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# Using phylogenetic diversity to explore the socioeconomic and ecological drivers of a tropical, coastal urban forest

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ABSTRACT

Relatively little is known about the dynamics of tropical urban forests, their phylogenetic diversity, as well as the socioeconomic and ecological factors that influence overall diversity across the urban landscape. However, permanent forest inventory and monitoring plot networks are increasingly being established across forests and cities of the world to monitor structural and functional attributes of urban forests, as well as ecosystem services. We analyzed a tropical, coastal urban forest in San Juan, Puerto Rico using metrics of phylogenetic diversity (PD), plant diversity, and available permanent plot data from an urban forest inventory and monitoring system. In total, we found 152 species belonging to 119 genera and 44 families in San Juan. PD tended to be highest in forest remnant areas. We also explored correlations between socioeconomic factors and taxonomic diversity and found that plant species richness was correlated with population density and housing price. We found marginally significant relationships between housing price, population density, and several PD metrics. Our results further suggest mixed evidence of luxury and legacy effects, two factors that have been linked to the plant diversity of anthropogenic ecosystems in other research. Overall, despite centuries of human influence, the existing urban forest diversity in San Juan - although perhaps not the particular species composition - is likely to be primarily the result of climate, biome, and multi-scale socioeconomic contexts and not legacy effects. The approach used and findings from this study could be used to better understand the application of PD metrics for assessing urban biodiversity and other beneficial attributes and traits of urban forests.

## 1. Introduction

The introduction of non-native plants into rapidly expanding urban ecosystems can substantially alter plant community species richness and overall biodiversity (Knapp, 2010) and leads to novel species assemblages (Hobbs et al., 2006). To date, there are relatively few studies of plant community composition and diversity characteristics of tropical and subtropical coastal urban ecosystems (Lima et al., 2013; Zhao et al., 2013; Zhu et al., 2019a, 2019b; Cheng et al., 2020; Wang et al., 2020). These woody plant and palm assemblages, referred to as urban forests, are the sum of trees, shrubs, and palms that grow in and around human settlements in tropical and subtropical climates. Improved information about these urban forests and their species composition and diversity could be used to better understand their development trajectory, as well as their current and projected dynamics (Escobedo et al., 2015; Rudel et al., 2016).

In particular 'phylogenetic diversity' (henceforward, PD) can be a highly useful biodiversity metric for green infrastructure planning and biodiversity conservation strategies in urban ecosystems (Cadotte et al., 2012; Lopez et al., 2018; Cui et al., 2019). It is also analogous to measures of functional diversity in which functionally equivalent species are down-weighted (Knapp et al., 2008; Hooper and Dukes, 2010). Thus, PD can also be used as a direct proxy for functional diversity (Knapp et al. 2008), assuming that closely related species resemble one another in

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terms of functional ecological traits than do distant relatives (Hooper and Dukes, 2010; Blood et al., 2016). Studies have previously used functional trait diversity to assess biodiversity and ecosystem services (e.g., Vandewalle et al., 2010; Grote et al., 2016) and to link the functional diversity of plant communities to anthropogenic influences on the environment. Yang et al. (2017) showed that Haikou, China's urban plant taxonomic and functional diversity are influenced by both frequency and type of land use change. In addition, previous research suggests that human preferences, socio-economic conditions, and also 'legacy effects' can act as strong drivers of species distributions in urban areas (Hope et al., 2003; Knapp, 2010; Schwarz et al., 2015).

Urban forest plant assemblages are novel and frequently complex as they consist of a mixture of anthropogenically planted and naturally regenerating species, that can include the introduction and planting of exotic, often invasive, taxa (Dobbs et al., 2017). Indeed, numerous exotic plant species have colonized urban regions through global trade and landscaping practices (Hope et al., 2003). Such novel assemblages can affect not only the taxonomic composition but also the phylogenetic patterns of plant communities and their over- or under-dispersion. A study of eleven cities by Aronson et al. (2014) found that urban areas contained a median of 28 % exotic plants. Yang et al. (2015) also found that in 38 different urban forests, a median of 42 % of the tree population was non-native. Indeed, urbanization as an anthropogenic disturbance has been reported to lead to urban plant biotic homogenization within and among cities (Blood et al., 2016; Kühn and Klotz, 2006; Yang et al., 2015; Silva-Junior et al., 2018; Lopez et al., 2018; Zhu et al., 2019a, b; Cui et al., 2019).

The specific socio-ecological correlates of urban plant diversity can also be complex (Dobbs et al., 2017). Land use in particular has been shown to be an important predictor of urban biodiversity (Hope et al., 2003; Kinzig et al., 2005; Tait et al., 2005; Zhao et al., 2013). Other studies (e.g. Wang et al., 2016; Zhu et al., 2019a, b; Wang et al., 2020) have found a significant, positive correlation between socioeconomic inequity and plant diversity and urban tree and surface covers; a phenomenon that has been referred to as a 'luxury effect,' in which greater biotic diversity is positively associated with areas of higher household income (Hope et al., 2003; Kinzig et al., 2005; Schwarz et al., 2015). Tratalos et al. (2007), and Escobedo et al. (2006, 2015) have shown that land use dynamics and socioeconomic factors affect tree diversity. Finally, Yang et al. (2017) and Zhao et al. (2013) showed that Chinese urban and peri-urban plant diversity was closely related to local environmental factors and human management, which can also vary with socioeconomics.

The growing interest in urban forests, their biodiversity, and the ecosystem functions and services that are provided by urban trees has led to the use of inventory and monitoring systems that collect urban woody plant field data across different cities of the world for different purposes (For examples from China, North America, and South America, and their applications see: Yang et al., 2015 and citations therein; Zhao et al., 2013; Lima et al., 2013; Nowak et al., 2008; Blood et al., 2016 and citations therein; and Escobedo et al., 2006; Wang et al., 2020a, 2020b). The increasing availability of this urban forest taxonomic data in turn provides us with a unique opportunity to examine novel urban forest plant assemblages.

