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Research paper

The luxury of vegetation and the legacy of tree biodiversity in Los Angeles, CA

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HIGHLIGHTS

- We evaluate determinants of vegetation cover and tree diversity in Los Angeles.
- Land use governance influence vegetation patterns and α and β diversity.
- High income, low density neighborhoods have the highest vegetation cover.
- Tree biodiversity increases with age and high income has an interactive effect.
- Our results contrast with arid cities, likely due to differing historical patterns.

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ABSTRACT

Urban vegetation cover and biodiversity provide ecosystem services to city residents, though the mechanisms affecting managed vegetation cover and biodiversity across varying urban land uses are not well understood. To evaluate competing mechanisms influencing urban vegetation cover and tree biodiversity, we collected data from 350 plots in the City of Los Angeles, CA. Alpha (α) and beta (β) tree biodiversity were quantified using sample based rarefaction curves. Hypotheses of independent climate, land use, luxury and legacy effects were evaluated with residual regression analysis and best models were chosen using AIC. Residential land use had the highest α biodiversity at all sampling scales, but the lowest β diversity, possibly indicating a limited plant pool for managers. Increased median household income was independently related to each type of vegetation cover, supporting a luxury effect. Regression models explaining the most variation in cover also included population density. In contrast, tree species richness was only positively related to housing age, supporting the legacy effect. Median income had no independent effect on tree biodiversity, which contrasts with patterns in other arid cities. However, age and income had an interactive effect. The highest α and β tree diversity were found in old, high-income locations. Managing for ecosystem services provided by vegetation should prioritize low income neighborhoods for increasing cover, while managing for biodiversity should maintain existing diversity in older neighborhoods and encourage new species in newer neighborhoods.

1. Introduction

Urban vegetation may increase the quality of life for residents by moderating extreme climates, reducing energy usage, and improving esthetics (Akbari, Pomerantz, & Taha, 2001; Fraser & Kenney, 2000; Jenerette, Harlan, Stefanov, & Martin, 2011; McPherson & Simpson, 2003). Perennial trees and shrubs are particularly important for ecosystem services of climate change mediation and adaptation (McPherson, Simpson, Xiao, & Wu, 2011; Nowak & Greenfield, 2012). The urban plant communities providing these ecosystem services are often highly diverse and contain unique species assemblages without analogs in unmanaged regions (Pickett et al., 2011; Whitney & Adams, 1980). In dryland regions, urban areas are frequently more species diverse than native landscapes when irrigation is provided (Grimm et al., 2008; Nowak, Hoehn, Crane, Weller, & Davila, 2011; Walker, Grimm, Briggs, Gries, & Dugan, 2009). A more diverse urban plant community can offer a broader range of ecosystem services, including food, shade, and esthetics (Lohr, Pearson-Mims, Tarnai, & Dillman, 2004; McCarthy, Pataki, & Jenerette, 2011). While landscape studies of urban ecosystems have increased in recent years (Pickett et al., 2011), patterns of managed plant ground cover and biodiversity within individual cities remain difficult to predict as human and natural processes interact in unexpected ways (Alberti, 2005; Grimm et al., 2008). The purpose of our study is to improve understanding of urban vegetation communities by evaluating urban vegetated cover and tree biodiversity patterns within Los Angeles, CA and identifying

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Table 1
Alternative hypotheses and mechanisms for urban vegetative cover and tree biodiversity.

Hypothesis	Vegetation cover	Tree biodiversity	Stated generally	References
1. Climate gradient	Tree cover will be higher in warmer inland regions due to demand for shade; shrub and herbaceous cover is expected to increase in coastal climates because of ease of management and decreased resident density	Tree biodiversity will increase near the coast as the mild climate can support trees from multiple biomes. If trees are low maintenance, managers may be more likely to plant them	Mild coastal climates may preclude fewer managed species and will contain more kinds of vegetative cover	Vegetation: Akbari et al. (2001), Jenerette et al. (2007) and McCarthy et al. (2011) Diversity: Lohr et al. (2004), Schoenherr (1995) and Tilman (2004)
2. Land use	Land uses with fewer inputs will have decreased vegetation cover, while Residential locations will have the highest because of individual value placed on vegetation	Tree biodiversity is expected to be highest in residential land uses due to intensive management and species decisions by multiple residents	Differing management decisions between land uses create patterns of vegetation and diversity	Alberti (2005), Cook et al. (2012), Hope et al. (2003), Lowry et al. (2012), Luck et al. (2009), and Thompson et al. (2003)
3. Luxury effect	All vegetation covers will be influenced by the "luxury effect" and will increase in high income neighborhoods because of increased property space and resources to invest in complex vegetation cover	Tree biodiversity will increase with income because heterogeneous environments with more species require more resources and property space to maintain.	Land managers have the resources to support large, heterogeneous green spaces in high income neighborhoods	Vegetation: Jenerette et al. (2007), Kinzig et al. (2005), McPherson et al. (2011) Diversity: Grove, Troy, et al. (2006), Hope et al. (2003), and Walker et al. (2009)
4. Legacy effect	Perennial vegetation cover will increase with development age due to longevity and difficulty of removal, while herbaceous vegetation may decrease due to urban fragmentation	Tree biodiversity will increase with development age because of long term establishment of trees with multiple managers and legacies of evolving species availability and city policy	Older urban neighborhoods may have heavily fragmented herbaceous vegetation, but retain legacies of cover and diversity in long lived perennials.	Vegetation: Boone et al. (2010), Cook et al. (2012), Luck et al. (2009), Troy et al. (2007) Diversity: Larsen and Harlan (2006) and Kirkpatrick et al. (2011)

their relationships with distributions of biophysical and social variables.

Multiple biophysical and social factors may influence urban vegetated cover and biodiversity (Table 1). Climate suitability may provide a fundamental constraint to the potential tree species pool (Tilman, 2004), though management may mitigate this constraint for some species (Grimm et al., 2008; Pickett et al., 2001). Governance and management regimes – e.g. commercial vs. residential zones – may directly and indirectly influence the structure and size of urban green spaces (Smith, Gaston, Warren, & Thompson, 2005; Thompson et al., 2003). The "luxury effect," hypothesis contends that higher income provides greater resources for managing extensive plant assemblages (Hope et al., 2003; Kinzig, Warren, Martin, Hope, & Katti, 2005; Lowry, Baker, & Ramsey, 2012; Walker et al., 2009). Proximate mechanisms for the income-diversity relationship may be choices associated with lifestyle (Grove, Troy, et al., 2006), maintaining social status in higher income neighborhoods by managing complex, biodiverse landscapes (Cook, Hall, & Larson, 2012; Larsen & Harlan, 2006; Robbins, 2007), and increased education level, which is connected to desire for tree related ecosystem services (Kendal, Williams, & Williams, 2012; Kirkpatrick, Daniels, & Davison, 2011). Income–diversity relationships have been extensively evaluated for perennial plants in the arid City of Phoenix, AZ (Hope et al., 2003; Kinzig et al., 2005; Walker et al., 2009) with limited data from other cities for comparison. Finally, a legacy hypothesis suggests activities by prior land managers persist throughout urban development and influence current vegetation cover and diversity (Boone, Cadenasso, Grove, Schwarz, & Buckley, 2010; Larsen & Harlan, 2006). The effect of legacies can vary by city. For example, older neighborhoods in Baltimore, MD, have increased tree canopies (Grove, Troy, et al., 2006; Troy, Grove, O'Neil-Dunne, Pickett, & Cadenasso, 2007), while in Phoenix, AZ, older neighborhoods have decreased tree canopy (Hope et al., 2003).

