forest equations from Parresol (2005) and Brandeis et al. (2006). Aboveground carbon (Mg C/ha) was estimated as 50% of the aboveground tree dry weight biomass.

2.4. Species diversity and composition variables

We characterized species richness and diversity at the plot-level. Species richness was calculated as the number of trees species found in each plot. Diversity was calculated with the

Table 1
Equations used for predicting aboveground[a] biomass in San Juan, Puerto Rico, where AGB = aboveground biomass in oven-dry kilograms, DBH = diameter at breast height in cm at 1.37 m, Ht = total tree height in meters.

Forest life zone or species	Equation	Source
Subtropical dry forest	$AGB = \exp(-1.94371 + 0.84134*\ln(DBH^2\ Ht))$	Brandeis et al. (2006)
Subtropical moist forest	$AGB = \exp(-1.71904 + 0.78214*\ln(DBH^2\ Ht))$	Parresol (2005)
Bucida buceras, all forest-type groups	$AGB = \exp(-1.76887 + 0.86389*\ln(DBH^2\ Ht))$	Brandeis et al. (2006)
Prestoea montana (palm), all forest-type groups	$AGB = -10.0 + 6.4*Ht$	Frangi and Lugo (1985), Brown (1997)
Rhizophora mangle, mangrove	$AGB = (125.957*DBH^2\ Ht^{0.8577})/1000$	Cintrón and Schaeffer-Novelli (1984)
Laguncularia racemosa, mangrove	$AGB = (70.0513*DBH^2\ Ht^{0.9084})/1000$	Cintrón and Schaeffer-Novelli (1984)
Avicennia germinans, mangrove	$AGB = 0.14*DBH^{2.4}$	Fromard et al. (1998)

[a] Aboveground biomass is in oven-dry kilograms of all live aboveground tree pools, including stem, stump, branches, bark, seeds, and foliage, as estimated from allometric equations that predict aboveground biomass from individual tree DBH and total height (Ht) measurements.

Shannon–Wiener index (H) using tree and shrub counts in each plot with the following equation:

$$H' = -\sum_{i=1}^{k} p_i \log p_i$$

where p_i is the proportion of ith species in the plot. We also determined plot-level species composition following the methods outlined in Jonsson and Wardle (2009), utilizing a principal component analysis (PCA) with the number of tree and shrub individuals/species in each plot. The PCA, performed using the covariance matrix of number of tree and shrub species in each plot, partitions the variability in number of species and abundance of each plot into orthogonal axes. As such, the first principal component axis or primary ordination axis explains most of the variation in the data and is therefore used as the measure of species composition for our analysis. To characterize plot-level stand density, we used the number of trees (trees/ha) and basal area (m^2/ha) per hectare.

2.5. Statistical analyses and path analysis/structural equation modeling

In PA, a diagram is first developed to show the path of causal relationships among variables based on a priori knowledge of the analyzed system (Bollen, 1989; Shipley, 2000). This hypothesized model (Fig. 2) gives an expected covariance matrix which is then compared with the observed covariance matrix of data to test whether the hypothesized model is true. A straight single-headed arrow in a path diagram indicates a *unidirectional causal* relationship between variables, while a double-headed straight arrow indicates *correlation* between variables. Unexplained variation, due to chance or variables not in the model, is indicated when no arrow is shown between variables. The path coefficient is a standardized partial regression coefficient that describes the direct effect of a predictor on the target variable after keeping all other variables constant. In PA, variables that are only predictors (arrows pointing away from them) are called *exogenous variables*, whereas dependent variables (those that have an arrow pointing toward them) are called *endogenous variables*. Thus, a variable can be both exogenous and endogenous in a path model. In contrast to a direct path (i.e. directly from the variable to the dependent), indirect pathways are indicated in the model by the presence of intermediary variables.

