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RESEARCH ARTICLE

Drivers of plant species richness and phylogenetic composition in urban yards at the continental scale

Josep Padullés Cubino · Jeannine Cavender-Bares · Sarah E. Hobbie · Diane E. Pataki · Meghan L. Avolio · Lindsay E. Darling · Kelli L. Larson · Sharon J. Hall · Peter M. Groffman · Tara L. E. Trammell · Meredith K. Steele · J. Morgan Grove · Christopher Neill

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Abstract

Context As urban areas increase in extent globally, domestic yards play an increasingly important role as potential contributors to ecosystem services and well-being. These benefits largely depend on the plant species richness and composition of yards.

Objectives We aim to determine the factors that drive plant species richness and phylogenetic composition of cultivated and spontaneous flora in urban yards at the continental scale, and how these potential drivers interact.

Methods We analyzed plant species richness and phylogenetic composition of cultivated and spontaneous flora of 117 private yards from six major metropolitan areas in the US. Yard plant species richness and phylogenetic composition were expressed as a function of biophysical and socioeconomic variables and yard characteristics using linear mixed-effects models and spatially explicit structural equation modeling.

Results Extreme temperatures largely determined yard species richness and phylogenetic composition at the continental scale. Precipitation positively

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J. Padullés Cubino (✉) · J. Cavender-Bares ·
S. E. Hobbie
Department of Ecology, Evolution and Behavior,
University of Minnesota, 1479 Gortner Ave., St. Paul,
MN 55108, USA
e-mail: padulles@umn.edu

D. E. Pataki
Department of Biology, University of Utah,
Salt Lake City, UT 84112, USA

M. L. Avolio
Department of Earth & Planetary Sciences, John Hopkins
University, Baltimore, MD 21218, USA

L. E. Darling
The Morton Arboretum, Lisle, IL 60532, USA

K. L. Larson
School of Geographical Sciences and Urban Planning and
School of Sustainability, Arizona State University,
Tempe, AZ 85287-5302, USA

S. J. Hall
School of Life Sciences, Arizona State University,
Tempe, AZ 85287-4501, USA

P. M. Groffman
City University of New York Advanced Science Research
Center at the Graduate Center, New York, NY 10031,
USA

P. M. Groffman
Cary Institute of Ecosystem Studies, Millbrook,
NY 12545, USA

predicted spontaneous richness but negatively predicted cultivated richness. Only the phylogenetic composition of the spontaneous flora was associated with precipitation. The effect of lower temperatures and precipitation on all yard diversity parameters was partly mediated by yard area. Among various socioeconomic variables, only education level showed a significant effect on cultivated phylogenetic composition.

Conclusions Our results support the hypothesis that irrigation compensates for precipitation in driving cultivated yard plant diversity at the continental scale. Socioeconomic variables among middle and upper class families have no apparent influence on yard diversity. These findings inform the adaptation of US urban vegetation in cities in the face of global change.

Keywords Private gardens · Socioeconomics · Horticulture · Homogenization · Spatial autocorrelation · Structural equation modeling

Introduction

A majority of the US population lives in cities (Cohen et al. 2015). Private yards often represent a large fraction of the urban vegetated area, depending on the characteristics of the cities in which they are located (Gaston et al. 2005; Loram et al. 2007; Goddard et al. 2010). Therefore, urban yards contribute to the provisioning of economically important ecosystem services (Cameron et al. 2012; Cook et al. 2012) and general well-being (Freeman et al. 2012). These benefits largely depend on different aspects of yard biodiversity, such as structure or composition (Balvanera et al. 2014). For example, locally adapted plants may have the potential to mitigate episodes of extreme hot temperatures (Tsiros 2010) and flood risk (Dunne et al. 1991). In this regard, understanding the factors and interactions that determine the biodiversity of private yards is crucial to better predict the consequences of global change for urban ecosystem function.

Urban flora comprises both human-cultivated and spontaneously occurring (establishing without human assistance) species (Pearse et al. 2018). Each pool of species is subject to distinct ecological and human influences with consequences at both the local and continental scale (Knapp et al. 2012; Aronson et al. 2016). Spontaneous species are influenced by historical biogeographic processes which can be altered by climate, pollution, soil, and other biophysical constraints (Williams et al. 2009; Groffman et al. 2014). The spontaneous species pool may also increase due to escaped cultivated species (Dehnen-Schmutz 2011), and human management activities such as mowing, fertilizing or the application of herbicide (Dahmus and Nelson 2014). Dispersal limitations in urban environments may prevent species from reaching certain sites and ultimately local spontaneous species pools may be dominated by a few generalists (McKinney 2002; but see Aronson et al. 2014).

The distribution of cultivated plants, unlike that of native vegetation, is influenced by many factors beyond biophysical variables such as temperature or precipitation (Kendal et al. 2012b). For example, cultural and socioeconomic factors, including family income, education and residents' age, influence yard plant diversity (reviewed in Cook et al. 2012). A well-known phenomenon that illustrates the importance of socioeconomics in driving urban flora is the "luxury effect", which describes the tendency of plant diversity in urban greenspace to increase with increasing socioeconomic status (Hope et al. 2003; Martin et al. 2004; Leong et al. 2018). Management choices, usually influenced by residents' beliefs and norms as well as population and housing density (Martini et al. 2015), may also affect the composition of cultivated species, especially in urban yards (Politi Bertoncini et al. 2012).

Despite the vast scientific literature describing the influences of these multiple drivers on urban flora at the local scale (McKinney 2006; Grimm et al. 2008;

T. L. E. Trammell
Department of Plant and Soil Sciences, University of Delaware, Newark, DE 19716, USA

M. K. Steele
Department of Crop and Soil Environmental Sciences, Virginia Tech, Blacksburg, VA 24061, USA

J. M. Grove
Baltimore Field Station, USDA Forest Service, Baltimore, MD 21228, USA

C. Neill
Woods Hole Research Center, Falmouth, MA 02540, USA

Newbold et al. 2015), few studies have examined them at the continental scale (e.g., Kendal et al. 2012b; Jenerette et al. 2016; Pearse et al. 2018), and none has explored the interactions among these factors in driving yard plant diversity and composition.