Reinforcing and competing effects of different variables – climate gradients, land-use, luxury effects, and legacies – likely create complex patterns of vegetative cover and diversity. The link between vegetative cover and income can grow stronger over time (Luck, Smallbone, & O'Brien, 2009) as cultural historical legacies and management have been shown to jointly influence neighborhood biodiversity (Kinzig et al., 2005; Walker et al., 2009). Neighborhood age and household income can interact to influence residential tree cover patterns (Lowry et al., 2012). Tree abundances in arid Australian cities were best explained by combining both climatic and socioeconomic variables (Luck et al., 2009; Kirkpatrick et al., 2011). Furthermore, the most influential mechanisms affecting landscape patterns may be land-use specific. For example, resident choices about private vegetation may be more sensitive to luxury effects than institutionally managed park vegetation (Kinzig et al., 2005; Martin, Warren, & Kinzig, 2004).

To better understand how multiple potentially interacting variables influence urban vegetation patterns, our study collected data from land-use stratified plots across the City of Los Angeles, CA (LA). In conducting this research, we asked: how do patterns of managed vegetation cover and tree biodiversity in LA vary in response to changes in environmental and social variables? Though many studies focus on residential neighborhoods or remnant native habitat (Cook et al., 2012; Lowry et al., 2012) our research evaluates patterns across multiple land governances. The results of this study will contribute to a growing body of literature that addresses how interacting mechanisms influence urban vegetation and will better inform city planners about neighborhood biodiversity and cover.

2. Study location

LA covers 1214 km^2 with approximately 3.8 million residents, (10% of California) and a population density of 3100 people per km^2 (2010 U.S. Census). Overall median income is ~$50,000 with census tract scale income varying between $10,000–$200,000. One-fourth of LA families with children live below the poverty line ($18,000 for a family of four; 2010 U.S. Census). While European development began in 1765, LA was officially founded in 1781 and by 1900 it was a major metropolis with over 100,000 people (Ríos-Bustamante, 1992). The majority of LA's residential neighborhoods were built during two periods (1955–1965 and 1975–1990).

The climate is Mediterranean with rainfall occurring primarily from November to March (Morris, 2009). Chaparral and coastal sage scrub characterize the regional flora. There is a strong coastal to inland gradient in both precipitation and temperature. Annual precipitation ranges from 330 mm at the coast to 380 mm in downtown. The gradient also manifests as an increased inland temperature range and mean; monthly temperature min/max (T_{min}/T_{max}) range from 9 to 25 °C at the coast and from 10 to 29 °C downtown (Morris, 2009; NOAA). At a smaller scale, T_{max} for neighborhoods 5 km closer to the ocean can be up to 1 °C cooler, with 25 mm less annual rainfall than more inland regions (Patzert, LaDochy, Willis, Mardirosian, 2007). Average annual maximum temperatures in LA have also warmed 2.8 °C from 1906 to 2006 due to overall climate change, decreased vegetation cover, and increased human structures (Akbari et al., 2001; Tamrazian, Ladochy, Willis, & Patzert, 2008).

3. Methods

3.1. Data collection

358 circular 0.04 ha plots were placed within the boundaries of LA using a stratified random sampling design based on local land-use (Nowak & Crane, 2000) – mapped by the City of Los Angeles and confirmed by the surveyor on site – to evaluate local zoning and management differences. Eight of these locations were either missing census information or could not be properly surveyed, reducing the sample size to 350 fully surveyed locations (Fig. 1). Criteria for distinguishing land-uses followed standardized classification by US Forest Service for urban areas (Urban Forestry Effects manual accessible at http://www.itreetools.org/eco/). Common land-uses included single-family homes (Residential), business uses (Commercial), educational and religious organizations (Institutional), major freeways and roads (Transportation) and multi-family housing (Multi-family). Less common uses were agriculture, golf courses, graveyards, parks, utilities and vacant land. Plots were visited in the summers of 2007 and 2008, and their locations were determined in the field using a portable GPS unit. Since many plots were located on private land, access permission was obtained from the owner before surveying. If unavailable, plots were moved to a nearby accessible area with similar tree and ground cover. For 25 plots without trees and inaccessible for survey (e.g. airplane runways), aerial surveys using Google Earth were conducted. The ground cover in these plots was simple with no trees and easily estimated using publically available imagery. Ground cover was divided into pervious and impervious covers. Tree and shrub cover were assessed independently of ground cover as they often shaded herbaceous vegetation. To distinguish between covers in our analysis, we use "herbaceous" to describe all non-woody vegetation, "perennial" to describe woody (tree and shrub) vegetation cover, and "vegetation" to describe the combination of tree, shrub, and herbaceous cover. Trees were defined as woody vegetation tall enough for measurement of diameter at breast height (dbh, measured at ~1.37 M), with a central bole of no less than 2.5 cm dbh, and no more than six stems. All trees within each plot were measured and identified. Other woody vegetation was classified as shrub cover and not identified. Proper tree identification was ensured through voucher specimens, taken to the University of California, Riverside herbarium for expert identification and archiving.

We grouped land-uses into classes representing management style, ground cover, and urban structure: CI: Commercial and Institutional (large number of public trees, high impervious cover); R: Residential; MT: Multi-family and Transportation (similar vegetation cover and socioeconomic variables); O: Other Pervious (high pervious cover: golf courses, graveyards, vacant land, etc.). For vegetation cover analysis, we only used non-vacant plots (n = 300) because of the predominance of shrublands in vacant land and lack of development influences on ground cover. For quantifying tree biodiversity, vacant lots were included (n = 350). Trees in vacant lots are protected by city and state laws, and therefore, tree biodiversity in these plots reflect governance and management decisions, making them important to include in our analysis.

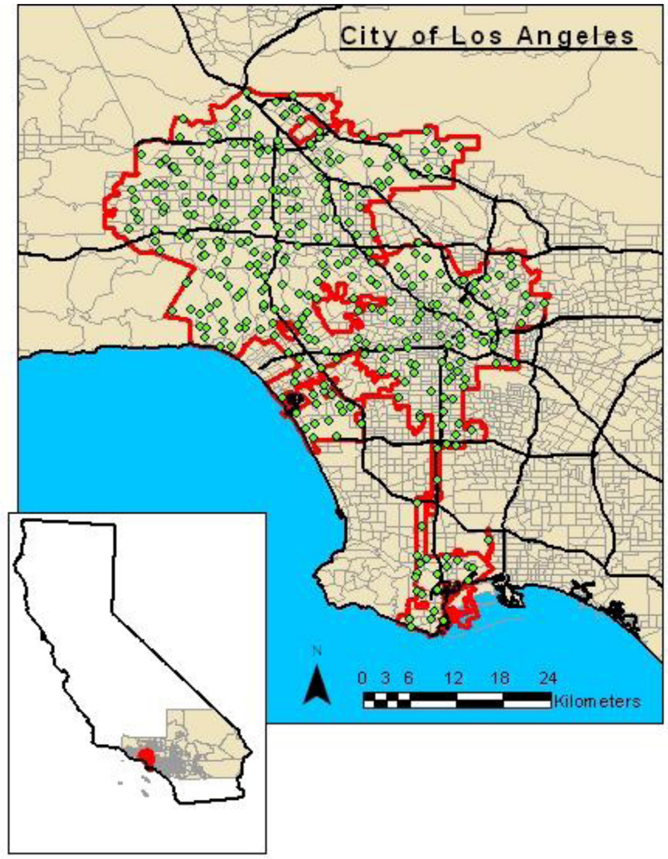

Fig. 1. Map of study area. Red line represents the Los Angeles city boundary, green dots are the study sites, black lines represent major freeways, and gray lines represent census tract boundaries within LA county. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Access to backyard plots in private residences was restricted, which often required relocating plots to the front yard. In residential areas, this may have increased the frequency of asphalt and cement ground covers. To address this concern, original and relocated plots were compared using Google Earth imagery and field observation to maintain similar vegetation density and tree presence. This may have affected species composition, as backyard and front yards can have different planting practices due to differing policies in acceptable "public" landscapes (Smith et al., 2005; Larsen & Harlan, 2006). Future studies of urban biogeography should incorporate long-term resident involvement to ensure property accessibility.