We tested two different PA models of aboveground carbon stores based on commonly reported relationships in the urban forest carbon literature. In the first model, we tested the effect of percent vegetation (i.e. tree and/or herbaceous-grass) cover, species composition, species diversity, species richness, number of trees per hectare, and basal area per hectare on aboveground carbon. The second model was similar to the first, except that we

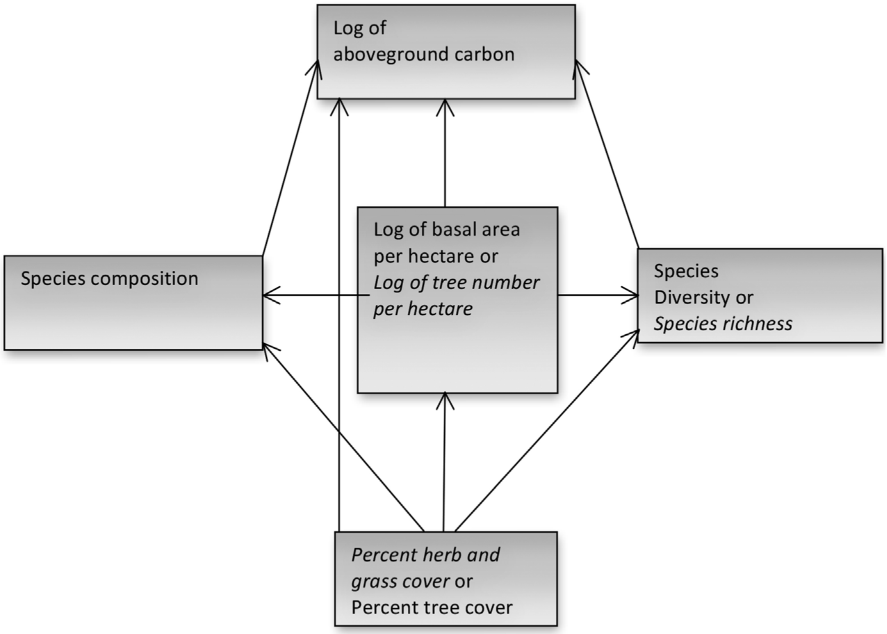

Fig. 2. Hypothesized path of aboveground carbon stores in San Juan, Puerto Rico's urban forest (Model 1). Variables in italics are endogenous variables that were tested in the hypothetical model but not included in subsequent analyses.

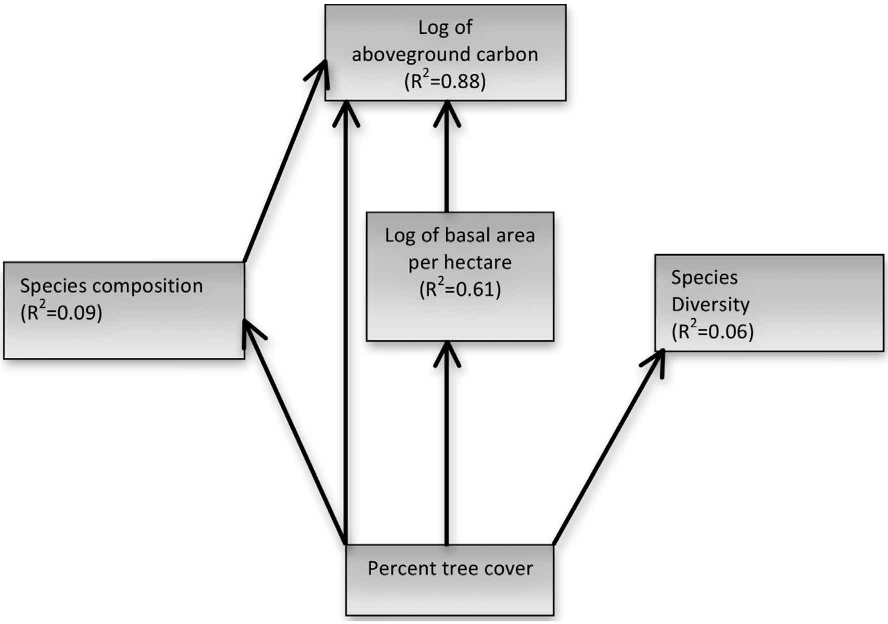

Fig. 3. Model 1 with significant paths for predicting aboveground carbon stock in the urban forest of San Juan, Puerto Rico.