Evaluating the strength of forces that homogenize or differentiate the urban flora at a continental or even worldwide scale provides critical context for understanding the composition and level of urban biodiversity. Although recent studies have shown that urban areas in disparate regions of the globe retain regionally distinct plant assemblages (Aronson et al. 2014; La Sorte et al. 2014), it has been hypothesized that urban communities have become homogenized at local scales, presenting less taxonomic variation than the native ecosystems they have replaced (McKinney 2006; Groffman et al. 2014). This pattern is hypothesized to occur, in part, because people select a relatively uniform mixture of grass, trees, and ornamental plantings for cultivation (Groffman et al. 2014). This homogenization, however, is not limited to cultivated areas, but also occurs in spontaneous communities (Tredici 2010; Knapp et al. 2012). In the US, there is support for the homogenization of private lawns (Wheeler et al. 2017) and different aspects of urban yard diversity, composition and structure (Knapp et al. 2012; Groffman et al. 2014; Pearse et al. 2018). We seek to disentangle and quantify the role of socioeconomic influences on plant assemblages in urban yards, incorporating phylogenetic composition (phylogenetic dissimilarities among yards) to the study of yard biodiversity at the continental scale.

The phylogenic composition of species in private yards has received relatively little attention (but see Knapp et al. 2012; Pearse et al. 2018), which contrasts with the considerable amount of literature assessing the factors influencing yard composition based on species frequency or cover (Luck et al. 2009; Kendal et al. 2012a; Padullés Cubino et al. 2017) and plant species richness (Hope et al. 2003; Bigirimana et al. 2012; van Heezik et al. 2013). While urban areas often have more species than natural areas (Pyšek 1993; Kühn and Klotz 2006; Grimm et al. 2008), the total number of species in a community may not predict ecosystem properties and functions as well as phylogenetic diversity (DÍaz and Cabido 2001; Cadotte et al. 2008). Moreover, phylogenetic composition incorporates phylogenetic relatedness information into traditional methods of studying communities (e.g., ordination approaches), which normally treat all species as independent and equally dissimilar. Both Knapp et al. (2012) and Pearse et al. (2018) found that, in comparison to species in natural areas, spontaneous yard species were more closely related to each other. This pattern can likely be explained by environmental limitations in urban areas that restrict which species can disperse, become pollinated and persist, affecting some lineages more than others (Knapp et al. 2012). However, the fundamental question remains as to how environmental and anthropogenic factors interact to drive species assembly and distributions at different spatial scales.

Here we present results from a survey of plant species richness and phylogenetic composition in yards of six major US cities (Boston, Baltimore, Los Angeles, Miami, Minneapolis-St. Paul and Phoenix). Previous work from Knapp et al. (2012) established for the Minneapolis-St. Paul region that spontaneous yard species were more closely related to each other than expected and showed reduced phylogenetic diversity in comparison to assemblages in natural areas. The effect of water stress (aridity) on yards' plant species richness and phylogenetic diversity at the city level for both the cultivated and spontaneous pool of species at the continental scale was tested by Pearse et al. (2018), who found no variation in these two variables across regions. Also, Wheeler et al. (2017) explored lawn composition at the continental scale and concluded that both management and regional climate shaped lawn species composition. Here, we substantially expand on these studies by combining socioeconomic data collected at the household level with environmental and yard characteristics to answer the following questions: (1) what factors drive plant species richness and phylogenetic composition of the cultivated and spontaneous flora in urban yards at the continental scale? And (2) to what extent do these factors interact?

For the first question, we hypothesize that plant species richness and phylogenetic composition of both cultivated and spontaneous species pools should positively correlate with climatic stress following well-established diversity-climate relationships (e.g., Currie 1991; Fine 2015). If human preferences, transport, or management (e.g., irrigation) moderate the constraints imposed by climate barriers (Williams et al. 2009; Jenerette et al. 2016), we expect cultivated pools to be less affected by biophysical conditions than spontaneous pools (Fig. 1). Consequently, we anticipate that socioeconomic influences, measured here through income, education and age of residents, should also be more important in explaining cultivated species richness (Hope et al. 2003; Martin et al. 2004) and composition (Luck et al. 2009; Kendal et al. 2012b; Padullés Cubino et al. 2017) than the same parameters for spontaneous pools. In terms of yard characteristics, we suspect that soil nitrate concentration (reflecting fertilizer application) will be associated with lower spontaneous plant species richness and diversity following previous studies assessing fertilizer application or nitrogen deposition on plant diversity in both urban (Dickson and Foster 2011; Wheeler et al. 2017) and natural areas (Isbell et al. 2013). We also posit that the amount of available habitat per plot (i.e., total vegetated area) will positively influence plant species richness within yards (Loram et al. 2008), but that species richness of spontaneous species will increase more with yard area than cultivated species (Knapp et al. 2012). To a lesser extent, we expect yard area to influence phylogenetic composition by increasing the likelihood of encompassing phylogenetically distinct species. In terms of interactions among drivers, we expect (1) yard area to largely mediate the effect of biophysical and socioeconomic gradients on yard plant diversity and (2) soil nitrate concentration to be positively associated with income and education, given previously findings that households with higher socioeconomic status fertilize more (Martini et al. 2015). An expanded version of our research hypothesis can be found in Table S1.