Accordingly, our study aim is to examine the effects of a number of frequently studied socioeconomic and ecological factors on the PD of a tropical, island urban forest in the Caribbean region of North America. Specifically, we focus on two objectives: 1) to measure the patterns of species PD across different land use types; and 2) to explore socioeconomic correlates (such as population densities and property premiums) and their effect on urban woody plant PD in this coastal tropical urban environment.

This approach using available urban forest inventory and monitoring data and PD metrics can also be employed to explore the influence of the luxury and legacy effects and biotic homogenization; hypotheses that have been reported to influence the biodiversity of urban ecosystems in other research (Hope et al., 2003; Yang et al., 2017). The methods and findings of our study will also complement the growing number of studies that use PD, as well as alternative approaches (e.g., functional traits), in both management practices and to help identify beneficial urban forest attributes (Vandewalle et al., 2010).

## 2. Methods

### 2.1. Study area

Our case study city is San Juan, Puerto Rico in the North American Caribbean. The study area is on the northeast coast of the Caribbean island of Puerto Rico (Fig. 1) at 28′0″N, 66° 7′0″W. This dynamic urban area has the 216.6 km$^2$ San Juan Bay Estuary watershed at its core and encompasses San Juan Bay, several large lagoons and channels, and extensive wetlands and forests, all in close proximity to a densely populated city. San Juan has a borderline tropical and subtropical climate with mean annual precipitation between 1500 and 1700 mm and an average annual temperature of 25.9 °C (Lugo et al., 2011). Historically, forests covered the area. Mangrove forest composed of *Rhizophora mangle* L., *Avicennia germinans* (L.) L., and *Laguncularia racemosa* (L.) Gaertn.f. fringed the bays and lagoons. A diverse mix of species including *Casearia guianensis* (Aubl.) Urban, *Calophyllum brasiliense* var. *antillanum* (Britton) Standl., *Coccoloba acapulcensis* Standl., *Manilkara bidentate* (A. DC.) A. Chev., *Sideroxylon foetidissium* Jacq., and *Tabebuia heterophylla* (DC.) Britt., occur throughout the moist coastal plain forests and scattered karst hills that are found farther inland (Wadsworth, 1950).

In 2010, the San Juan metropolitan area had a total population of approximately 2.5 million inhabitants (U.S. Census Bureau, 2011). Population density averages 3215 persons/km$^2$, but in some areas can exceed 8300 people/km$^2$ (Villanueva et al., 2000). Land use cover in the San Juan area is both complex and dynamic. Historically, land cover and land use in and around San Juan generally followed the same patterns of change observed across the island. First, deforestation characterized the European colonization in the early 1500s, then agricultural development continued until the middle of the twentieth century at which time socioeconomic policies led to a widespread abandonment of agricultural lands, and, finally, natural regeneration of forest on fallow lands began to occur, accompanied by even greater expansion of urban areas (Parésramos et al., 2008). Recent hurricanes have also severely impacted the island. The long legacy of human settlement following colonization and continued change due to socio-ecological disturbances (e.g. economics, hurricanes, proximity to mainland United States) makes the San Juan metropolitan area an interesting case study on the North American continent.

### 2.2. Sampling design and field data

The Land Use and Land Cover (LULC) types for San Juan are listed in Table 1. We used data from a systematically sampled inventory based on a hexagonal sampling grid of fixed plot sizes. Table 2 shows the 2011 sampling characteristics for San Juan. The sampling protocol for our data is given in more detail in Brandeis (2003) and Brandeis and Turner (2013). The Forest Inventory and Analysis (FIA) program overlays a hexagonal sampling grid over the area to be inventoried, in which each hexagon has an area of approximately 2400 ha with a sampling plot either in the center of each hexagon, or located at a random distance and azimuth from that center (Reams et al., 2005). The San Juan Bay Estuary watershed is covered by 11 standard-sized FIA hexagons. Therefore, we intensified the base grid (decomposed it into smaller hexagons) by a factor of 12, giving us 108 sampling points, once we removed points that fell into water, within the watershed boundaries. Land use/cover types were also identified and corroborated in the field.

A standard FIA subplot cluster was installed in areas that met the Caribbean FIA criteria for forested land at the sampling point: a

