Climate tolerances and trait choices shape continental patterns of urban tree biodiversity

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ABSTRACT

Aim We propose and test a climate tolerance and trait choice hypothesis of urban macroecological variation in which strong filtering associated with low winter temperatures restricts urban biodiversity while weak filtering associated with warmer temperatures and irrigation allows dispersal of species from a global source pool, thereby increasing urban biodiversity.

Location Twenty cities across the USA and Canada.

Methods We examined variation in tree community taxonomic diversity, origins and production of an aesthetic ecosystem service trait in a cross-section of urban field surveys. We correlated urban tree community composition indicators with a key climate restriction, namely mean minimum winter temperature, and evaluated alternative possible drivers: precipitation, summer maximum temperature, population size and the percentage of adults with a college education.

Results Species accumulation curves differed substantially among cities, with observed richness varying from 22 to 122 species. Similarities in tree communities decreased exponentially with increases in climatic differences. Ordination of tree communities showed strong separation among cities with component axes correlated with minimum winter temperature and annual precipitation. Variation among urban tree communities in richness, origins and the provisioning of an aesthetic ecosystem service were all correlated with minimum winter temperature.

Main conclusions The urban climate tolerance and trait choice hypothesis provides a coherent mechanism to explain the large variation among urban tree communities resulting from an interacting environment, species and human decisions. Reconciling the feedbacks between human decision making and biophysical limitations provides a foundation for an urban ecological theory that can better understand and predict the dynamics of other linked biotic communities, associated ecosystem dynamics and resulting services provided to urban residents.

Keywords Biodiversity, ecosystem service, environmental filter, macroecology, tree, plant trait, urban.
INTRODUCTION

Cities harbour novel communities of extensive plant biodiversity that are partially to completely created by humans and include naturalized species in open spaces and cultivated species in highly managed spaces (Savard et al., 2000; Pickett et al., 2001; Hobbs et al., 2006; Knapp et al., 2012). Together, the naturalized and cultivated components of urban plant biodiversity are connected to broader community assembly processes through influences on trophic and competitive interactions (Faeth et al., 2005) and to ecosystem functioning through influences on biogeochemical cycling and energy flows (Kaye et al., 2004). The ecosystem services provided by naturalized and cultivated urban vegetation are highly valued by many urban residents and include climate regulation, food production and aesthetic opportunities (Lovell & Taylor, 2013; Avolio et al., 2015a; Jenerette et al., 2016). While urbanization frequently leads to local extinctions in plant communities (Hahs et al., 2009), it also often leads to complex patterns of biodiversity through the importation of new species (Smith et al., 2006; Clarke et al., 2013). Improved understanding of the processes limiting biodiversity and shaping the composition of urban vegetation will provide a foundation for a more general theory of urban plants and their closely connected community and ecosystem processes.

The species distributions of both naturalized and cultivated plants vary among cities, and this variation has led to alternative hypotheses for describing urban plant macroecology. In some analyses urban plant community distributions are broadly organized along global temperature and biome gradients (Kendal et al., 2012a; Nock et al., 2013; Ramage et al., 2013; La Sorte et al., 2014) consistent with the widely used hardiness zone classifications (e.g. the USDA hardiness map; http://planthardiness.ars.usda.gov/PHZMWeb/). These findings support an urban biome matching hypothesis, which predicts a high contribution of species to the urban community that are regionally native or from a biome similar to that city’s geographical location (Aronson et al., 2014; La Sorte et al., 2014). Alternatively, the global reach of human commerce (Hulme, 2009) and increasing convergence of urban abiotic conditions (Pouyat et al., 2007; Jenerette & Potere, 2010; Hall et al., 2016) have led to the development of an urban homogenization hypothesis. This hypothesis predicts urban communities include less variation in species than corresponding native analogue communities (McKinney, 2006; Knapp et al., 2012; Groffman et al., 2014).

Neither of the dominant hypotheses can accommodate the extreme diversity of urban vegetation found both among and within cities. In Murmansk, Russia, a high-latitude European city within a cold boreal biome, the tree community includes fewer than 20 species, which are all strongly matched to the local subarctic climate conditions (McBride & Douhovnikoff, 2012). Conversely in Los Angeles, CA, a highly irrigated city in a dry subtropical climate and Mediterranean biome, the urban tree community includes more than 200 species, representing nearly all the world’s biomes and more than an order of magnitude more tree species than the native analogue community (Clarke et al., 2013; Pincetl et al., 2013). These comparisons highlight the importance of biome matching in some regions and biome insensitivity in other regions. Similarly, the low number of expected shared species between these cities and the importation of species from new biomes suggest a restricted influence of urban homogenization on tree communities. Reconciliation and extension of alternative hypotheses describing urban plant macroecology are needed.