Our sampling approach is consistent with prior surveys conducted by the USDA Forest Service (Nowak & Crane, 2000) and similar to urban vegetation sampling conducted in the Central Arizona-Phoenix Long Term Ecological Research site (CAP-LTER) (Hope et al., 2003; Walker et al., 2009). Studies at CAP-LTER have been used as a benchmark for research in arid cities (Cook et al., 2012). A comparison of our sampling methods to those in Phoenix shows that while our plots were half the size of Phoenix plots, we sampled more points (LA: 350 vs. Phoenix: 206) in a smaller area (LA: 121,400 ha. versus Phoenix metropolitan area: 640,000 ha). Support (total area sampled/extent of landscape) was 3 times higher for LA (3.0×10^{-5}) than Phoenix (1.0×10^{-5}). Furthermore, fewer than 100 plots were sampled within urbanized Phoenix, while urban locations made up 300 of LA's 350 sampled locations. Therefore, our high density of plots compensates for what our study may lack in individual plot coverage. We further incorporate rarefaction curves in biodiversity analyses for cross-scale comparisons.

Field measurements were geospatially linked to physical and socioeconomic variables (ArcGIS 9.2). Demographic variables (median household income and population density) were obtained at a census tract scale from a Geolytics data product, which compiled the 2000 U.S. census tract information. These variables are median values at a larger scale than each of our plots or land-uses, and represent the regional characteristics near each plot. For that reason, dense populations may exist near a "Commercial/Industrial" location, though that point contains no residents. Environmental variables of distance from coast and elevation were calculated individually for each plot. The age of a building structure or land development date was obtained from public records accessed through a commercial real estate service (http://www.redfin.com/) and addresses based on the plot GPS locations. The ages of most residential land were determined according to recorded "built date." Otherwise, the median age of 5–10 houses nearby was used in lieu of a built date. Outside of residential areas, we used establishment date for businesses and freeway extension date for transportation land. In undeveloped locations, there were no housing ages; instead, the census tract scale variable of "median housing age" was used to determine the general year that urbanization began to influence wildland management.

3.2. Biodiversity Indices

Diversity indices and rarefaction analyses were calculated using EstimateS 8.20 (http://viceroy.eeb.uconn.edu/EstimateS). Species abundance and evenness were evaluated using Shannon's diversity index (H'; Weaver & Shannon, 1949). Cumulative H' values were calculated for all plots and land-use classes. Evenness (E) was calculated as $E = \ln(H')$. Species unique to each land class were determined using similarity analyses in EstimateS and visual comparison of species lists. Sample based rarefaction curves, randomized and smoothed species accumulation curves, were constructed for each land-use classes to compare both α diversity (overall biodiversity) and β diversity (turnover between plots). Rarefaction curves are produced by repeatedly re-sampling the pool of N samples, so measures of α biodiversity can be directly compared at any sampling intensity (Colwell, Mao, & Chang, 2004; Gotelli & Colwell, 2001). Rarefaction curves can be described using a power law function, $y = Cx^z$, where C is a constant and z is the slope of the function (Koellner, Hersperger, & Wohlgemuth, 2004). The exponent, z, is a measure of β diversity in each land class, as it describes the rate of species accumulation (Arita & Rodríguez, 2002; Zhao, Ouyang, Xu, Zheng, & Meng, 2010). The slope of z ranges from 0 to 1, with 1 indicating that there are no shared species between plots within a given land class (high β diversity) and 0 indicating identical species in each plot within a land class (low β diversity). We also estimated overall species richness for all plots and each land class using the first order jackknife estimator, which minimizes bias in richness estimates and allows estimation of total species without an asymptotic species accumulation curve. This estimator is a function of rare species; with every rare (n) species found, the jackknife estimate is $1/n(n-1)$ more than the total number found (Heltshe & Forrester, 1983). As a check for spatial independence, we conducted a semi-variogram using ArcGIS 9.2 on plot location and species composition to determine the extent of spatial autocorrelation.

3.3. Data analysis

We evaluated the individual contributions of environmental, socioeconomic, and legacy regulation on biodiversity and cover while accounting for likely cross-correlation. Environmental variables considered were distance from coast (DFC) and elevation. Median household income (noted as income) was used to indicate socioeconomic status, similar to other studies (Hope et al., 2003; Martin et al., 2004). Education level has been shown to influence species diversity and vegetation cover (Kirkpatrick et al., 2011; Kendal et al., 2012), but we excluded education data because of the strong correlation with income (Cilliers, Siebert, & Davoren, 2012). Legacy effects were accounted for with development age. Finally, tract-level population density (noted as density) was also included. A principal components analysis indicated that elevation and DFC were correlated in complex ways because of coastal and inland mountains, so we retained the simpler variable of DFC to describe climatic gradients. It also showed that income was related negatively to both population density (−0.51), and age (−0.31), though age and density were not related to each other. Combining all three of these into a single variable would remove individual variable contributions. Instead, we used SPSS 16.0 to run regression models on cover against income, age, and population density and then regressed individual variables against model residuals. This allowed us to observe the independent effect of income while controlling for age and density and the effect of age or density while controlling for income.

3.4. Vegetation cover analysis

Independent regression models were run on tree, shrub, and herbaceous cover values for the 300 non-vacant plots to determine the effect of age, population density, and income. For models where age, population density, or income had a detectable effect on a particular cover, we regressed that variable against the residuals of related variables. As DFC was not related to other variables, no residual variable analysis was necessary. Age and density were regressed against residuals of income-cover regressions, and income was regressed against residuals from an age and density model. We report the best models chosen by AIC, to assess the independent contribution of each variable. Regressions were repeated in each land-use class to test if land use change altered expected luxury and legacy patterns (Table 1). We also used a structured regression to quantify the contribution of each independent variable to best-fit models. This analysis allowed us to identify changes in model explanatory value (R^2) as variables were added (Appendix A). Pearson product moment correlation was conducted between independent variables and tree, shrub, and herbaceous cover. Analysis of variance (ANOVA) was used to compare tested variables and cover between land use classes.

3.5. Diversity analysis

Due to the small size of our sampled plots (11.3 m radius), we found, on average, less than one tree species per plot. Analyzing biodiversity patterns and conducting regressions with individual plots (similar to Hope et al., 2003) was not possible with these data. Therefore we binned all sampled plots ($n = 350$) into 20 bins (17–18 plots each), effectively increasing our sampling area from 0.04 ha to ~0.7 ha. We binned plots four times based on each independent variable (DFC, density, income, and age). For example, when we binned by the age variable, the 18 oldest plots were placed in bin

Table 2
Tree biodiversity indices and estimates for major land-use classes. H' = Shannon's diversity index (Weaver & Shannon, 1949); H_{max} = ln(# of species); evenness = ln(H'). Unique species indicate species found only in that land-use class. Estimated richness is based on the first order jackknife estimator.

Land-use class	# of plots	# of species	Estimated richness	# of trees	% of plots with trees	Unique species	H'	H_{max}	Evenness
Commercial/Institutional	70	36	65.5 ± 6.5	103	40%	14	2.97	3.58	0.83
Multi-family/Transportation	43	18	33 ± 4	44	35%	6	2.66	2.89	0.92
Other Pervious	74	22	39 ± 4.5	90	28%	11	2.38	3.09	0.77
Residential	163	109	169 ± 9	438	84%	67	4.17	4.69	0.89
Total	350	140	214 ± 10	675			4.33	4.94	0.87

#20 and the 18 youngest plots were placed in bin #1. We investigated bins in each organization more than two standard deviations away from the mean of all other plots to identify outliers. To isolate the effect of each independent variable, we conducted independent regressions and correlations between the average value of the variable in each bin and total bin diversity, but only when the data were binned by that independent variable. For example, regression and correlation of average housing age with species diversity was only conducted for the 20 bins organized by age (bin #1 is young, bin #20 is old). In this way, we show both correlative and linear relationships between age, income, density and diversity for comparison to similar studies (e.g. Hope et al., 2003). Because of this necessary limitation, residual regression models to determine independent variable effects were not possible for biodiversity analyses. Instead, we used rarefaction to quantify interactions between variables.