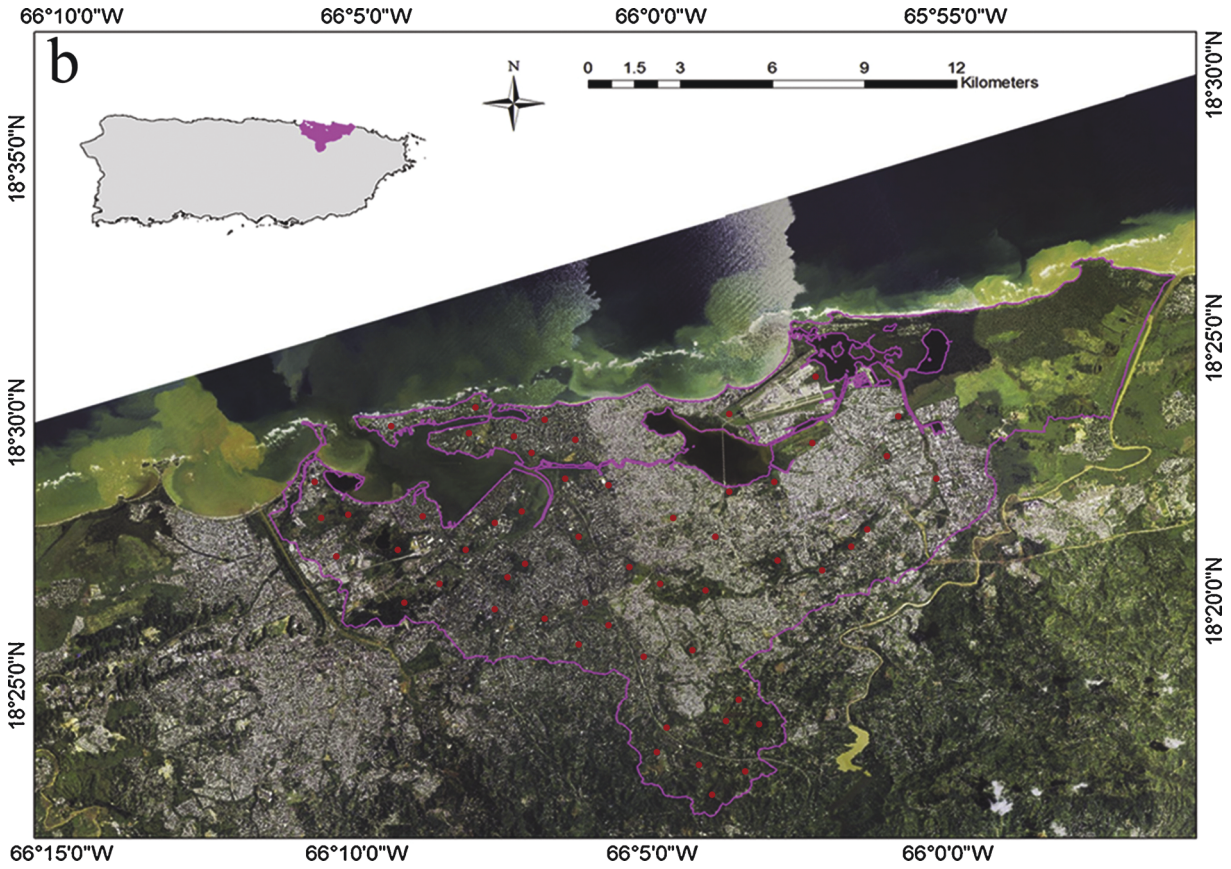


**Fig. 1.** Study area and sampling sites in San Juan, Puerto Rico.

**Table 1**
Land use and land cover types for San Juan, Puerto Rico.

| | # plots | Area ($m^2$) |
|---|---|---|
| Vacant | 11 | 3185 |
| Forest | 9 | 2548 |
| Institutional | 9 | 2336 |
| Parks | * | – |
| Agriculture | 8 | 1274 |
| Other | na | – |
| Multi-family residential | * | – |
| Commercial/industrial | 23 | 4459 |
| Transportation | * | – |
| Residential | 34 | 7856 |

* Institutional and Park land uses were combined into one category; Multi-family residential was combined with Residential, and Transportation was combined with Commercial/Industrial due to small sample sizes. The Wetland/Water/Agriculture land use category was primarily seasonally flooded pasture land. Forest was primarily mangroves and upland secondary moist forest cover types.

**Table 2**
San Juan Puerto Rico's original Land use and land cover types and sampling characteristics.

| Land use cover types | Number -All plots | Sampled area (ha) | Land use area (ha) | % area |
|---|---|---|---|---|
| Commercial/industrial/ transportation | 23 | 1.55 | 4459 | 20.6 |
| Institutional/park | 9 | 0.61 | 2336 | 10.8 |
| Mangrove forest | 3 | 0.20 | 1486 | 6.9 |
| Residential | 34 | 2.29 | 7856 | 36.3 |
| Moist forest | 6 | 0.40 | 162 | 4.9 |
| Vacant | 11 | 0.74 | 3185 | 14.7 |
| Wetland/water/ agriculture | 8 | 0.54 | 1274 | 5.9 |
| Total | 94 | 6.34 | 21,658 | 100.0 |

contiguous area > 0.4 ha., or >30 m wide for forested strips, with >10 percent canopy coverage in trees (Brandeis et al. 2003). In 2011, additional urban forest inventory data were collected on the FIA-style plots following FIA urban forest inventory protocols (Lima et al., 2013). Single 14.6-m-radius circular (670 $m^2$) plots used to collect data are part of the Urban Forest Effects (UFORE) and i-Tree ECO models and thus urban forest inventories were installed in urban and agricultural lands that did not meet minimum requirements for forest under FIA's definitions (Nowak et al., 2008). Small patches (> 0.4 ha) of tree-covered land that did not meet the minimum area requirements were considered urbanized and usually categorized as vacant. Ninety 670 $m^2$ plots, or a total of 6.3 ha in the study area, were sampled in San Juan. Trees (woody vegetation that was at least 2.5 cm DBH) and shrubs (< 2.5 cm DBH) had to be at least 30 cm tall to be included in the estimates. For each tree within the plot, tree status (live, dead, or removed), and species taxonomic identity were noted, and DBH was measured at 1.4 m. Specific and detailed protocols on the vegetation and tree measurements, plot criteria, LULC designation, and overall sampling design can be found in Brandeis (2003); Lima et al. (2013) and Nowak et al. (2008).

### 2.3. Phylogenetic data

We used two available programs, *Phylomatic* and *Phylocom*, to obtain a phylogenetic tree, estimate branch lengths, and calculate relevant phylogenetic metrics (Webb et al., 2008). We derived our phylogenies from the most recent informal supertree available from the Angiosperm Phylogeny Website (http://www.mobot.org/MOBOT/research/apweb/). We then used *Phylocom* to assign ages to nodes for which

dating information was available (Wikström et al., 2001), after which we estimated the remaining branch lengths using the smoothing algorithm, *bladj*, as implemented in *Phylocom*. Finally, we removed all singleton (non-dividing) nodes from our tree. Since the resolution was coarse and many polytomies remained at the genus and species level, we also used *phyloGenerator* (Pearse and Purvis, 2013) to estimate a second tree based on the *BioPython* framework (Talevich et al., 2012). The *phyloGenerator* program automates the retrieval of sequence information from Genbank, undertakes multiple sequence alignment, and estimates a phylogenetic tree using Maximum Likelihood as implemented in the software *RAxML* (Stamatakis, 2014). We computed PD using the *picante* package (Kembel et al., 2010) in the statistical computing software R (R Core Team, 2018).