Here we propose a climate tolerance and trait choice (CT-TC) hypothesis of urban community assembly that includes cultivated and naturalized components and can account for the large variation in urban plant communities. We hypothesize that the interaction between climate-imposed restrictions moderated by local land management activities such as irrigation and the desire for specific ecosystem services serve as dual regulators of urban tree biodiversity. When evaluating causes of species distributions, a framework of community assembly filters has been used in many contexts to relate plant traits to species presence and survival through a series of filters associated with distinct processes, including dispersal, habitat suitability and biotic interactions (Funk et al., 2008; Williams et al., 2009; Lebrija-Trejos et al., 2010; Lasky et al., 2013). In urban ecosystems, both biological (Duncan et al., 2011; Nock et al., 2013) and ecosystem service-based (Kendal et al., 2012b; Pataki et al., 2013; Avolio et al., 2015a) traits can be important determinants of plant biodiversity. Combining filters, traits and human choice, the CT-TC hypothesis predicts that when an environmental filter is strong then urban vegetation will primarily include species and ecosystem service-based traits from local biomes. However, when the filter is weak and coupled with the potential for global urban dispersal, CT-TC predicts that urban plant species will originate from non-local biomes and include an ecosystem service trait, showy reproductive parts, that is otherwise restricted in the local native community. That is, physiological and biotic constraints on plant growth and survival interact with the desire of urban residents for plant traits and provisioning of environmental and cultural benefits for urban residents.

Frequently, climate is a critical filter for community richness and composition (Currie & Paquin, 1987; Kleidon & Mooney, 2000; Francis & Currie, 2003; Qiao et al., 2015). Notably, while a climate-based physiological tolerance hypothesis has been suggested from both theory (Kleidon & Mooney, 2000) and observations (Wang et al., 2011), dispersal limitation may result in fewer species than predicted in warmer environments (Currie et al., 2004). In urban environments, the potential for global transportation of trees may overcome effects of dispersal limitation and emphasize the effects of climate tolerances. Potential climate filtering processes could include responses to the frequency of freezing, maximum temperatures or precipitation. We expect the influence of irrigation to mitigate filtering through both high maximum temperatures and limited precipitation. However, cold temperatures and their influence on species freezing
tolerances (Wang et al., 2011) are not similarly mitigated through management and may represent a fundamental constraint on the distribution of urban plant biodiversity.

We evaluate predictions from CT-TC using a continental scale cross-section of urban tree plot surveys. Trees influence community dynamics and ecosystem functioning, grow from both natural reproduction and intentional propagation, persist across multiple growing seasons and provide many valued ecosystem services. Urban tree communities provide an important starting point for the evaluation of macroecological hypotheses of urban vegetation. We tested the prediction that a city's minimum winter season temperature is positively correlated with biodiversity, species from outside the local biome, non-native species and the frequency of trees with showy reproductive parts. This suite of dependent variables provides insights into the variation of tree community composition and the production of a widely desired aesthetic ecosystem service (Kendal et al., 2012b; Pataki et al., 2013; Avolio et al., 2015a; Clarke & Jenerette, 2015). As a further test, we also evaluated the possible role of alternative sources of environmental and social variation that have been found to be important drivers of urban plant communities at within city scales (Hope et al., 2003; Avolio et al., 2015b).