tested the effect of land use instead of vegetation cover. Since preliminary analyses performed separately by land use indicated that models of Commercial, Industrial, and Residential land uses were very similar, we collapsed these land uses accordingly by classifying plots as either forest or non-forest. Two important assumptions underlying PA are that there is a linear relationship between variables and that variables have a normal distribution, so we used logarithmic transformations when needed to meet these assumptions.

We used the SAS procedure PROC TCALIS (SAS version 9.2) to estimate the paths that best explained plot-level aboveground tree carbon. To determine the most robust model, we started with a hypothetical model using the following variables and their interrelationships: aboveground carbon, percent tree cover, percent herbaceous and grass cover, tree and shrub diversity and composition, tree species richness, basal area per ha, number of trees per hectare, and land use. We then followed a stepwise procedure guided by Akaike's Information Criteria (AIC) to select the most parsimonious model (Jonsson and Wardle, 2009; Figs. 2–4). Model fit was tested using the chi-square statistic and its associated *p*-value (a high *p* value indicates good model fit), standardized root mean square residual (SRMSR; <0.05 indicates good model fit), root mean square error of approximation (RMSEA; <0.05 indicates good model fit), and a comparative fit index (CFI; >0.90 indicates good model fit). Several fit statistics explained above were used to balance model fit with model parsimony, and ensure that the models were not biased.

3. Results

Overall urban forest structure and composition characteristics in the study area are reported in Tucker Lima et al. (2013). Two different forms of our hypothesized model without land use

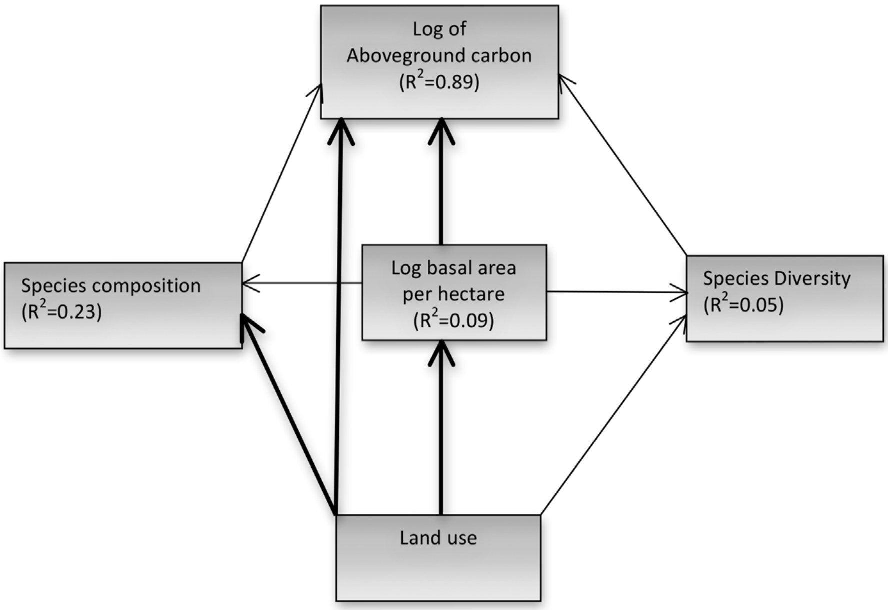

Fig. 4. Model 2 with significant paths (bold arrows) for predicting aboveground carbon in the urban forest of San Juan, Puerto Rico.

Table 2
Parameter estimates, Standard Error (SE), and t-values for paths in Model 1 (Fig. 2) that determines the log of aboveground carbon per hectare in San Juan, Puerto Rico.