### 2.4. Socioeconomic variables

We extracted our variables from datasets collected by FIA, as well as from available United States Census data (U.S. Census Bureau, 2011). Land use or cover, population density, housing price, and building age have all been found to be correlated with urban plant diversity in prior research (e.g., Wang et al., 2016; Dobbs et al., 2017). These variables are readily available for San Juan; consequently, we analyzed each one as a potential correlate of PD.

San Juan's socioeconomic variables were all measured on site or were extrapolated based on available geospatial data from the United States' Census (U.S. Census Bureau, 2011), and included LULC as measured on site following Brandeis and Turner (2013). Only 94 of the 108 sampling locations could be visited due to access limitations (e.g., permission not granted by landowner or inaccessible mangrove forests). Of the 94 plot locations, only 60 had trees or shrubs. We overlaid the U. S. Census Bureau (2011) census-block level spatial data on plot locations to determine socio-economic characteristics for each plot including: total population, median owner-occupied housing unit price (USD$), and the median year a structure was built on the plot. We determined population density for each block by dividing total population by census block area.

### 2.5. Data analyses

We measured PD using three different metrics: abundance-weighted mean nearest taxon distance (MNTD); abundance-weighted mean phylogenetic distance (MPD); and standard phylogenetic diversity (PD). Although abundance-weighting can complicate the comparison of phylogenetic diversity between communities (Tucker et al., 2017), we felt that differences in relative abundance between sites was an important dimension of variation in our data that we did not want to overlook. Furthermore, our standard PD and raw species richness measures do not include information about relative abundance of species.

The MNTD measures the mean phylogenetic distance from each species to its closest relative in the community. This metric focuses on the minimum phylogenetic similarity between co-occurring taxa. The underlying idea of this metric has been that if ecological community assembly is governed by competition, then perhaps minimum phylogenetic distance is more important in determining whether a species can be added to the community than (for example) mean phylogenetic distance to all community members (Silva-Junior et al., 2018; Lopez et al., 2018; Zhu et al., 2019a, 2019b; Cui et al., 2019).

By contrast, MPD measures PD by calculating precisely this latter-most quantity: the mean phylogenetic distance between all species in a community. With regard to community assembly, this metric assumes that ecological competition can occur between all species, not just between close relatives, but once again that competition, and thus the possibility of competitive exclusion, is strongest between closely related taxa (Lopez et al., 2018; Silva-Junior et al., 2018; Cui et al., 2019; Zhu et al., 2019a, 2019b). The advantage of MPD is that it may capture functional diversity of the community (if distant relatives tend to exhibit more distinct ecological roles than do closely related taxa) in a way that MNTD cannot. Nonetheless, in practice the two metrics tend to be correlated. Both measures take into account differences in relative abundance among species such that, just as with traditional diversity metrics, measured diversity using MPD or MNTD is higher for greater evenness in relative abundance among species. Each metric is sensitive to changes in tree topology and size in different ways, and are thus often used as complementary descriptors (Kraft et al., 2007; Cadotte et al., 2010, 2012). Accordingly, in subsequent sections, we report results for both MNTD and MPD separately.

Finally, in addition to MNTD and MPD, we also calculated traditional PD as the simple sum of the total branch lengths of the tree pruned to contain only the taxa of the local community (Faith, 1992). Henceforward, whenever we refer to multiple PD metrics, we will identify traditional PD as *standard PD* or simply *PD*, and the abundance-weighted measures described above as *MNTD* or *MPD*.

For our first objective and all three PD metrics, we calculated standardized PD (i.e., z-scores) by computing the difference between the observed measure for a community and the mean PD from randomly assembled communities, divided by the standard deviation of PD across the same set of random species assemblages. We generated random communities by sampling a total number of species equivalent to the species richness of the local community from the regional species pool, repeating this procedure multiple times, and each time recalculating PD. We also estimated the statistical significance of PD, for all three metrics, by comparing observed PD to the same null distribution obtained by randomly assembling communities from the regional pool. A standardized PD value significantly in excess of zero indicates phylogenetic overdispersion of a local community compared to the degree expected by chance. Conversely, standardized PD significantly less than zero suggests phylogenetic clustering of species in an assemblage relative to the regional pool.

For our second objective, we tested for normality of our standardized PD scores using a Kolmogorov-Smirnov test. If normality was rejected, then we used a Johnson transformation to normalize each variable using Minitab 16. We next tested for collinearity of predictor variables for our linear models of PD as a function of our various aforementioned socioeconomic and environmental variables. Following Johnson et al.'s (2015) approach, we only retained predictor variables that had correlation coefficients to the other variables in the model that were less than 0.8. We then analyzed PD as a function of herbaceous, water, tree and shrub, and impervious surface cover, and of longitude and latitude. We also analyzed PD as a function of population density, housing price, and housing age.

To evaluate spatial autocorrelation of our PD measures we used Moran's I. We calculated Moran's I in R 4.0.2 using functions in the *ape* library (Paradis and Schliep, 2019). We generate a matrix of inverse distance weights to calculate Moran's I, at first, we generate a distance matrix, and then take the inverse of the matrix values and replace the diagonal entries with zero. By doing so, we have created a matrix where each off-diagonal entry $[i, j]$ in the matrix is equal to $1/$(distance between point $i$ and point $j$). Based on these results, we can reject the null hypothesis that there is zero spatial autocorrelation present in the variable whose alpha value $= 0.05$. As such, we kept Housing age, Housing price and Population density as socioeconomic variables, considering them as the most meaningful for our study questions.

Given the number of predictor variables analyzed, we used a Principal Components Analysis (PCA) to reduce the dimensionality of our dataset in analyzing the relationships between plant diversity (e.g., plant richness, phylogenetic diversity, MPD, NMTD, etc) and the explanatory variables in our model (e.g. housing price, Housing age etc.), and to ordinate the spatial and socioeconomic data using R (R Core Team, 2018). To explore the relationships between community structure and environmental variables, we first computed a distance matrix in which distances represent the differences in abundance across species between sites. We then ordinated this distance matrix using non-metric

multidimensional scaling (NMDS), and we extracted canonical NMDS scores. Finally, we used the *envfit* function of the *vegan* R package to identify vector combinations of our environmental predictor variables (specifically, housing price, Housing age, and population density) that best explained variation in our NMDS scores.