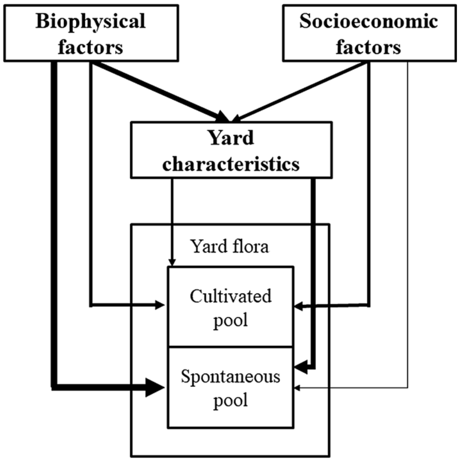

Fig. 1 Schematic representation of the hypothesized influences of the different drivers of yard flora considered in our study. Width of the arrows represents the hypothesized strength of the relationship

Materials and methods

Sample selection

The present work was part of a collaborative research project addressing the ecological homogenization of urban America (Groffman et al. 2014, 2016; Polsky et al. 2014; Hall et al. 2016; Larson et al. 2016; Trammell et al. 2016; Wheeler et al. 2017; Pearse et al. 2018). For this part of the study, surveys were conducted in six metropolitan statistical areas (MSAs): Boston, MA (BOS), Baltimore, MD (BAL), Los Angeles, CA (LA), Miami, FL (MIA), Minneapolis-St Paul, MN (MSP), and Phoenix, AZ (PHX) (Fig. S1). MSAs were chosen to represent six different ecological biomes and major climatic regions across the USA. More details on MSAs characteristics can be found in Trammell et al. (2016).

The study cities were stratified using the PRIZM marketing classification scheme (CLARITAS 2013), which classifies each Census Block Group in the United States into a single group based on analysis of the areal unit's population density, affluence and life-stage (Polsky et al. 2014). Using this primary selection, we first contacted > 100,000 households and identified > 13,500 where the respondent was over 18 years of age and their home had either a front or back yard. Approximately 70% of these respondents completed a 32 multi-part question telephone survey. Telephone interviews were conducted between November 21 and December 29, 2011. Of the 9480 survey respondents, 5797 agreed to be contacted for follow-up fieldwork. To recruit participants for the present study, the agreeable households were first sent information letters and were later contacted by phone (Larson et al. 2016). Different attempts were made during diverse periods of the day until a sample of 20–30 households from each MSA was obtained (see Fig. S1 for final number of households of each MSA). This field-based sample of residents comprised the base vegetation survey data analyzed in this paper.

Data collection

We expect that cultivated and spontaneous plant species richness and phylogenetic composition of the yards would be explained by a set of ten predictor variables (Tables 1 and S1). All response (vegetation parameters) and predictor (biophysical, socioeconomics, and yard characteristics) variables were collected as described in following paragraphs. All statistical procedures were performed in R version 3.4.1 (R Core Team 2017). Significance was established at $\alpha < 0.05$.

Table 1 Summary of response and predictor variables used in the analysis

Variables	Code	Units	Transformations/categories	Mean[a] ± SD	Moran.I
Response					
Cultivated species richness	C.Rich	Number of species		39.87 ± 24.87	0.219***
Spontaneous species richness	S.Rich	Number of species		47.10 ± 34.03	0.374***
NMDS axis 1 for cultivated species	C.MDS1	Dimensionless			0.616***
NMDS axis 2 for cultivated species	C.MDS2	Dimensionless			0.450***
NMDS axis 1 for spontaneous species	S.MDS1	Dimensionless			0.714***
NMDS axis 2 for spontaneous species	S.MDS2	Dimensionless			0.275***
Predictors					
Biophysical					
Maximum temperature of warmest month	MaxT.wm	°C		31.20 ± 5.33	0.902***
Minimum temperature of coldest month	MinT.cm	°C		− 1.60 ± 10.30	0.918***
Mean temperature of driest quarter	MenT.dq	°C		14.43 ± 11.66	0.908***
Precipitation of wettest month	Prec.wm	mm		107.88 ± 58.83	0.928***
Precipitation of warmest quarter	Prec.wq	mm		239.47 ± 172.42	0.938***
Socioeconomics					
Income		$/year	Under 25,000	4 (3.42)	0.133**
			25,000–50,000	17 (14.53)	
			50,000–100,000	48 (41.03)	
			Over 100,000	48 (41.03)	
Education		Level of education	Less than high school	3 (2.56)	− 0.003
			High school graduate	12 (10.26)	
			Some college	20 (17.09)	
			College graduate	48 (41.03)	
			Postgraduate work	34 (29.06)	
Mean age of household residents	Mean age	Years		42.96 ± 15.57	− 0.013
Yard characteristics					
Total vegetated area	log TVA	m^2	log (x)	6.66 ± 1.41	0.245***
Soil nitrate concentration	log NO_3	mg/kg	log (x)	1.60 ± 1.00	0.164***

,*Significant at $P \leq 0.01$ and 0.001, respectively

[a] Actual number of households and % in brackets are provided for income and education variables