Paths		Estimate	SE	t-value
From	To			
Percent tree	Species composition	0.40	0.16	2.37[*]
Percent tree	Species diversity	0.01	0.004	2.05[*]
Percent tree	Basal area (m^2/ha)[a]	0.06	0.006	9.21[*]
Percent tree	Aboveground carbon (Mg C/ha)[a]	0.014	0.004	3.37[*]
Species composition	Aboveground carbon (Mg C/ha)[a]	0.004	0.002	2.10[*]
Basal area (m^2/ha)[a]	Aboveground carbon (Mg C/ha)[a]	0.47	0.05	9.05[*]

[a] Natural log of the variable.
[*] Significant at $\alpha = 0.05$.

Table 3
Standardized estimates of direct and indirect effects of factors in Model 1 (Fig. 3) that determine the log of aboveground carbon (Mg C/ha) in San Juan Puerto Rico.

Factors	Total effect	Direct effect	Indirect effect
Percent tree	0.83[*] (0.00)	0.25[*] (<0.001)	0.57[*] (0.00)
Basal area	0.69[*] (0.00)	0.69[*] (0.00)	0
Species composition	0.10[*] (0.03)	0.10[*] (0.03)	0

Values in parentheses are p values.
[*] Significant effects at $\alpha = 0.05$.

(Model 1) were tested since some plot cover values were highly correlated. The first included percent herb and grass cover as the exogenous variable while the second included percent tree cover as the exogenous variable (Fig. 2); however all other variables and paths were kept constant for both forms. Our analyses show that the best model for predicting aboveground carbon (log) without land use (Model 1) was the second form that included percent tree cover, species composition, species diversity, and basal area per hectare (log; Fig. 3 and Table 2). This was indicated by the lowest AIC value (−5.31), a p-value of 0.61 for the Chi-square test, a SRMSR of 0.04, RMSEA of <0.01, and a CFI of 1.0. Paths included in model 1 (Fig. 3) were statistically significant ($p < 0.05$). We also tested species diversity and richness in the model, but neither variable was significant in predicting aboveground tree carbon storage. The number of trees per hectare was tested instead of basal area, but the model with basal area performed better (Fig. 3 and Table 2), explaining 88% of the variation in aboveground carbon in the study area where trees were present.

The paths indicated that percent tree cover had a significant ($p < 0.05$), positive effect on composition, diversity, basal area, and aboveground carbon (Table 2). Tree cover explained 61% of the variation in basal area of trees, but only 9% of the variation in species composition and 6% of the variation is species diversity. Indeed, species composition and basal area also affected aboveground carbon positively. However, percent tree cover had both direct and indirect effects on aboveground carbon (Table 3), with the indirect effect via tree basal area and composition being more influential (0.57) than its direct effect (0.25; Table 3). The effects of basal area (0.69) and species composition (0.10) on aboveground carbon were direct (Table 3) and did not affect either species composition or species diversity (Fig. 3).

Model 2 included the effect of land use on aboveground carbon. Like Model 1, the best fit (lowest AIC = −2.07) model included species composition, species diversity, and basal area per hectare (log; Fig. 4 and Table 4); however not all paths were significant. Since removing non-significant paths from the model resulted in an increase in AIC value and poorer fit indices, paths that were statistically insignificant in the model were kept (Fig. 4; paths shown in bold are statistically significant). The Chi-square test indicated good model fit ($p = 0.38$), as did the model SRMSR (0.03), RMSEA (0), and CFI (1.0). Overall the model explained 89% of variation in aboveground carbon in the study area where trees were present.