Rarefaction analysis, conducted in EstimateS, was used to examine the correlative effect of age and income on biodiversity. Plots were separated into two factor groups with old (built before 1960) and young (built after 1960) housing and again into poverty (below \$20,000), low (\$20–40,000), Average (\$40–65,000), and high incomes (above \$65,000). The year 1960 was chosen as it separates the 1950 and subsequent 1980 housing booms. Rarefaction curves were created from these unequally sized groups to accurately compare biodiversity in each. Power law exponents, z, were then calculated for comparison of β diversity. This analysis was repeated in the Residential land class, as we hypothesized biodiversity in resident owned locations would be more sensitive to income variability. Because no young residential areas existed in impoverished locations, we only examined three income levels (low, median, and high) for cross comparison.

4. Results

4.1. Diversity indices and land-use comparisons

Overall, 140 different tree species and 675 individual trees were recorded in LA. We estimated there are 214 (±10) species in LA based on the jackknife estimator (Table 2). The residential land class was the most diverse with 109 different tree species, 67 of which were unique to this land-use class (Table 2). The residential land-use class contains over 60% of the total number of trees found in our study. Estimated number of species was highest in Residential (169 ± 9), followed by Commercial/Institutional, Multi-family/Transportation, and Other Pervious. Other Pervious was the least diverse despite containing high number of trees, due to homogenous stands of wild oak and walnut in vacant plots. Across all land-use classes, species evenness was high (above 70%).

Rarefaction curves showed that residential plots had higher α diversity than any other land class at any sampling intensity, with the lowest biodiversity in Commercial/Institutional and Multi-family/Transportation classes (Fig. 4 and Table 2). Conversely, β diversity was highest in Commercial/Institutional (0.933) and Multi-family/Transportation classes (0.922; Table 3). Residential locations had the lowest β diversity of any land class (0.747). A spherical semi-variogram of each land-use class showed no spatial auto-correlation in species diversity at our sampling scale. The lack of spatial auto-correlation is consistent with high β diversity values in all land-use classes.

4.2. Vegetation cover

Herbaceous land cover was abundant in every land class, while tree cover was low (Fig. 2). Land-use classes all had significantly different percentages of herbaceous cover ($p < 0.001$), with Commercial/Institutional containing the least and Other Pervious the most. Land-use class differences were less distinct for tree and shrub cover, with the highest tree cover in Residential ($p < 0.05$) and lowest shrub cover in Commercial/Institutional ($p < 0.05$). Land-use classes showed significant differences in income, DFC, density, and age. Income was highest in Residential and Other Pervious classes ($p < 0.05$; Fig. 3a). Multi-family and Transportation plots are closest to the coast ($p < 0.05$; Fig. 3b). Other Pervious plots had the lowest tract population density ($p < 0.05$; Fig. 3c) and contained recently urbanized plots ($p < 0.05$; Fig. 3c).

Residual regressions indicate independent effect of income apart from age/density on herbaceous ($R^2 = 0.048$; $p < 0.001$), tree ($R^2 = 0.047$; $p < 0.001$) and shrub covers ($R^2 = 0.057$; $P < 0.001$). Density was only independently influential on tree cover ($R^2 = 0.014$; $P = 0.024$). Density and income combined was the best model for shrub cover ($R^2 = 0.63$; $P < 0.001$), while combined age, density, and income was the best model for herbaceous cover ($R^2 = 0.121$; $P < 0.001$) and tree cover ($R^2 = 0.066$; $P < 0.001$) (Table 4). Tree cover had poor predictive value compared to shrub and herbaceous cover models. Our analysis showed no effect of DFC on cover values for all land-use classes. In the Residential land class, income had an independent effect on herbaceous ($R^2 = 0.038$; $p = 0.007$) and

Table 3
β diversity based on power law relationship of rarefaction curves ($y = Cx^z$), where z is a proxy for β diversity. Values can range from 0 to 1. Values closer to 1 mean that plots in that land-use class or age/income group have high species turnover between plots.

Group	# of plots	Exponent z (β diversity)
Land-use class (Fig. 4)		
Commercial/Institutional	70	0.933
Multi-family/Transportation	43	0.922
Other Pervious	74	0.876
Residential	163	0.747
Total	350	0.741
Age/income group (Fig. 6A and B)		
Old_poverty	54	0.873
Old_low	73	0.846
Old_average	49	0.886
Old_high	19	0.941
Young_poverty	16	0.922
Young_low	32	0.766
Young_Average	56	0.935
Young_High	51	0.922
Residential age/income group (Fig. 6C and D)		
Old_low	64	0.799
Old_average	36	0.894
Old_high	16	0.942
Young_low	9	0.939
Young_Average	23	0.902
Young_High	15	0.963

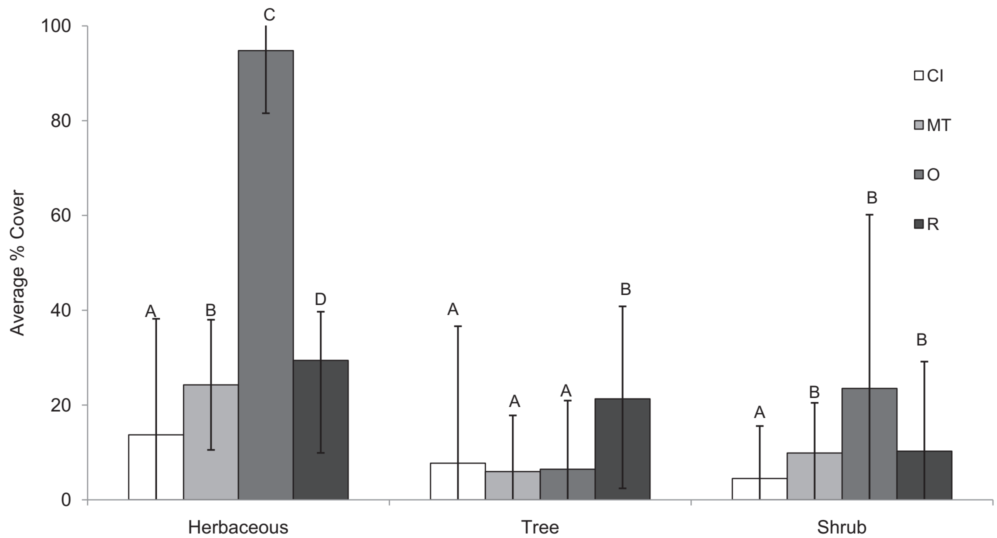

Fig. 2. Vegetation cover data for the major land use classes: Commercial and institutional (CI), Multi-family/Transportation (MT), Other Pervious (O) and Residential (R). Bar heights indicate mean percent cover at plots within each land use class and error bars represent standard deviation. Significant differences ($p < 0.05$) between classes are represented by different letters. All the classes were significantly different in herbaceous cover, tree cover was highest in residential areas, and shrub cover was lowest in Commercial/Institutional areas.