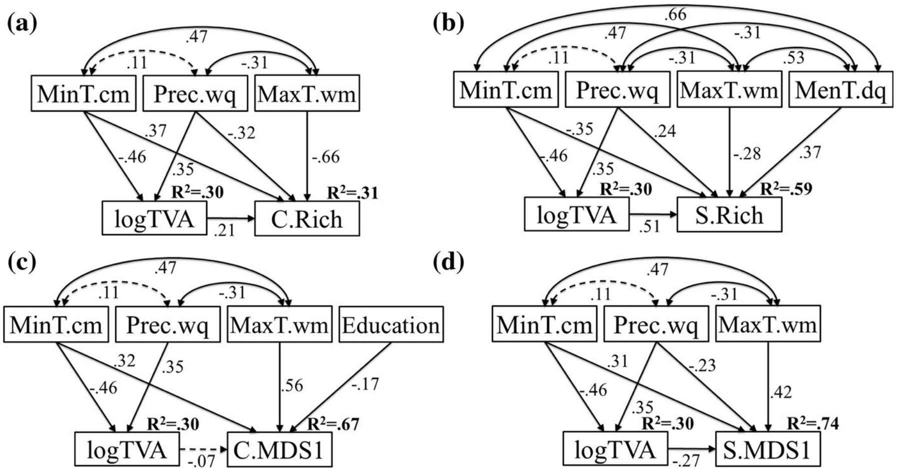

Fig. 2 Final structural equation models explaining cultivated (**a**) and spontaneous (**b**) species richness, and cultivated (**c**) and spontaneous (**d**) phylogenetic composition (NMDS axis 1) of 117 private yards of six major metropolitan areas of the US. R^2 values are shown for the dependent variables. Numbers associated with directional paths are standardized regression coefficients while numbers associated with double-headed arrows are correlation coefficients. Dashed arrows indicate non-significant path coefficients ($P > 0.05$). *C.Rich* = cultivated species richness, *S.Rich* = spontaneous species richness, *C.MDS1* = cultivated phylogenetic composition as predicted from NMDS axis 1, *S.MDS1* = spontaneous phylogenetic composition as predicted from NMDS axis 1, *MinT.cm* = minimum temperature of the coldest month, *MaxT.wm* = maximum temperature of the warmest month, *MenT.dq* = mean temperature of the driest quarter, *Prec.wq* = precipitation of the warmest quarter, *logTVA* = natural logarithm of the total vegetated area

Vegetation

We recorded plant species presence in each yard of a total of 145 households for which socioeconomic data was available. We sampled all areas during the growing season (spring for LA and PHX; summer for BAL, BOS, MIA and MSP). All sampling in BAL, BOS, MIA, MSP, and PHX was done in 2012. All Los Angeles locations were sampled in 2013. The entire area of each yard was surveyed except where there was an unmanaged vegetation or woodland/woodlot component, which was sampled with a 2 m wide transect across the full yard or 100 m, whichever was shorter. While yard plants are often subspecies or cultivars, we did not attempt to classify plants below the species level. For those plants that could not be identified at the species level (~ 15%), the genus was recorded. Species were classified as cultivated or spontaneous based on homeowner interviews and observations of placement; a given species could be documented as both spontaneous and cultivated if different individuals of that species fell into different categories. Land-use and land-use history were considered in the designation. For example, species in woodlots and unmanaged vegetation components were generally considered spontaneous. Species that were not designated as either cultivated or spontaneous in the field were later classified in the lab based on records for the same species in other sampled yards. Species names were matched to The Plant List (http://www.theplantlist.org) version 1.1, using package *Taxonstand* (Cayuela et al. 2017). A phylogeny produced by Qian and Jin (2016), which expands that from Zanne et al. (2013), was used for all phylogenetic metrics, and species missing from this phylogeny were added at the genus level using the 'congeneric.merge' function in R package *pez* (Pearse et al. 2015). Hybrids were reduced at the genus level and species for which there were no phylogenetic data (~ 1.5%) were excluded from the analysis.

Biophysical

We extracted three measures of temperature and two of precipitation from the 30 arc-second WorldClim database (available at http://www.worldclim.org/) for each household: 'MaxT.wm' (maximum temperature of the warmest month), 'MinT.cm' (minimum temperature of the coldest month), 'Ment.dq' (mean temperature of the driest quarter), 'Prec.wm'