We found that land use had both significant direct (0.23) and indirect (0.27) effects on aboveground carbon stores (Tables 4 and 5 and Fig. 4). As land use shifted from non-forest to forest, the amount of aboveground carbon per hectare increased (Tables 4 and 5). The direct effect of land use was lower than its indirect effect via stand density (i.e. basal area; Table 5); however, because the species composition and diversity paths to aboveground carbon were not significant, we can assume that the indirect effect was through stand density. In contrast to Model 1 (Fig. 3), our land use Model 2 (Fig. 4) did not show a significant effect of either species composition or diversity on aboveground carbon; however, land use did have a significant effect on species composition. Land use explained 23% of the variation in species composition. Similar to the effect of non-forest versus forest land use, increasing stand density significantly increased aboveground carbon (Tables 4 and 5). Most of the effect of stand density on the aboveground carbon was direct (0.83), but a small, insignificant indirect effect (0.005; Table 5) did exist.

Table 4
Parameter estimates, standard error (SE), and t-values for paths (Fig. 3; Model 2) determining the log of aboveground carbon per hectare in San Juan Puerto Rico.

Paths		Estimate	SE	t-value
From	To			
Land use	Species composition	28.08	8.53	3.29[*]
Land use	Species diversity	0.12	0.27	0.45
Land use	Basal area (m^2/ha)[a]	1.30	0.54	2.37[*]
Land use	Aboveground carbon (Mg C/ha)[a]	0.68	0.14	4.66[*]
Basal area (m^2/ha)[a]	Species composition	2.49	2.03	1.22
Basal area (m^2/ha)[a]	Species diversity	0.09	0.06	1.50
Species diversity	Aboveground carbon (Mg C/ha)[a]	−0.05	0.07	−0.75
Species composition	Aboveground carbon (Mg C/ha)[a]	0.001	0.002	0.65
Basal area (m^2/ha)[a]	Aboveground carbon (Mg C/ha)[a]	0.57	0.03	17.99[*]

[a] Natural log of the variable.
[*] Significant at $\alpha = 0.05$.

Table 5

Standardized estimates of direct and indirect effects of factors for Model 2 (Fig. 3) that determines the log of aboveground carbon (Mg C/ha) in San Juan Puerto Rico.

Factors	Total effect	Direct effect	Indirect effect
Land use	0.50* (0.0)	0.23* (0.0)	0.27* (0.01)
Basal area	0.84* (0.0)	0.83* (0.0)	0.005 (0.56)
Species diversity	−0.01 (0.71)	−0.01 (0.71)	0
Species composition	0.03 (0.51)	0.03 (0.51)	0

Values in parentheses are *p* values.

* Significant effects at $\alpha = 0.05$.

4. Discussion

Several recent urban forest ecosystem studies have analyzed carbon storage in temperate and subtropical urban forests according to land uses and discussed sources of variability in carbon storage estimation methods (Churkina et al., 2010; Davies et al., 2013; Escobedo et al., 2010; Raciti et al., 2012; Russo et al., 2014; Strohbach and Haase, 2012; Timilsina et al., 2014; Zhao et al., 2010b). Other studies have also related land use and urban tree cover to carbon stores and generally assumed a direct effect between these (Davies et al., 2013; Nowak and Crane, 2002; Nowak et al., 2013). But, to our knowledge, no studies have parsed out the causal influence, in terms of directionality and covariances, of different drivers such as plot-level tree cover, land use, composition, density and diversity on urban forest carbon stores.