We explored the relationships between plant diversity metrics and our socioeconomic variables using Generalized Linear Models (GLMs) with stepwise model selection in R4.0.2 using functions in the step library (R Core Team, 2018). First, we constructed a multivariate GLM, in which we included all explanatory variables with $p$-values $< 0.1$ in their individual bivariate GLMs. Next, we conducted stepwise selection using our full multivariate GLM to identify the model with the lowest Akaike Information Criterion (AIC) score and when the variables' coefficients passed the significance test ($p < 0.05$).

Second, we fit linear models for the most correlated plant diversity indices and our socioeconomic variables. We used the results from this analysis to understand the relevance and influence of the frequently mentioned luxury, legacy, and biotic homogenization hypotheses on tropical, coastal island urban forests. We use property premiums as a proxy for the luxury effect and land use land cover and the number of years since a structure on the plot was built as the proxy for the legacy effect. Finally, we used a structural equation model based on Partial Least Squares using R package "pls" to explore the influence of location and socioeconomic factors (i.e., Latitude, Longitude, Population density, Housing price and Age) on the analyzed plant diversity metrics (i.e., PD, MNTD, NTAXA, MPD).

## 3. Results

### 3.1. Plant taxonomic diversity in San Juan

We found 152 tree, shrub, and palm species in our study area belonging to 119 genera and 44 families. Note that as previously mentioned, we analyzed only 60 of 94 San Juan plots because the remaining 34 did not contain any trees or shrubs. Our results also show that the number of species was highest in Forest ($13.11 \pm 8.31$, $n = 9$), and lowest in Institutional/parks ($2 \pm 0$, $n = 2$; Table 3). Vegetation was predominantly tropical coastal, island flora. For example, *Spathodea campanulate* P. Beauv (Bignoniaceae) dominated in Vacant LULCs while *Rhizophora mangle* L. (Rhizophoraceae) and *Avicennia germinans* L. (Verbenaceae), both mangrove forest species, were abundant in Forest LULCs.

### 3.2. Plant phylogenetic diversity in San Juan

In our analysis of phylogenetic diversity, we found that standard PD was highest in Forests ($1214.17 \pm 582.42$, $n = 9$) and lowest in Institutional/parks LULCs ($306.63 \pm 1.15$, $n = 2$). MPD was highest in Forests ($185.55 \pm 54.15$, $n = 9$), and lowest in Other areas ($66.85 \pm 16.86$, $n = 2$). Finally, MNTD was greater in Commercial/industrial LULCs ($333.81 \pm 43.14$, $n = 2$) relative to Forests ($160.88 \pm 72.55$, $n = 9$; Table 3).

The Plant richness, PD, MPD.obs, and MNTD.obs in residential areas (R) is more than those in multi-residential areas (MR). The Plant richness, PD, MPD.obs, and MNTD.obs in R in our study was $6.15 \pm 4.42$, $756.39 \pm 461.37$, $181.64 \pm 60.84$ and $215.51 \pm 72.88$ ($n = 20$), respectively. The PD, MPD.obs, and MNTD.obs in MR in our study was $3.17 \pm 2.75$, $498.96 \pm 290.09$, $154.13 \pm 68.77$ and $241.45 \pm 76.91$ ($n = 7$), respectively. It indicates that residential areas could harbor more plant species than that in multi-residential areas (MR), possibly because greater building heights result in much harsher environments for local species to survive. Further analyses and discussion of our PD metrics are presented in the following sections.

### 3.3. Urban forest diversity, land use covers, and socioeconomic factors

In our PCA of herbaceous, water, tree and shrub cover, impervious surface cover, and other explanatory variables, the first four PC axes explained 72.9 % of the variation. Population density, tree and shrub cover, water cover, and median housing price loaded most positively on PC 1, while longitude and herbaceous cover loaded most strongly and positively on PC2 (Fig. 2). Our NMDS analysis found that plant species richness was correlated with population density (Table 4, $p < 0.05$) and housing price (Fig. 3).

Results from our GLM analysis found weak but marginally significant (all $0.05 < p < 0.10$) negative correlations between housing price and MNTD as well as between population density and MNTD (Fig. 4a, b). We

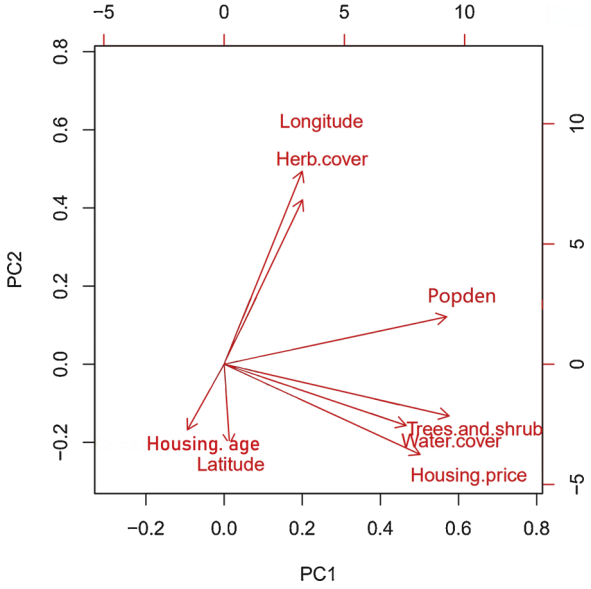


**Fig. 2.** Principle Component Analysis results for San Juan, Puerto Rico's urban forests.

**Table 3**
The number of taxa (NTAXA), phylogenetic diversity (PD), mean phylogenetic distance (MPD), and mean nearest phylogenetic taxon distance (MNTD) in San Juan, Puerto Rico according to land use and land cover (LULC) types.