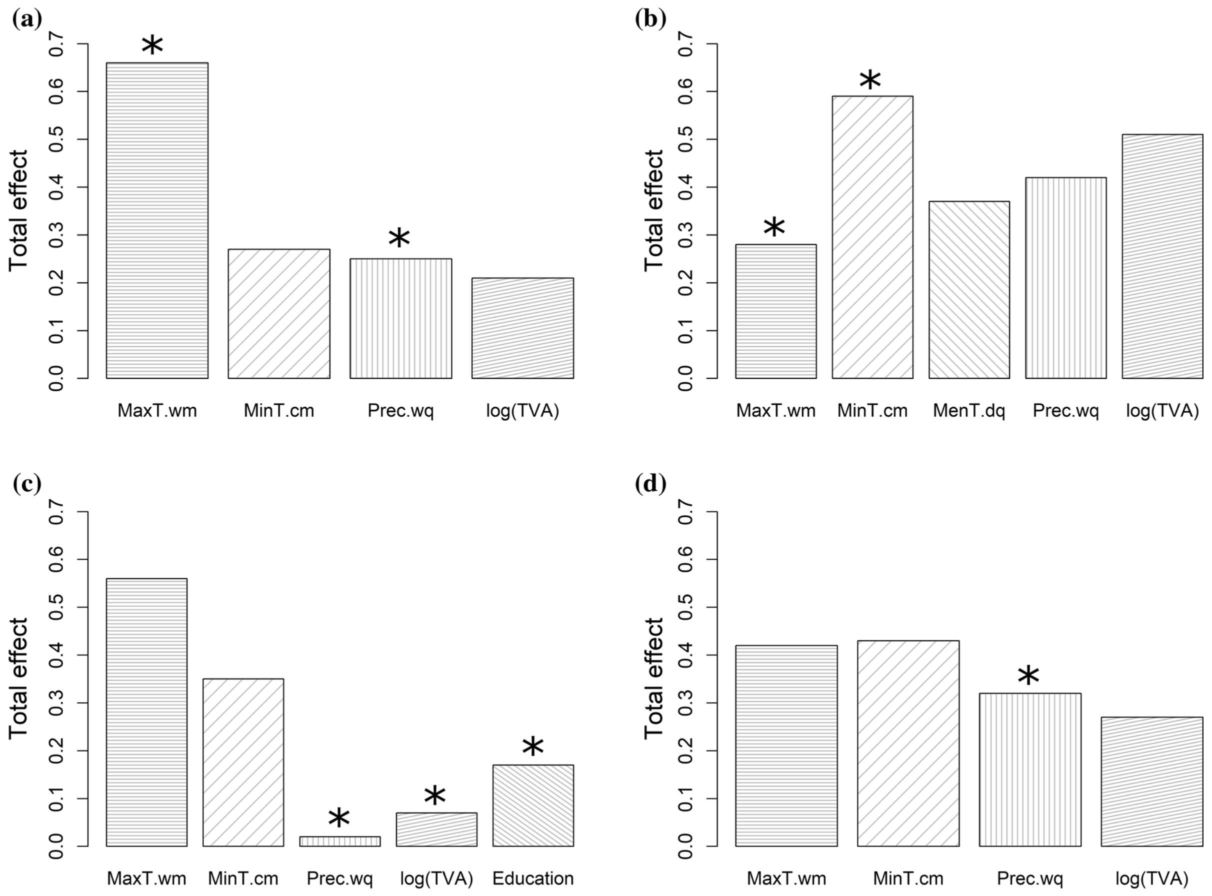

Fig. 3 Total effects of variables on cultivated (**a**) and spontaneous (**b**) species richness, and cultivated (**c**) and spontaneous (**d**) phylogenetic composition (NMDS axis 1) of 117 private yards of six major metropolitan areas of the US. Total effects are defined as the sum of the direct and indirect paths between variables (exclusive of paths denotated by double-headed arrows). To allow for the comparison of total effects among variables, negative coefficients are indicated with asterisk (*). *MinT.cm* = minimum temperature of the coldest month, *MaxT.wm* = maximum temperature of the warmest month, *MenT.dq* = mean temperature of the driest quarter, *Prec.wq* = precipitation of the warmest quarter, *logTVA* = natural logarithm of the total vegetated area

(precipitation of the wettest month), and 'Prec.wq' (precipitation of the warmest quarter) (Table S2). These variables were selected to account for maximum climatic variation among regions and to include the effect of extreme climatic events. Data extraction for each household was performed using R package *rgdal* (Bivand et al. 2017).

Socioeconomics

Different socioeconomic aspects of the household, among other information, were collected during telephone surveys. Particularly, income and the level of education were retained for this part of the study as categorical variables (Table 1). Further, during the summer of 2012, we conducted 134 in-person interviews with the selected residential homeowners. The age of all household members was also collected during the interviews. Due to the skewed nature of the interview sample (Tables S3, S4 and S5, and additional description in the Supporting Information) our analysis is only generalizable to white middle and upper class families in the US.

Yard characteristics

Total vegetated area (TVA) of yards was digitized and measured using orthoimages in ArcGis version 10

(ESRI 2017). Information gathered during the vegetation surveys was also used to complement the digitization process. Two soil cores divided into four soil depth intervals (0–10, 10–30, 30–70 and 70–100 cm) were sampled in each yard during the middle of the growing season in either 2012 or 2013 to obtain soil nitrate (NO_3^-) concentrations. Soil cores were extracted from two random locations on lawn areas when possible. Samples were shipped to the Cary Institute of Ecosystem Studies in Millbrook, NY, where they were extracted with 2.0 M KCl. Extracts were analyzed colorimetrically for NO_3^-- + NO_2^--N and NH_4^+-N. For detailed methods, consult Raciti et al. (2011). Mean values of these measurements in each yard are reported in this study.

Data analysis

A final set of 117 cases was included in the analysis after removing those with missing values and checking the dataset for errors (Fig. S1). TVA and soil nitrate concentration were log-transformed to reduce skewness and improve the normality of the residuals. Plant species richness per yard was defined as the total number of plant species inventoried in the yard. Phylogenetic beta diversity was calculated through the unweighted UniFrac metrics using R package *picante* (Kembel et al. 2010). Based on the phylogenetic tree, the UniFrac metric measures the distance between two or more samples in terms of the overall branch length that is unique to each sample. We then performed a Non-Metric Multidimensional Scaling (NMDS) analysis to visualize phylogenetic distances between every pair of yards (constrained to two dimensions, using R package *vegan*; Oksanen et al. 2017). In traditional species composition ordinations, where species are treated independently, if two closely related species have disjunct distributions, they could cause communities to be very different. However, using a phylogenetic approach, their close relationship will cause these communities to be more closely clustered (see Figs. S2 and S3). Plant species richness and phylogenetic composition (phylogenetic dissimilarities among yards; site scores of the two NMDS axes) of the two targeted categories (cultivated and spontaneous species) constituted the response variables in this study.

Species distribution data is inherently spatially structured and thus especially affected by spatial autocorrelation (Guisan et al. 2006; Kissling and Carl 2007). Spatial autocorrelation in ecological data is a common phenomenon as observations at closer locations are usually more similar that would be expected by chance (Legendre 1993; Legendre and Legendre 1998). Spatial dependencies in yard floras may be present because households' land management activities may not occur in socio-spatial isolation. For example, householders may be affected by their neighbors' behaviors (Nassauer et al. 2009). Moran's I implemented in the R package *ape* (Paradis et al. 2004) was used to check for spatial autocorrelations between response and predictor variables and geographic distances between each pair of yards. Distances in kilometers between each location were calculated using the great-circle method in the R package *fields* (Nychka et al. 2017). Correlograms for response variables were produced using the R package *letsR* (Vilela and Villalobos 2015).

We used linear mixed-effect models with 'lme' function in R package *nlme* (Pinheiro et al. 2018) to investigate relationships between response variables and continental (biophysical) and local-scale (socioeconomics and yard characteristics) predictor variables separately. Interactions among both sets of predictors were investigated further using spatially explicit structural equation models. In all models the random effect of 'MSA' was included to cluster households in different MSAs and account for spatial autocorrelation. Variograms incorporating geographic structure did not improve the models fit in any case and therefore were not used in this analysis. Because we initially considered all possible sets of predictors to be equally likely to explain variation in dependent variables, all possible combinations of variables together with the null model were considered in the final candidate set of models. Yard characteristics were also modeled as a function of biophysical and socioeconomic variables separately using the same technique. Multicollinearity was assessed using the Variance Inflation Factor (VIF) with function 'vif' in the R package *usdm* (Naimi et al. 2014). Models with $VIF > 5$ were discarded and subsequently removed from further analysis (Hair et al. 1995). We calculated the AICc (the small-sample-size-corrected Akaike's Information Criterion; Anderson 2008) values of each candidate model set and ranked them by their Akaike weights using the R package *AICcmodavg* (Mazerolle 2017). The function 'modavgd' in the same package was used to compute the standardized model-averaged coefficients (Mazerolle 2017). To assess model fit, we calculated marginal and conditional R^2. Since our primary focus was on the significant factors determining yard diversity, the results from this part of the analysis have been allocated to the Supporting Information.