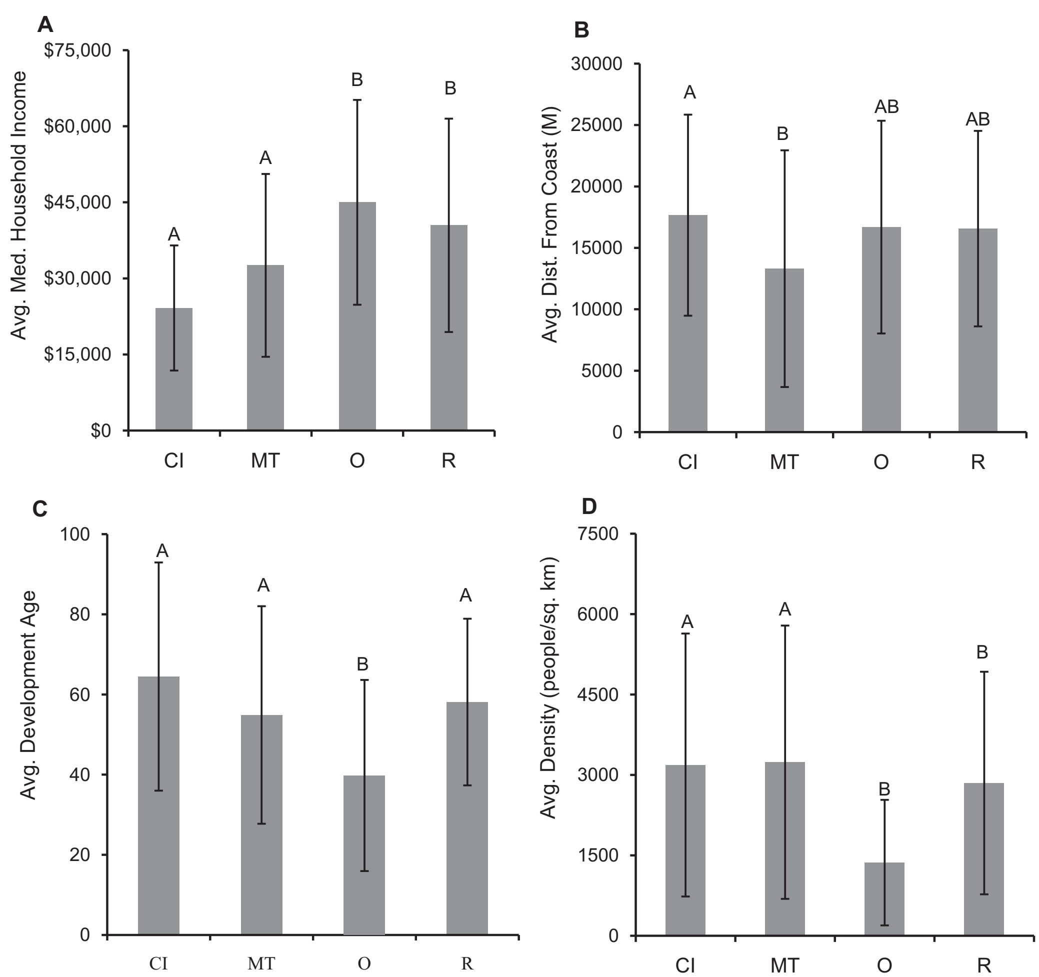

Fig. 3. Descriptive statistics of social and environmental variables by land use class. Bar heights indicate mean values of income (A), distance from coast (DFC) (B), development age (C) and population density (D) in each land use class. Error bars represent one standard deviation of that variable in each class. Significant differences ($p < 0.05$) between classes are represented by different letters. Income was highest in the Other and Residential land use class, DFC was slightly lower in the Multi-family/Transportation class, and the Other class was both the youngest and least dense of all the plots.

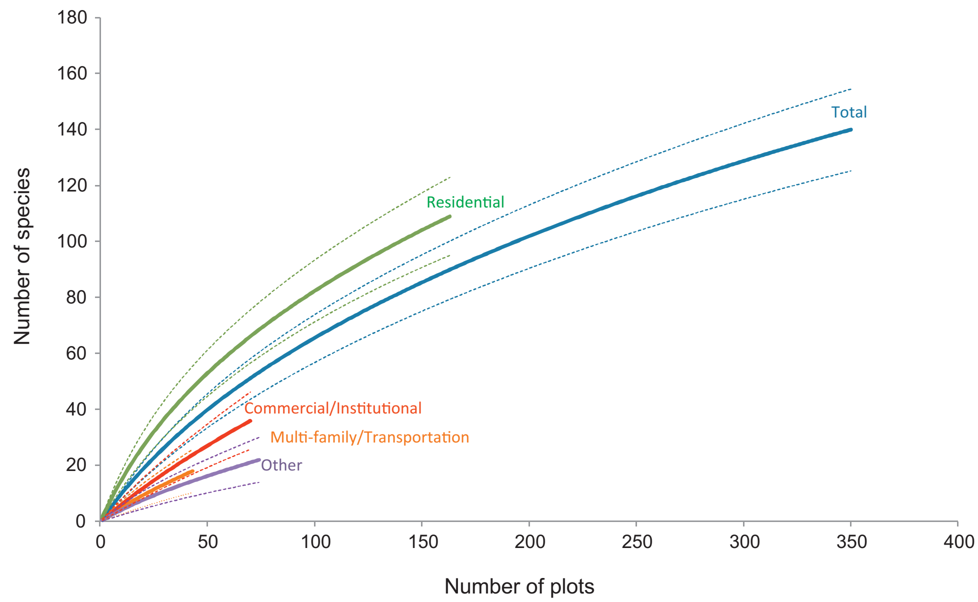

Fig. 4. Sample-based rarefaction curves for each land use class, calculated using EstimateS (Colwell et al., 2004). Dotted lines of the same color represent 95% confidence levels. Power law relationship fits and β diversity slopes based on these data are reported in Table 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

shrub cover ($R^2 = 0.054$; $p = 0.002$), but not on tree cover. Income was the best model for Residential tree cover, though R^2 was quite low ($R^2 = 0.024$; $P = 0.048$). The Multi-family/Transportation land class showed an independent effect of income only on shrub cover ($R^2 = 0.077$; $p = 0.04$), and a strong effect of age on tree cover ($R^2 = 0.175$; $p = 0.003$). The income model for shrub cover ($R^2 = 0.077$; $P = 0.04$) and age model for tree cover ($R^2 = 0.171$; $P = 0.003$) were not significantly different than controlled residual regressions. Commercial/Industrial and Other Pervious plots had no significant models for any cover.

These models are consistent with Pearson's product moment correlation (Table 5). The strongest negative relationship was between age and herbaceous cover (−.187), though it is also related to income and density (.337, −.139). Vegetation cover overall was positively related to income, while density was the most negatively correlated to herbaceous cover, as shown in the structured regression models. Individual regressions of cover types are shown plotted against the main effects of luxury and legacy to illustrate the linear aspect of this relationship (Fig. 5c and d).

4.3. Diversity regression models

Because of the binning requirement to analyze diversity data, a critical evaluation of available data was necessary. Since diversity was only correlated with variables used for that specific binning, it was important that bins accurately represent the variable's range. In the age binned plots, the oldest bin with plots before 1920 included the lowest income points and the fewest trees because of co-occurring old structures and low local maintenance. Therefore, we excluded this final bin, leaving 19 age bins. We also excluded one plot in a 210-year-old graveyard, as it was the oldest location by over 100 years and did not reflect overall data. For the income bins, the 2nd and 3rd highest income bins were outliers with 25 and 28 tree species. On further examination, the increase in species came from only two plots in each bin, all built in the 1930s, with 10–17 species each. The outliers represented a legacy instead of a luxury effect, as younger plots at the same income level contained less than 5 species each, making these outliers in income bins. We removed these four points, leaving 16 plots in each income bin.