Urban forest assessments generally use tree cover as a direct proxy for estimating carbon stores (Nowak and Crane, 2002; Nowak et al., 2013). Landscape-scale studies on urban forest function such as those of Hutyra et al. (2011), Davies et al. (2013), and Zhao et al. (2010b) have used plot data, stratified according to land use and land cover, for estimating and analyzing carbon storage and sequestration. Other studies of subtropical urban forests have used this same plot data and ancillary spatial data such as socioeconomic (e.g. United States Census, land tenure) and remote sensing (e.g. LANDSAT, field measured overstory) to determine correlates of urban forest structure (e.g. tree cover, species composition, and diversity; Szantoi et al., 2012; Zhao et al., 2013). However, we found that tree cover had a significant positive effect on species composition, species diversity, basal area, as well as tree carbon stores (Table 2); when land use was not considered. However, tree cover had both direct and indirect effects on tree carbon stores (Table 3), with indirect effects via tree basal area and composition being more influential. This has implications for other studies and the use of tree cover as the sole metric for functionality. For example, Nowak and Crane (2002) and Nowak et al. (2013) have used carbon storage to tree cover-factors (kg C/square meter trees cover) to estimate national level urban forest carbon stores. However, our findings show that the tree cover-carbon storage relationship can be more complex. Davies et al. (2013) also report that scaling up plot-level carbon densities, using remote sensing data, to city-wide estimates can result in imprecise carbon storage estimates.

In our analysis, tree-shrub diversity did not significantly influence carbon stores. But, we found that species composition – as defined by the first principal component axis performed on the covariance matrix of number of tree and shrub species in each plot – was an important variable; therefore, high tree cover in areas dominated by a single species (e.g. plot in a vacant residential area dominated by invasive trees) and similar tree cover in a nearby mixed species area (e.g. plot in an occupied residential area) will have different effects on aboveground carbon storage. Similar dynamics have been observed in tropical natural forests in Panama by Ruiz-Jaen and Potvin (2011) who found that functional dominance and diversity explained more of the variation in carbon storage than did diversity, or species richness; but, species richness in a mixed species plantation was, however, positively related to the carbon storage.

Our results demonstrate the importance of tree species present in the plot. For example, two introduced and invasive tree species, *Spathodea campanulata* and *Syzgium jambos*, had the highest loading on the first principal component axis. Higher plot-level PCA scores indicate a higher occurrence of these two species and subsequent increased aboveground carbon storage. *Spathodea campanulata* is fast-growing, shade-intolerant, and readily colonizes areas disturbed by human activities, particularly in the coastal areas and soils with higher fertility (Abelleira Martinez and Lugo, 2008; Brandeis et al., 2009). Similarly, Escobedo et al. (2010) reported that *Melaleuca quinquinervia*, an invasive tree, was influential in urban forest carbon sequestration in subtropical Florida US; however the study did not quantitatively analyze the effects of species composition or diversity on carbon storage. In tropical natural forests and plantations, functional characteristics (e.g. shade tolerant versus intolerant) of the dominant species was found to also be more important than diversity for predicting carbon storage (Kirby and Potvin, 2007; Ruiz-Jaen and Potvin, 2010). In our models, species diversity did not significantly affect aboveground carbon storage. But, our results did show that areas with higher tree cover had higher tree-shrub species diversity. Our measure of species diversity included both shrub and tree diversity, hence their inclusion might have confounded this effect, as higher stand density has been shown to reduce understory diversity (Burton et al., 2013).

Additionally, species composition – as defined in this study – and basal area both affect aboveground carbon positively (Table 2). In fact, all basal area effects on carbon stores were much greater than those of species composition (Table 3). The relationship between basal area and carbon stores is expected, but our findings regarding the use of species composition as a driver of urban forest carbon stores has important management implications. Specifically, care is warranted when applying the normative assumption that tree species diversity will lead to increased carbon stores in urban forests (Zhao et al., 2010b). As such, the importance of species composition as opposed to diversity in our study suggests that the types of trees present – in our case, invasive *Spathodea* and *Syzgium* spp. – is more important than the number and abundance of specific tree species when predicting higher carbon values. Functional dominance (i.e. shade tolerance versus intolerance) and diversity have also been identified as being more important in determining carbon stores in tropical natural forests (Kirby and Potvin, 2007; Ruiz-Jaen and Potvin, 2010).