Spatially explicit structural equation modeling (SE-SEM)

Direct and indirect influences of significant predictors on response variables were further analyzed using spatially explicit structural equation modeling (SE-SEM) in R packages *sesem* (Lamb et al. 2014) and *lavaan* (Rosseel 2012). SEM models were built only for vegetation response variables for which interactions with yard characteristics were detected in regressions: plant species richness and phylogenetic composition (NMDS axis 1) of both cultivated and spontaneous species (Tables S8 and S9). A set of candidate SEM models were produced for each of these response variable using all predictors included in models with ΔAICc < 2, as well as only significant predictors (Table S11). Only models with the lowest AIC are shown here.

In general, SEM provides a more appropriate means of specifying causal relationships when there is substantive information available to guide the development of theoretically justified models (Grace 2006). Compared with techniques such as multiple regression, SEM allows a closer inspection of indirect effects and the interactions among factors (Grace 2006, 2008). Although SEM is commonly applied in ecology, the spatial information commonly found in ecological data is difficult to model in a SEM framework. To deal with this issue, SE-SEM incorporates spatially explicit dependent causal relationships and provides readily interpretable plots of the change in path coefficients across scale (Lamb et al. 2014). In this regard, while standard SEM is based on the analysis of variance–covariance matrices, the SE-SEM method fits the same SEM model to a series of variance–covariance matrices calculated for different lag distances (Lamb et al. 2014). Since our primary research interest on spatial autocorrelation at the local scale, lag distances in SE-SEM were assessed for the first 600 km, which largely exceeds the maximum distance found between households within any MSA.

SEM uses maximum likelihood to solve path equations simultaneously (Grace 2006, 2008). In the analysis, we present standardized path (or connection) coefficients, which allows comparison of path strengths (Grace 2008). We also report model fit as Chi square and its associated *P* value, with *P* values greater than 0.05 indicating an acceptable fit (Hooper et al. 2008). As Chi square can be influenced by sample size, we also report the root mean square error of approximation (RMSEA), where smaller values indicate more parsimonious models, and values < 0.07 suggest an adequate model fit (Hooper et al. 2008).

Results

The most frequently cultivated plant families in each MSA were Poaceae and Rosaceae for BAL, Poaceae and Asteraceae for BOS, Crassulaceae and Asteraceae for LA, Arecaceae and Asparagaceae for MIA, Asteraceae and Rosaceae for MSP, and Fabaceae and Poaceae for PHX (Table S6). Poaceae and Asteraceae were the most frequent spontaneous plant families for all MSAs, except for MSP where Asteraceae and Rosaceae dominated (Table S7).

The NMDS analyses ordinated both cultivated and spontaneous phylogenetic dissimilarities with a final stress solution of 0.165 and 0.180, respectively (Fig. S2). Moran's I test results revealed significant spatial autocorrelation in all response and predictor variables, except for education and the mean age of the residents (Table 1; Fig. S4). Highest Moran's I values for response variables corresponded to spontaneous species NMDS axis 1 (0.71) and cultivated species NMDS axis 1 (0.62). In terms of predictor variables, values of Moran's I were highest for the precipitation of the warmest quarter ('Prec.wq') (0.94) and the precipitation of the wettest month ('Prec.wm') (0.93).

Spatially explicit structural equation models

The nonspatial final SEM models had an adequate fit for both cultivated ($\chi^2 = 0.029$; df = 1; P = 0.864; RMSEA = 0.000) and spontaneous ($\chi^2 = 1.060$; df = 2; P = 0.589; RMSEA = 0.000) species richness, and cultivated ($\chi^2 = 9.018$; df = 6; P = 0.173; RMSEA = 0.066) and spontaneous ($\chi^2 = 0.029$; df = 1; P = 0.864; RMSEA = 0.000) phylogenetic composition as predicted by NMDS axis 1 (Fig. 2). The influence of the minimum temperature of the coldest month (‘MinT.cm’) and ‘Prec.wq’ on logTVA explained 30% of the variation. ‘MinT.cm’ exhibited a negative direct effect on logTVA ($\beta = -0.46$) and ‘Prec.wq’ a positive direct effect ($\beta = 0.35$) (Fig. 2).

While the model for cultivated species richness explained 31% of the variation, the model for spontaneous species richness explained up to 59% (Fig. 2a, b). ‘MinT.cm’ had a positive direct effect on cultivated species richness ($\beta = 0.37$) and ‘Prec.wq’ a negative direct effect ($\beta = -0.32$). The sign of path coefficients changed for spontaneous species richness, with ‘MinT.cm’ having a negative direct effect ($\beta = -0.35$) and ‘Prec.wq’ a positive direct effect ($\beta = 0.24$). The maximum temperature of the warmest month (‘MaxT.wm’) showed a negative direct effect on both cultivated ($\beta = -0.66$) and spontaneous ($\beta = -0.28$) species richness. The mean temperature of the driest quarter (‘MenT.dq’) exhibited a positive direct effect on spontaneous species richness ($\beta = 0.37$). LogTVA had a positive direct effect on both cultivated ($\beta = 0.21$) and spontaneous ($\beta = 0.51$) species richness. Highest total effects (standardized coefficients > 0.5) corresponded to ‘MaxT.wm’ for cultivated species richness, and ‘MinT.cm’ and logTVA for spontaneous species richness (Fig. 3).