Plot age was positively related to biodiversity in both Pearson product moment correlation and linear regression ($p = 0.024$; $r = 0.516$; $R^2 = 0.33$; Fig. 5a and Table 5) within age-binned plots. Conversely, when bins were sorted into income levels, there was no linear relationship between income on number of species per bin ($p = 0.369$; $R^2 = 0.045$; Fig. 5b) and correlation was also non-significant (Table 5). Density and DFC showed no relationship with species diversity in their respective binning organizations.

4.4. Luxury and legacy interactive effect

Rarefaction curve analysis showed that luxury and legacy effects interacted for a large effect on α biodiversity (Fig. 6a and b). Old plots in the two highest income groups had higher α diversity than any other group (Fig. 6b), while young, poverty locations had the lowest (Fig. 6a). Within a single age group, high and average income plots in young and old locations contained higher α diversity than low income/poverty areas (Fig. 6a and b). Residential land class had similar results, with older and younger areas showing an association between α diversity and higher income (Fig. 6c and d). β diversity did not follow patterns of income, but was generally higher in younger areas (Table 3). The exception to this was old, high-income locations, which had similar β diversity to young, high-income areas in both general (old, high: 0.941; young, high: 0.935) and residential rarefaction comparisons (old, high: 0.942; young, high: 0.963).

5. Discussion

Our results show the luxury effect is the dominant influence on perennial and herbaceous cover, with significantly more vegetation cover in high income plots (Tables 4 and 5 and Fig. 5d). Lower population density also predicted higher cover in association with income (Table 4). In contrast, legacy effects emerged as the dominant influence over tree diversity with more species in older neighborhoods (Table 5 and Fig. 5a). Biodiversity in residential plots was influenced by both the luxury and legacy effect, with the highest diversity in old, high-income neighborhoods (Fig. 6b). Distance from coast also had no detectable effect on urban

Table 4
Residuals (predicted − actual) from the relationship of each major variable (income, age, density) with each vegetation cover class (Herbaceous, Tree, and Shrub) regressed against related variables. Significant results indicate that the tested variable independently influences that cover value. As only Residential and Multi-family land-use classes had significant models, they are the only classes reported. Overall best model combinations based on AIC are reported below each reported regression. No residuals were done with Distance From Coast, as it was not independently significant. All, all non-vacant plots; R, Residential; MT, Multi-family/Transportation. Variables: income, median household income; DFC, distance from coast; density, population tract density.

Tested model		All locations (n = 300)		
Residual	Variables	Herbaceous	Tree	Shrub
Age; density	Income	Adj. R^2 = 0.048 P < 0.001*	Adj. R^2: 0.047 P < 0.001	Adj. R^2: 0.057 P < 0.001
Income	Age	–	–	–
Income	Density	–	Adj. R^2: 0.014 P = 0.024	–
Best model				
Density; income		–	Adj. R^2 = 0.063 P < 0.001	Adj. R^2 = 0.135 P < 0.001
Age; density; income		Adj. R^2 = 0.121 P < 0.001	–	–
Residual	Variables	Residential land-use class (n = 163)		
Age; density	Income	Adj. R^2: 0.038 P = 0.007	–	Adj. R^2: 0.054 P = 0.002
Income	Age	–	–	–
Income	Density	Adj. R^2: 0.018 P = 0.048	–	–
Best model				
Income		–	Adj. R^2: 0.024 P = 0.048	–
Density; income		Adj. R^2: 0.081	– P = 0.005	–
Age; density; income		–	–	Adj. R^2: 0.185 P < 0.001
Residual	Variable	Multi-family/transportation land-use class (n = 43)		
Age/density	Income	–	–	Adj. R^2: 0.077 P = 0.04*
Income	Age	–	Adj. R^2: 0.175 P = 0.005*	–
Income	Density	–	–	–
Best model				
Age		–	Adj. R^2: 0.171 P = 0.003	–
Income		–	–	Adj. R^2: 0.077 P = 0.04
		Other Pervious, commercial/industrial (No significant models)		

* Not significantly different than independent regressions of indicated variable vs. cover.

vegetation cover or diversity, despite its influence on native vegetation (Schoenherr, 1995). Our results show how socioeconomics and history have shaped LA's vegetation structure with differing effects on plant cover and diversity.

5.1. Biodiversity and trends

LA contains an impressive tree diversity (141 present; 214 projected), with a diverse Residential land-use class (109 present; 169 projected). High species evenness (Table 2) indicates a large number of unique species (ones found in only a single location). This result is supported by β diversity values of above 0.7 in each land-use class (Table 3). Previous research on β diversity shows that the slope of the exponent ranges from 0.2 to 0.4 for heterogeneous forests (Connor, McCoy, & Cosby, 1983; Koellner et al., 2004). The high β diversity values in LA support hypotheses that urban heterogeneity occurs primarily between rather than within parcels (Jenerette, Wu, Grimm, & Hope, 2006). Surprisingly, though α diversity is highest in the Residential land-use class, β diversity is lowest and is instead high in Commercial/Institutional and Multi-family/Transportation land-use classes (Fig. 4 and Table 3). Though residential plots contain species unique to that land-use class (Table 2), there is overlap between plots in multiple neighborhoods. In contrast, land-use classes governed and managed by city, commercial, or multi-family housing managers have little to no overlap of tree species between locations. Homeowners may have a more limited pool of available species accessible for planting than other land-use managers, creating more overlap between spatially separate neighborhoods.

LA is projected to have more than three times the tree species diversity of Southern California (Magney, 2000). Similar amounts of

Table 5
Pearson's product moment correlation between independent variables and all covers and diversity. Diversity correlations are based on 20 bins binned by each independent variable, with inputs equal to total biodiversity and average variable value for each bin.

	Income	Density	Age	DFC
Tree cover	.217***	–	–	–
Shrub cover	.331***	–	−.161**	–
Herbaceous cover	.337***	−.139*	−.187**	–
Species (grouped by variable)	–	–	.516*	–

* p < 0.05.
** p < 0.01.
*** p < 0.001.