| LULC | NTAXA | PD | MPD | MNTD |
|---|---|---|---|---|
| Vacant | 8.67 ± 3.21 | 1018.05 ± 333.86 | 181.92 ± 61.69 | 170.14 ± 45.57 |
| Forest | 13.11 ± 8.31 | 1214.17 ± 582.42 | 185.55 ± 54.15 | 160.88 ± 72.55 |
| Institutional | 2 ± 0 | 306.63 ± 1.15 | 113.55 ± 7.94 | 236.7 ± 2.31 |
| Parks | 2 ± 0 | 342.01 ± 48.87 | 147.1 ± 58.24 | 307.45 ± 97.75 |
| Agriculture | 3 ± 0 | 354.48 ± 0 | 126.83 ± 0 | 142.15 ± 0 |
| Other | 3.5 ± 0.71 | 447.56 ± 116.72 | 66.85 ± 16.86 | 220.01 ± 3.2 |
| Multi-family residential | 3.71 ± 2.75 | 498.96 ± 290.09 | 154.13 ± 68.77 | 241.45 ± 76.91 |
| Commercial/ industrial | 4 ± 1.41 | 621.92 ± 91.53 | 211.1 ± 5.51 | 333.81 ± 43.14 |
| Transportation | 6 ± 4.42 | 657 ± 457.41 | 124.99 ± 33.99 | 95.85 ± 12.47 |
| Residential | 6.15 ± 4.42 | 756.39 ± 461.37 | 181.64 ± 60.84 | 215.51 ± 72.89 |

**Table 4**
Non-metric Multi-Dimensional Scaling (NMDS) of urban forests in San Juan, Puerto Rico after Johnson transformation in Minitab 16. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1, Permutation: free, Number of permutations: 999. The input data are plant composition or the plant species and plot matrix with each species' abundance in each plot.

| | Housing age | Housing price | Population density |
|---|---|---|---|
| NMDS1 | −0.30 | −0.12 | −0.22 |
| NMDS2 | 0.95 | 0.99 | 0.98 |
| $r^2$ | 0.09 | 0.10 | 0.12 |
| Pr(>\|r\|) | 0.10 | 0.06 | 0.04 * |

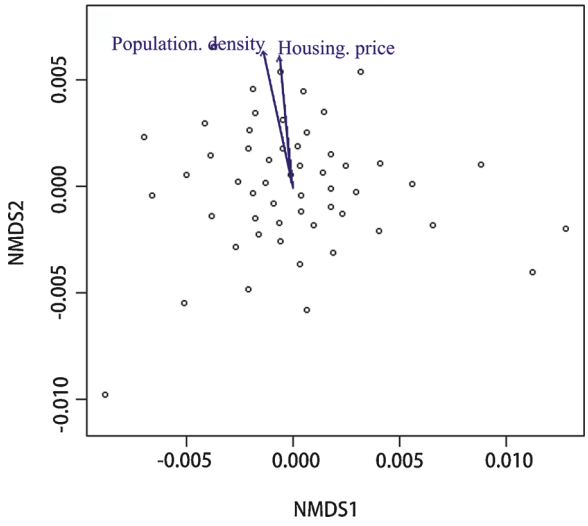


**Fig. 3.** *envfit* analysis of our non-metric multidimensional scaling (NMDS) socres for all species across all sampling sites in San Juan, Puerto Rico. Plot-level environment variables (population density and housing price) that were significantly related to each ordination ($P < 0.05$) are indicated in the figure panel.

also found weak but marginally significant positive correlations between population density and both traditional PD and total herbaceous species richness (NTAXA; Fig. 4c, d). Our structural equation modelling found that NTAXA, PD, MPD.obs, and MNTD.obs were mostly influenced by Housing price, followed by Population density, Age, and Latitude and Longitude. Specifically, Longitude and Age negatively influenced ntaxa, PD, MPD.obs, and MNTD.obs; while Latitude, Population density, and Housing price positively influenced ntaxa, PD, MPD.obs, and MNTD.obs (Table 5).

## 4. Discussion

Our findings are in general agreement with other studies and clearly show that different cities will have differing distributions and areas of LULCs across space, even within equivalent sampling plots and in similar climates (Rudel et al., 2016; Dobbs et al., 2017). Inevitably, this results from different human management systems, land planning priorities, and other socio-economic factors. Socio-ecological context in particular will determine the extent to which woody plants and palms are used for aesthetic, environmental, and climate mitigation purposes in urbanized areas (Lundholm and Richardson, 2010; Escobedo et al., 2011; Zhao et al., 2013). In this study we found that PD was highest in Forest LULCs. We suspect that the distribution of San Juan's LULC types are driven primarily by a combination of physical restrictions to expansion along its northeastern boundary by a protected forest reserve and wetlands (see Fig. 1) and socioeconomic conditions on the island. The population of San Juan is currently in a phase of contraction as more Puerto Ricans immigrate to the continental United States due to the recently unfavorable economic conditions on the island.

The results from our research can help inform future analyses that may wish to draw comparisons with other urban forests with different socio-ecological contexts. Complications can arise in studies of PD, however, when data from different sites are obtained using different inventory and monitoring systems. For instance, in our data, percent cover of small trees/seedlings is included in the shrub cover estimate. This is important as seedling plants are likely to be conspecific to other more mature trees and plants in the plot, thus not increasing PD (and perhaps even decreasing PD, had we used abundance-weighting). Second, we see plots in mangrove forests (tree, shrub and water cover) at the extreme end of the PCA axis in Fig. 2. Mangrove plots, which inherently have only a few species, often grow on standing water and include a mangrove seedling layer that is counted as shrub cover.