SEM models for cultivated and spontaneous phylogenetic composition NMDS axis (1) explained 67% and 74% of the variation, respectively (Fig. 2c, d). Both ‘MaxT.wm’ and ‘MinT.cm’ had a significant direct effect on both cultivated ($\beta = 0.56$ and $\beta = 0.32$, respectively) and spontaneous ($\beta = 0.42$ and $\beta = 0.31$, respectively) phylogenetic composition. ‘Prec.wq’ only had a significant direct effect on spontaneous phylogenetic composition ($\beta = -0.23$). Education showed a significant direct effect on cultivated phylogenetic composition ($\beta = -0.17$). The influence of logTVA on plant phylogenetic composition was only significant for the spontaneous pool ($\beta = -0.27$). Highest total effects (standardized coefficients > 0.5) corresponded to ‘MaxT.wm’ for cultivated phylogenetic composition (Fig. 3). ‘MinT.cm’ and ‘MaxT.wm’ had the highest total effects of any variable on spontaneous phylogenetic composition (0.43 and 0.42, respectively) (Fig. 3).

The spatially explicit models had a reasonably good fit across all lag distances (Figs. S5, S6, S7 and S8). There were no average modification indices greater than 4, further demonstrating that the path model was valid across all lag distances (Lamb et al. 2014).

Discussion

Factors influencing yard vegetation richness

Cultivated and spontaneous species richness was driven largely by climatic gradients in white middle and upper class households. For example, cultivated species richness observed in yards decreased as the maximum temperature of the warmest month, a proxy for summer thermic severity, increased (even when yard area was kept constant) and the minimum temperature of the coldest month, a proxy for winter thermic severity, decreased. Thus, the number of cultivated species decreased with increasing extreme thermic conditions, likely reflecting limited availability of ornamental species adapted to severe thermic episodes (Kendal et al. 2012b; Jenerette et al. 2016; Pearse et al. 2018). Interestingly, the amount of precipitation of the warmest quarter, which could be interpreted as inversely related to water stress in the summer months, impacted cultivated species richness such that there were more cultivated species in yards located in water-stressed areas than those in areas receiving more summer rainfall. This result supports the idea that irrigation may overcome water limitation to a large extent, supporting a much larger pool of cultivated species in arid regions than would otherwise persist and providing evidence for previously hypothesized patterns (Groffman et al. 2016). Thus, consistent with Kendal et al. (2012b), precipitation gradients may not be appropriate predictors for cultivated species richness unless all other water sources are accounted for. In this regard, although research has studied how irrigation practices impacts urban flora, more comparative research is needed to understand continental-scale impacts, including in cool, dry regions.

In accordance with previous studies (Loram et al. 2008; Marco et al. 2008; van Heezik et al. 2013), the number of cultivated species was positively associated with yard area. The strong positive association between yard vegetated area and species richness might be attributed to a greater diversity of yard components (e.g., lawn, wetlands, flower beds, etc.) in larger yards, as found by Smith et al. (2005) in yards in the UK. Furthermore, we have demonstrated that yard area mediates the effect of climatic gradients on yard vegetation at a wide range of scales. In particular, yards located in drier (lower ‘Prec.wq’) and hotter (higher ‘MinT.cm’) regions tend to have less vegetated surface, which appears to result in fewer cultivated and spontaneous species. No associations were found between yard area and socioeconomic factors, although Troy et al. (2007), using remote sensing data, found that vegetated yard area in Baltimore was determined by the sociodemographic characteristics of homeowners. In our study, such a relationship could not be established at the continental scale, possibly due to the bias of our dataset towards households in higher socioeconomic classes. Likewise, the positive relationship between household income and yard plant species richness, first described by Hope et al. (2003), i.e., ‘luxury effect’, and reaffirmed by many others (Martin et al. 2004; Bigirimana et al. 2012), was not found in our study, suggesting that the influence of socioeconomic factors varies among geographical regions and spatial and temporal scales. For example, Brelsford and Abbott (2017) reported for the city of Las Vegas a trend towards a decline in the vegetation area in households in neighborhoods established between 1997 and 2007. Also, in a recent review examining the ‘luxury effect’, Leong et al. (2018) concluded that this phenomenon is amplified in arid cities and as neighborhoods age. Nevertheless, by accounting for spatial autocorrelation and considering the effect of different lag distances in our models, we now have a better understanding of trans-scale drivers. Further research is needed to test the consequences of these drivers across an expanded range of socioeconomic classes.

In terms of spontaneous species, the number of species increased as both the maximum temperature of the warmest month (more extreme hotter conditions) and the minimum temperature of the coldest month (more extreme colder conditions) decreased. Extreme climate variations may limit the distributions of plant species across a wide range of habitats (O’brien et al. 2000; Jenerette et al. 2016), including in urban yards. While higher summer temperatures seem to impose a constraint on the number of spontaneous species, lower winter temperatures appear to promote spontaneous plant species richness. This finding suggests that the range of coolest temperatures for the US cities included in our study were not extreme enough to limit the number of spontaneous species growing in the yards. Moreover, yards located in areas with the lowest minimum temperatures are also those not experiencing extreme hot conditions in the summer. The high correlation between the minimum temperature of the coldest month and the mean temperature of the driest quarter (‘MenT.dq’) also reinforces this idea. In contrast to cultivated species richness, summer precipitation showed a positive influence on the number of spontaneous species, suggesting that precipitation gradients are important in explaining spontaneously assembled vegetation in urban yards. Nonetheless, microclimatic conditions in yards—although not measured in this study—may have a critical influence beyond the effects of macroclimate and may favor certain species within each pool.

As previously stated, the total effects of extreme cold conditions and summer precipitation on the number of spontaneous species were also partly mediated through the total vegetated area of the yard, indicating that climate and yard area covary. Furthermore, the reduction in total vegetated area in drier and hotter areas could also be associated with a reduction in lawn surface (Hilaire et al. 2008). Previous studies have shown that lawn species that are not the primary planted turf grass are usually dominated by spontaneous forbs (Politi Bertoncini et al. 2012). Wheeler et al. (2017) found a positive association between lawn species richness and annual rainfall, but not with annual mean temperature.