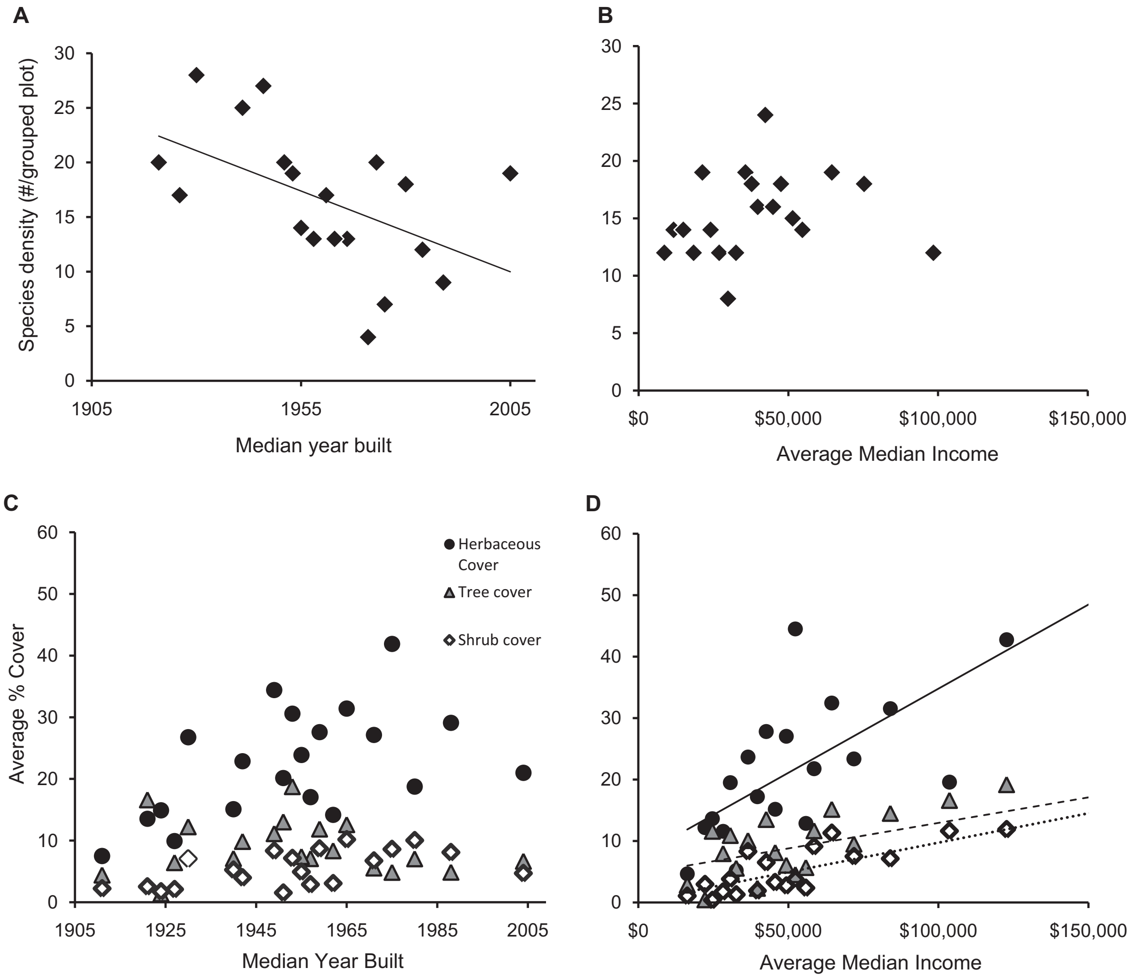

Fig. 5. Legacy and luxury effects on diversity and cover. Regression lines are based on twenty grouped points sorted by either age (A and C) or Income (B and D). Statistics for regressions are in Tables 4–6. (A) Diversity is positively related to age, with oldest areas containing the most species, with no effect of income (B). While younger areas have higher vegetation and shrub cover (C), hierarchical regression shows that age has no independent effect on cover (Tables 4 and 5). All vegetative covers increase with higher Income, indicating a strong luxury effect (D). Income is also shown to have an independent effect on all covers, especially shrub and pervious cover (Table 5).

high urban diversity have been found in other arid regions because of the influx of non-native species and resource addition to support them (Kirkpatrick et al., 2011; Walker et al., 2009). Exotic invasives in the managed plant pool can contribute to invasions of local wildlands. A common tree that we found in LA, *Schinus terebinthifolius*, invades Southern California waterways and displaces native species (CIPC, 2006). As multiple introductions can increase invasiveness, LA and other cities with exotics have the potential to be nuclei of invasion events (Reichard & White, 2001).

5.2. Climatic gradients and population density

Our analyses did not reveal any significant relationships between DFC and vegetation cover or tree biodiversity (Table 5). Instead, population density and income were the strongest influences on perennial vegetation cover (Table 4). In semi-arid regions such as LA, wildland vegetation diversity and abundance is expected to increase near the coast because of moderated temperatures and rainfall (Schoenherr, 1995). Higher temperatures near the city center (Tamrazian et al., 2008; NOAA) were expected to encourage perennial vegetation due to its climate mediating properties (McPherson et al., 2011). Instead, the higher population density near the city center had a limiting effect on cover due to reduced available planting space, a pattern also observed in other urban ecosystems (Godefroid & Koedam, 2007). For biodiversity, climate is more moderate closer to the coast (Patzert et al., 2007), which theoretically allows for a broader palette of tree species than more inland locations. We found no evidence for a coastal to inland tree diversity gradient in our analysis. Instead, we found exotic trees from tropical and deciduous forests across the city. Our results show the importance of social aspects within urban to rural gradient concepts (McDonnell & Pickett, 1990; McKinney, 2002), illustrating that climate gradients or population density alone are insufficient to explain managed vegetation.

5.3. Land-use, luxury, and legacy effects on vegetation cover

Land-use classes had significantly different patterns of herbaceous cover and the Residential land class had high perennial cover ($p < 0.05$; Fig. 2). California has one of the lowest urban tree covers across the U.S. at ~20% (Nowak et al., 2012) and only the Residential land class matches that statewide average at 21%. Salt Lake City, Phoenix, and Baltimore also have similarly high residential perennial cover (Boone et al., 2010; Lowry et al., 2012; Walker et al., 2009), which may reflect the universal appeal and value tree cover has for residential managers (Fraser & Kenney, 2000). Surprisingly, income showed no clear independent effect on Residential tree cover (Table 4) ($R^2 = 0.03$; $p = 0.032$). This may be reflective of how trees are socially perceived in residential neighborhoods. Residents may invest in a few large trees to present an esthetically

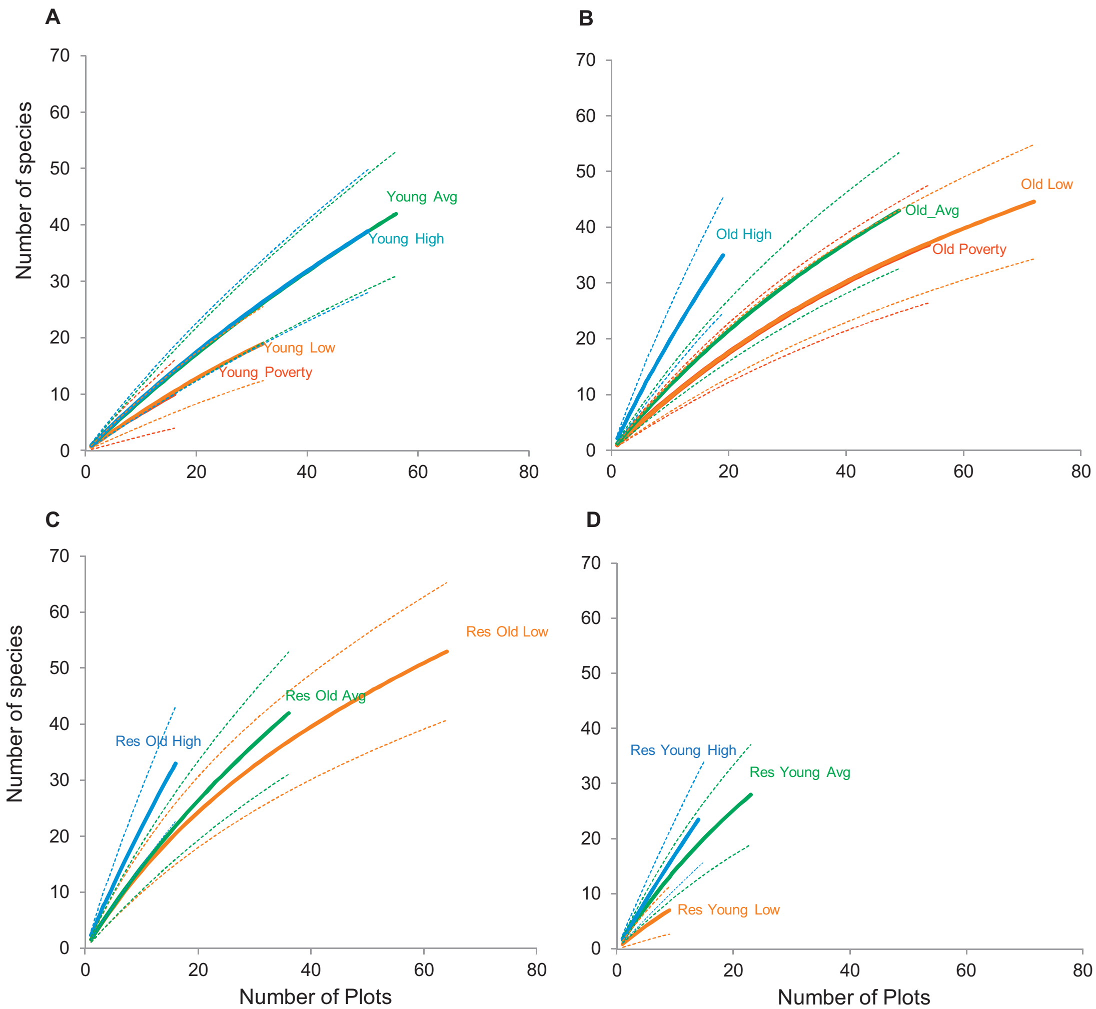

Fig. 6. Interactive effect of age and income on tree biodiversity. Sample-based rarefaction curves for each income class (poverty/low/average/high), separated into age groups. These include all locations (A) and Residential locations (C) built or developed after 1960 and all locations (B) and Residential locations (D) built or developed before 1960. Dotted lines of the same color represent 95% confidence levels. Power law relationship fits and β diversity slopes based on these data are reported in Table 3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