When ecosystems exhibit functional diversity, available vertical and horizontal spaces are generally occupied by a high number of species. However, in natural forests, it is not necessary that all the available spaces are utilized. In a stand where both shade tolerant and intolerant species grow together, shade tolerant species can grow in the understory and fill greater amount of vertical space available compared to a stand dominated by shade intolerants. *Spathodea campanulata* for example is expected to decline as canopies close and it is unable to regenerate due to its shade intolerance; eventually being replaced by more shade-tolerant native species.

We hypothesized that land use would affect carbon stores directly and indirectly through its effect on species composition, species diversity, and stand density. Land use shifts from non-forest to forest did increase tree carbon stores (Tables 4 and 5), corroborating findings that carbon stores decreased from peri-urban, natural areas to high-density urban areas (Hutyra et al., 2011). However, this effect was lower than its indirect effect via stand density. In our study, aboveground carbon was highest in dense forested plots and a positive relationship existed between stand density and aboveground carbon. Moreover, other studies have also shown that different models, classifications, field and remote sensing methods, and criteria used to differentiate urban from rural land use/land covers will affect sampling stratification, error, and subsequent estimates of urban tree C stores (Davies et al., 2013; Raciti et al., 2012; Russo et al., 2014; Timilsina et al., 2014).

Our inability to find any effect of species richness and diversity on aboveground carbon storage could also be due to our sampling and definition of ‘‘urban’’ that combined data from remnant natural forests in peri-urban areas, open-grown trees from dense, urban private tenure areas, and mangrove forests (Raciti et al., 2012). For example, mangrove forest plots had a maximum of four species present, were denser, and had more than 90% of the maximum observed carbon storage per hectare, but stems were smaller in diameter relative to trees from upland forests. Additional analyses that separate urban areas, from upland and mangrove forests will reveal different relationships and carbon storage values (Raciti et al., 2012; Timilsina et al., 2014). Further research is warranted on the effect of other biotic and abiotic drivers of carbon storage such as hurricanes, soil quality, human management systems, fertilization and land use polices and ordinances. However, our study's methods and findings contribute an approach to better understanding the complexities behind these processes and for developing management practices that can more effectively meet specific carbon storage goals in subtropical urban areas.

5. Conclusion

Increased atmospheric carbon dioxide concentrations have exacerbated climate change, and the effects of that change are of particular importance for the world's forests, coastal areas, and human settlements in the tropics. For example, cities in tropical and subtropical regions are increased emitters of anthropogenic carbon dioxide. Additionally, carbon stores in urban vegetation and soils are increasingly being affected by increasing human populations and socio-political changes as well as land use changes (i.e. urbanization) and other natural stochastic disturbances (Millennium Ecosystem Assessment, 2003).

This study, by analyzing the ‘‘paths’’ between independent (e.g. urban forest structure and function) and dependent (urban forest ecosystem service) variables can be used along with other findings from cited studies to better understand these complex relationships and influences of intermediate socio-ecological processes on management. The use of path analysis also presents a novel method to better analyze these direct and indirect effects of drivers on urban forest ecosystem services. This study's use of landscape-scale sampling, field measured data, and path analysis contribute toward the understanding of multi-scale socioeconomic (landscape-level land use) and biophysical (plot-level forest structure, species composition and diversity) variables affecting aboveground carbon storage. The method can also be used to determine if indeed these variables have direct or indirect effect through interactions with other biotic and abiotic factors.

Our results and approach have implications for the use of urban forest assessments that use tree cover or diversity alone as proxies for ecosystem functionality. Our findings show that the effects of tree cover on carbon stores is not direct and that species composition, species diversity and land use have much more complex relationships than previously reported in the urban forest literature. Findings might indicate that anthropogenic tree species selection, plantings and removals in urban forests might be minimizing the influential role of composition, richness, and diversity on carbon stores whereas functionality as defined by basal area and composition is much more important in predicting carbon stores. Care is also warranted as areas with a high number of invasive species (with higher carbon stores) are not desirable in the long run for sustainability and multiple use management objectives, as diversity will make for stands that are more resilient to natural disturbances assuring urban forest carbon stores for the long-term.

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