Factors influencing yard vegetation phylogenetic composition

Our study showed that the phylogenetic composition of both the cultivated and spontaneous pool of species reflects the influence of extreme climatic variation (Williams et al. 2009). As expected, these climatic influences explained more variation for spontaneous than for cultivated species (McKinney 2006). According to our ordination results, phylogenetic composition of cultivated plants in yards of Baltimore, Boston and Minneapolis-Saint Paul were more closely related than were those from the three southern urban regions: Los Angeles, Phoenix and Miami. These compositional differences between the two groups of cities were less pronounced for the spontaneous pool of species, suggesting that spontaneous species in the study yards were phylogenetically more closely related than cultivated species across the continent. Pearse et al. (2018) showed that cultivated and spontaneous species in most of the same yards we studied here come from a more limited set of lineages than do natural area species, resulting in phylogenetic similarity among cities, which they interpreted as a form of homogenization. This is most likely because of the high number of exotic species in urban yards, which can increase the phylogenetic relatedness of spontaneous yard flora in comparison to natural areas (Knapp et al. 2012). Cosmopolitan species tend to have a higher affinity for urban areas (Knapp et al. 2008), and they tend to represent lower taxonomic diversity than rare species (Ricotta et al. 2008).

The phylogenetic composition of cultivated species (both NMDS axis) was best explained by two of our biophysical variables describing extreme thermic events: the maximum temperature of the warmest month and the minimum temperature of the coldest month. This is in line with Kendal et al. (2012b), who explored the distribution patterns for all types of cultivated urban flora at the global scale and concluded that mean annual temperature was the most important predictor of cultivated composition. Jenerette et al. (2016) also found that the composition of urban tree communities across the US and Canada correlated with minimum winter temperature and annual precipitation. Moreover, lawn species in warm and cool regions across the US have been found to group separately when species composition is considered (Wheeler et al. 2017). Surprisingly, none of our measures of precipitation had a significant effect on cultivated phylogenetic composition, raising the hypothesis that irrigation may be compensating for precipitation (Groffman et al. 2016). It is worth highlighting that while our sampling was deliberately conducted during the period of peak flower activity, sampling during other time periods could result in different findings due to phenological variation and contrasting emergence times of different plant species.

Education was the only socioeconomic variable with a significant effect on cultivated phylogenetic composition. Although previous studies have shown the relevance of education in structuring yard floras (Luck et al. 2009; van Heezik et al. 2013; Padullés Cubino et al. 2017), none have examined this effect at the continental scale. Luck et al. (2009) pointed out that it is difficult to determine the direction of causality with regard to the relationship between education and plant diversity, even though education is assumed to indicate potential knowledge of land management and environmental issues. In our study, a link between education level and environmental awareness was not established, although this remains a plausible explanation for the significant effect of education. Furthermore, the underrepresentation of lower income and education segments in the study limits our ability to generalize the association between education and yard composition to a broader cross-section of the urban population. Additional social science research is needed to gain insight into the processes underlying the relationship between education and vegetation composition (i.e., how exactly knowledge and education affect plant choices) across all sectors of society that may illuminate mechanisms to promote environmentally friendly urban yards. Time lags and legacy effects of socioeconomic factors are also important to consider in future research on the distribution of yard flora across spatial scales. Recent studies suggest that spatial distribution of urban vegetation may be better predicted by previous rather than current socioeconomic factors (Luck et al. 2009; reviewed in Cook et al. 2012).

The entire set of biophysical variables significantly affected at least one component of spontaneous phylogenetic composition, indicating that the spontaneous pool of species is more susceptible to environmental change than the cultivated pool. In intensively managed landscapes, like urban yards, humans modify these filters, facilitating certain species and creating novel conditions that result in communities with a species composition that has not existed before (Hobbs et al. 2009; Aronson et al. 2016). Although no association was found between socioeconomic variables and spontaneous phylogenetic composition, other anthropogenic activities such as cultivation, weeding or herbicide application might have a direct effect (Polsky et al. 2014). In this regard, yard area was also revealed as a significant factor controlling for spontaneous phylogenetic composition. The remaining spatial variability in one of our models (S.MDS1) suggested that other traditional ecological processes possessing spatial structure, such as colonization, extinction and competition, and not included in this study, partly explain species distributions (Leduc et al. 1992).

Conclusion

Biophysical variables representing extreme climatic variation had a significant influence on yard vegetation diversity. This influence was much stronger for yard phylogenetic composition than for plant species richness. Also, we have demonstrated using data grouped at the household level that extreme biophysical conditions affect cultivated and spontaneous pools differently. For example, the lack of positive association between precipitation and cultivated yard diversity supports the hypothesis that irrigation is compensating for this environmental stress. Furthermore, the explanatory power of our models was larger for all spontaneous diversity parameters than for cultivated diversity, likely reflecting the importance of homeowners' actions in structuring cultivated yard floras. This idea is also supported by the higher spatial autocorrelation found in all spontaneous species response variables when compared to that of cultivated species.

To our knowledge, no study to date has examined the influence of socioeconomic factors on yard vegetation diversity at the continental scale. Contrary to our hypothesis, socioeconomic factors had no effect on species richness, and very little effect on cultivated phylogenetic composition. Due to the characteristics of our dataset, this conclusion only applies to middle and upper class households; further research should elucidate the extent to which it holds across a broader range of socioeconomic brackets. As expected, yard area largely mediated the effect of biophysical variables on yard species richness and, to a lesser extent, on phylogenetic composition.

SEM models provided an accurate description of the influences and interactions between predictor and response variables. We show these interactions for private urban yards, for the first time, and find them to hold at all considered lag distances, underscoring the relevance of our conclusions at the continental scale. These findings can inform the adaptation of US urban vegetation in cities in the face of global change.

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