Our research supports the "luxury effect" reported by previous studies (e.g. Hope et al., 2003; Zhu et al., 2019a, 2019b; Wang et al., 2020), i.e., more wealth equals more plant taxonomic species richness and phylogenetic diversity. In our study, Housing price is a predictor of local urban residents' income and overall higher wealth, as such these residents could invest more resources on their yards or nearby parks' plant species, which is consistent with Zhu et al. (2019a, 2019b) in Hong Kong. Furthermore, nearest taxon index (NTI) or NRI (net relatedness index) should be included to determine if the phylogenetic pattern was random or not.

The positive relationship between property premiums and vegetation abundance or plant diversity (i.e. the luxury effect) has also been reported in a number of prior publications (Hope et al., 2003; Escobedo et al., 2006, 2015; Wang et al., 2016). Affluent residents contribute to a larger tax base that can in turn be allocated to the planning and maintenance of public spaces. Similarly, well-maintained public spaces with diverse floras, or just high tree and shrub cover generally, may be more attractive to high-income buyers (Dobbs et al., 2017). In our GLMs, housing prices were not correlated with the diversity of tree, shrub, and herbaceous species richness (i.e. NTAXA in Fig. 4). However, species richness was greatest in San Juan's Forest LULCs (Table 3). With regard to species richness, our *envfit* analysis revealed only one significant correlation: between our NMDS axes and population density (Table 4). This result implies that, among all possible socioeconomic and environmental factors considered in this research, sites with similar population density also tended to have similar plant species richness.

The above results can also be used to explore the role of other ecological hypotheses in explaining the diversity in urban forests (Rudel et al., 2016). For example, we did not find support for the hypothesis that Housing age may serve as a proxy for the effect of legacy on diversity; rather, our results indicated that plant species richness was not correlated with Housing age (Table 4). Thus, our analysis would seem to indicate that the effects of legacy on the local-scale diversity of urban woody plants in the tropics might differ by context (Staudhammer et al., 2015; Yang et al., 2017). Similarly, regional, national, and local scale socioeconomic factors can drive changes in urban LULCs (Grove et al., 2006; Luck et al., 2009; Escobedo et al., 2006; Wang et al., 2015, 2016; Zhu et al., 2019a, b; Wang et al., 2020a). San Juan's coastal island location near major mainland economies means that it is highly influenced by global commerce, real estate markets, temporal emigration and immigration patterns. This in turn can affect LULC dynamics, particularly along near coastal areas, which might subsequently drive plant assemblage.

In other studies of the dynamics of vegetation phylogenetics in cities, Ricotta et al. (2010) compared PD across 20 European sites and found that, despite an increasing number of alien species introductions, there was little evidence of rapid promotion of floristic homogenization. However, despite showing how available forest inventory data and phylogenetic trees can be combined to study the PD of different urban forests, PD (as traditionally measured) appears to be less useful in determining whether or not biotic homogenization is underway (Cadotte et al., 2012). Other studies such as those of Blood et al. (2016)

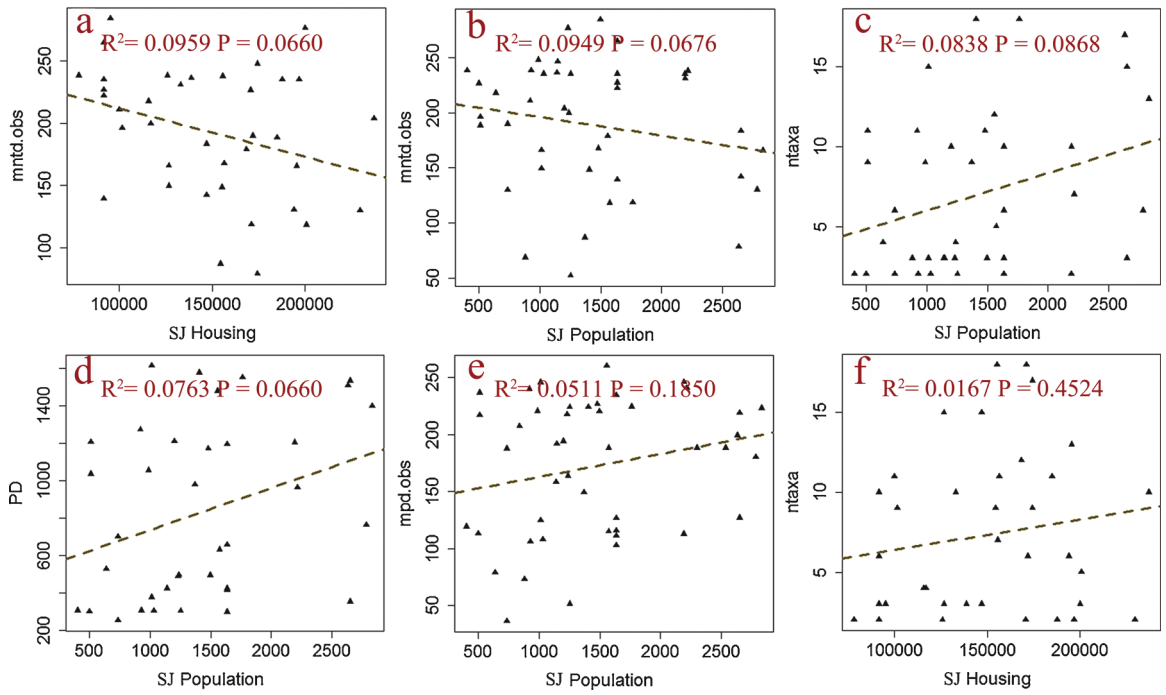


**Fig. 4.** Generalized Linear Model results showing the number of taxa (NTAXA), phylogenetic diversity (PD), mean phylogenetic distance (MPD), the abundance-weighted mean nearest taxon distance (MNTD), and their relationship with two socioeconomic variables: housing prices (SJ housing) and population density (SJ population) in San Juan, Puerto Rico.