pleasing yard, reflecting social status outside of income (Grove, Cadenasso, et al., 2006; Larsen & Harlan, 2006). Plots in the Commercial/Institutional land class were generally located in lower income neighborhoods (Fig. 3a) with few trees (Table 2).

In all vegetation regression models, predictive skill is low (Table 4), reflecting the intrinsic heterogeneity of urban ecosystems (Cadenasso, Pickett, & Schwarz, 2007), an issue also observed in other arid cities (Lowry et al., 2012; Martin et al., 2004; Walker et al., 2009). Since the size and available space for vegetated cover is dependent on legacies of city and neighborhood planning decisions, using present day manager socioeconomics to predict overall vegetation cover does not take into account historic decisions, in part explaining our low predictive capability in this analysis (Boone et al., 2010; Kirkpatrick et al., 2011).

The generality of our finding of a luxury effect on vegetation cover is corroborated by other studies of urban neighborhoods (Jenerette et al., 2007; Luck et al., 2009). Maintaining vegetation requires large resource and labor investment (Troy et al., 2007). Irrigation is necessary in Southwestern US cities for the maintenance of lawns and other high water use trees. Wealthier households can pay for increasing water costs and overage penalties (Pataki et al., 2011). These wealthy homeowners may influence more than just their own parcels and also contribute to maintenance of nearby public green space to increase neighborhood value (Grove, Troy, et al., 2006; Harlan, Yabiku, Larsen, & Brazel, 2009). A potential feedback to the luxury effect may arise from existing vegetation increasing housing value, therefore increasing the number of high-income homeowners (Mansfield, Pattanayak, McDow, McDonald, & Halpin, 2005).

In contrast, the legacy hypothesis for vegetation cover (Table 1) was not independently observed (Fig. 5c). While age was negatively correlated with both herbaceous and shrub covers (Table 5), residual regression indicated income and density were the only independently significant variables (Table 4) and no independent effect of age was evident. A few of the identified best fit models included age along with income and density to explain vegetation patterns (Table 4), which may have to do with the interrelated nature of those three variables. The only exception to this was tree cover in the Multi-family/Transportation land class, which showed a clear negative linear relationship between tree cover and age (Table 4). Older Multi-family/Transportation areas may exist in over-developed neighborhoods with little room for tree plantings and trees may be detrimentally affected by higher traffic patterns near these plots. The overall disconnect between age and land cover contrasts with patterns in other U.S. cities. In nearby Phoenix, perennial cover decreased in older areas (Hope et al., 2003; Larsen & Harlan, 2006); Salt Lake City and Denver tree cover are related both to income and age (Cook et al., 2012; Mennis, 2006). Variation in the vegetation legacy effect between cities may be linked to both housing booms and regional management.

5.4. Contrasting luxury vs. legacy effects for biodiversity in Southwestern metropolises

The most striking result from our study is the positive linear relationship between tree diversity and housing age in LA without an independent luxury effect (Table 5 and Fig. 5a). Age and income interact in neighborhoods with co-occurring high income, old locations – especially in the Residential land-use class – have the highest α and β diversity (Fig. 6). A lack of single-family homes in very low-income areas made for unclear comparisons between low and average incomes in Residential locations (Fig. 6). In contrast, studies in Phoenix, AZ, show a negative correlative and linear relationship between age and diversity and a strong luxury effect on perennial diversity (Hope et al., 2003; Walker et al., 2009). Temperate and tropical cities in other countries also show evidence of the linear relationship between plant diversity and luxury income (McConnachie, Shackleton, & McGregor, 2008; Melles, 2005). As Phoenix is another arid southwest metropolis with similar socioeconomic range as LA, the potential drivers of biodiversity were expected to be similar. Further, the urban homogenization effect suggests variables influencing diversity should be similar for most large cities (McKinney, 2002). Instead, our results show that contextual properties in urban ecosystems can create regionally varying results (Alberti, 2005; Pickett et al., 2011).

Cultural and historical legacies may explain some of the cross-city divergence in species patterns. LA, founded in 1781, is the oldest major metropolis in the southwestern U.S. Phoenix, Denver, and Salt Lake City were not established until after 1850. Changing marketing trends for certain tree species may have contributed to regional biodiversity. For example, city managers have halted planting the once popular *Ficus microcarpa* in LA neighborhoods because of their destructive nature (Brandt, 2008), though it lines the streets of older downtown LA. Comparatively, older Phoenix neighborhoods contain relatively homogenous high water use lawns and deciduous trees, originally valued for their cooling effect, while the advent of the air conditioner has been followed by xeric landscapes with a variety of desert perennials in newer neighborhoods (Walker et al., 2009).

Socioeconomic differences may also influence why the luxury effect may be dominant in other arid cities. Phoenix, Denver, and Salt Lake City have a lower cost of living than Los Angeles, increasing spending ability for tree maintenance (ACCRA Cost of Living Index, 2010). Tree removal on private property in LA can cost hundreds of dollars because of protections against tree destruction by the LA Urban Forestry Division. Since older houses are often in lower income areas, tree addition instead of subtraction over time may result. Studies in Denver (Mennis, 2006) and Salt Lake City (Lowry et al., 2012) show that age and income are both positively related to tree cover, supporting our result of tree diverse housing tracts in concurrently old and rich neighborhoods (Fig. 6). The very old, very high income plots removed from the income bin analysis represent extremes of these interacting variables, as they contained twice as many species as younger housing tracts of the same income level.

5.5. Implications for planning

Our study highlighted the high α and β diversity of urban trees in an arid city, a striking contrast to the surrounding species-poor wildlands. We also showed how LA tree diversity is primarily related to historical legacies in contrast to Phoenix, AZ. Our results suggest regional planners can better preserve tree biodiversity when accounting for both social and governance characteristics and sustaining existing diversity in older neighborhoods. For instance, policies that encourage tree planting of diverse species in land uses with little private open space (Nowak & Greenfield, 2012) or incentivizing neighborhood tree longevity (Kirkpatrick et al., 2011) can increase urban tree biodiversity. Vegetated cover can provide many ecosystem services for urban residents (McCarthy & Pataki, 2010; Pataki et al., 2011) including such critical functions as improving health and reducing energy usage. Our results show low vegetated cover in poor communities, indicating that they are the most at risk for reduced ecosystem services. For the largest increases in ecosystem services provided by vegetated cover, our findings suggest cities should expand green space in low-income neighborhoods (Huang, Zhou, & Cadenasso, 2011; Jenerette et al., 2011; Millennium Ecosystem Assessment, 2005). Our research opens up avenues to increase ecosystem services and enhance urban biodiversity as part of long-term regional studies across the U.S., providing better comparisons and predictions of vegetation dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2013.04.006.e

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