**Table 5**
Structural equation models based on Partial Least Squares analyzing the influence of location and socioeconomic factors (i.e., Latitude, Longitude, Population density, Housing price and Age) on the variation of several taxonomic and phylogenetic diversity metrics (PD, MNTD, NTAXA, MPD) in San Juan, Puerto Rico.

| Socioeconomic factor | Coefficient | NTAXA (y1) | PD (y2) | MPD.obs (y3) | MNTD.obs (y4) |
|---|---|---|---|---|---|
| | b0 | 7.01 | 798.34 | 184.71 | 240.48 |
| Latitude | b1 | −9.98E-13 | −1.13E-10 | −4.36E-11 | −7.85E-11 |
| Longitude | b2 | 3.27E-13 | 3.70E-11 | 1.43E-11 | 2.57E-11 |
| Population density | b3 | −4.96E-09 | −5.61E-07 | −2.17E-07 | −3.90E-07 |
| Housing price | b4 | −2.09E-06 | −0.0002368 | −9.15E-05 | −0.000164559 |
| Age | b5 | 1.18E-10 | 1.34E-08 | 5.18E-09 | 9.31E-09 |

and Yang et al. (2017) demonstrate more appropriate statistical methods and metrics for using diversity data from networks of urban forests plots to assess the extent biotic homogenization.

Indeed, we found that MNTD was negatively correlated with housing price and population density, while herbaceous species richness, PD, and MPD were positively correlated with housing price and population density (Fig. 4). That is, the socioeconomic filters (i.e. including population density and housing price) seem to play a negative role in driving changes in MNTD, while playing a positive role in PD, MPD, and herbaceous species richness in San Juan urban ecosystems, thus representing a luxury effect (more wealth equates to more plant diversity, as per Hope et al., 2003).

It's difficult to explain what may be driving the difference in pattern between these two different metrics of PD. The simple implication is that more affluent and more densely populated areas have higher species richness overall, while less affluent and less densely populated urban sites tend to have higher nearest taxon distances, and thus lower minimum evolutionary similarity between species. An entirely speculative explanation for this pattern is that dense, affluent areas are more highly structured by active planting (including of distantly related ornamental plants); while the species richness of less affluent, low density urban forest patches is driven by ecological competition – even if between exotic species. Though intriguing, testing this hypothesis is beyond the scope of the present study since all of our urban communities consist of a mixture of ornamental, exotic, invasive, and native taxa.

Traditionally, PD has been used to study community assembly under the assumption that closely related taxa tend to be ecologically similar, for example, in terms of life-history, floristics, nutrient demands, environmental tolerances, and so on (Rudel et al., 2016). Thus, compared to the regional species pool (i.e., relatively high PD), phylogenetic over-dispersion of a local community might be indicative of local communities, which have been structured in part by ecological competition and competitive exclusion, which in turn tend to be stronger and higher, respectively, among closely related species than between phylogenetically distant taxa.

By contrast, phylogenetic clustering of the local community compared to the regional pool (i.e., low PD) might correspond to ecological filtering or environmental conditions that permit only species with certain phylogenetically auto-correlated tolerances or attributes to assemble in the local community (Cadotte et al., 2012). Phylogenetic diversity is also used in conservation biology since it embodies the principal that not all species, and thus not all extinctions, are equal (Rudel et al., 2016). That is, the loss of a species that is evolutionarily unique, and thus has no particularly closely related extant relative (i.e., large PD loss), is more serious than the extinction of a species with a large number of extant, closely related kin (i.e., small PD loss).

However, in terms of using PD in urban ecosystem, we found that it offers the potential for an additional biodiversity metric for green infrastructure and urban biodiversity research. First, PD permits us to quantify the biological diversity of a local community while taking the

evolutionary relationships of the members of that community into account (Faith, 1992). Second, all PD metrics explicitly down-weight the contribution of closely related species and up-weight relatively distant (that is, phylogenetically or evolutionarily dissimilar) taxa. Finally, PD has been linked to conservation measures that value 'feature diversity' (Faith, 1992) as well as higher ecosystem function (Cadotte, 2013).

## 5. Conclusion

Our study approach shows how PD analyses can be used to better understand the socioeconomic and ecological dynamics that influence woody plant diversity in tropical urban forests and elsewhere. We used a forest inventory monitoring and analysis system and various analyses to calculate different PD metrics and we then proceeded to correlate the PD to a range of socio-economic factors using statistical analysis. As such we show how this approach and PD can be used as a complementary method to better understand the role of the luxury and other ecological hypotheses on tropical urban forests, as well as patterns of biotic homogenization in tropical coastal urban forests.

As a different dimension to measure plant taxonomic diversity, plant PD also provides us an insightful perspective of species relatedness at the molecular phylogenetic level from the evolutionary angle (Zhu et al., 2019a, 2019b). That is, we can judge the species in urban ecosystems that are close or far related from the phylogenetic trees, which would be useful for future species selection palettes in urban planning processes.

Our results also add to a growing literature of research that has explored the correlations between socioeconomic factors and urban forest structure, composition, and ecosystem function. Although most of this research has been undertaken in temperate urban areas in Europe, North America, and most recently, China; here we examine these effects in the neotropics. Future research on PD could incorporate aspects of landscape architecture and design to test how ecophylogenetics – the application of phylogenies in ecology – might aid in achieving desired outcomes for society relating to green infrastructure and Nature-Based Solutions.

## Author statement

Manuscript title: Using phylogenetic diversity to explore the socioeconomic and ecological dynamics of a tropical, coastal urban forest I have made substantial contributions to the conception or design of the work; or the acquisition, analysis, or interpretation of data for the work; AND I have drafted the work or revised it critically for important intellectual content; AND I have approved the final version to be published; AND I agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons who have made substantial contributions to the work reported in the manuscript, including those who provided editing and writing assistance but who are not authors, are named in the Acknowledgments section of the manuscript and have given their written permission to be named. If the manuscript does not include Acknowledgments, it is because the authors have not received substantial contributions from nonauthors.

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## Declaration of Competing Interest

The authors declare no conflict of interest.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at https://doi.org/10.1016/j.ufug.2021.127111.

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