METHODS

Database compilation

We compiled data from 20 cities in the United States and Canada where randomized field surveys had been conducted that included both naturalized and cultivated trees (Fig. 1, Table S1 in the Supporting Information). This network of 20 cities spans a climate gradient from cold and wet (e.g. Minneapolis, MN) and cold and dry (e.g. Kelowna, BC) to hot and wet (e.g. Tampa, FL) and hot and dry (e.g. Phoenix, AZ) sites. All surveys included in the analysis were carried out between 2000 and 2010. Each survey inventoried all trees occurring within sampling plots distributed through the region. All but two of the surveys (Phoenix and Boston, MA) were conducted using USDA Urban Forest Inventory protocols (Nowak et al., 2003). These protocols used circular 0.04-ha plots distributed in a stratified random sampling design based on local land use. For three surveys, Kelowna, Tampa and Roanoke the relative abundances of the species were obtained from Yang et al. (2015); for the remaining sites the original plot data surveys were used directly. The Phoenix and Boston surveys also used randomized field plot designs, although they differed in their stratification and plot size. Phoenix was sampled using 0.09-ha plots distributed in a spatially stratified design (Hope et al., 2003). Boston was sampled using 0.07-ha plots arranged along urbanization transects (Raciti et al., 2012). For both Phoenix and Boston, the extent of sample data was restricted to urban and suburban regions by visual inspection of each point on high-resolution imagery (Google Earth). Two surveys, Orange County (CA) and Riverside (CA), were focused on an urbanized subset of the county and centred on the cities of Irvine (CA) and Riverside (Avolio et al., 2015b). Differences between sampling designs, including definitions of ‘urban’, placement of plots and plot size, introduce some uncertainties. Nevertheless, the intensity of sampling within all cities, the broad bioclimatic distribution of cities and care in harmonizing the datasets yields a powerful test of alternative hypotheses of urban tree community organization.

For the entire dataset we adopted a standard definition of ‘tree’: a species consistently cultivated as an upright woody plant with a defined canopy and a central bole. These criteria were checked against online plant datasets including the USDA Plants Database (http://plants.usda.gov), the Flora of China (http://efloras.org/) and the Germplasm Resources Information Network (GRIN; http://www.ars-grin.gov). Only species fitting the definition of a tree were included in analyses.

For each tree species we assigned geographical origin and trait characteristics. To identify if tree species were native to tropical biomes we used a combination of information on biome distributions, species ranges and habitats. While our characterization is coarse-scale in nature because detailed species range maps were unavailable for many species in our dataset, especially those from outside North America or Europe, this approach should allow the binary identification of tropical origin more readily than a complete biome classification. We based our delineation of tropical biomes using previously developed mapping (Olson et al., 2001). We then used provincial-level ranges, habitat information and expert knowledge to identify trees with tropical origins. The natural ranges of individual species were identified to a country in the GRIN database from which we identified the corresponding biome. When species were found in more than one

Figure 1 Geographical distribution of cities included in study and 30-year normals for minimum January temperature. Each city is represented by a two-letter code: BA, Baltimore, MD; BO, Boston, MA; CH, Chicago, IL; DC, Washington, DC; ED, Edmonton, AB, Canada; KE, Kelowna, BC; LA, Los Angeles, CA; LO, London, ON, Canada; MN, Minneapolis, MN; OC, Orange County, CA; PH, Philadelphia, PA; PX, Phoenix, AZ; RA, Raleigh, NC; RI, Riverside, CA; RO, Roanoke, VA; SB, Santa Barbara, CA; SF, San Francisco, CA; SY, Syracuse, NY; TA, Tampa, FL; TO, Toronto, ON, Canada.
biome and included a tropical biome the species was coded as having a tropical origin. For Australia and the USA, GRIN also provided the states where the species were native and allowed refined biome classification. Otherwise, if the country of origin included multiple biomes a more refined range distribution was obtained from the Urban Forests Ecosystem Institute (UFEI) and Flora of China databases. For each city we also assessed if tree species were native to the specific state using the state ranges identified in GRIN and naturalized ranges identified from the USDA Plants Database.

For biological trait classification we used the UFEI Selectree tool (http://selectree.calpoly.edu), from which we developed a metric to identify an aesthetic ecosystem service trait by classifying trees with showy flowers or fruit (Kendal et al., 2012b). Fruit may also be desired for food rather than aesthetics, other plant parts may also provide aesthetic appeal and showy reproductive parts may further be associated with increasing disservices of litter production. Nevertheless, the showy reproductive trait score provides an indicator of an often important component of aesthetic appeal (Pataki et al., 2013; Avolio et al., 2015b). Showy flowers were ranked from 0 to 2, with 0 being inappreciable or no flowers (e.g. *Pinus* sp.), 1 for having small white or sparse flowers (e.g. *Citrus* sp.), and 2 for possessing large, colourful, showy flowers (e.g. *Koelreuteria paniculata*). Showy fruit was scored 1 for large, colourful fruit (a trait noted in the UFEI database) or otherwise scored as 0. Flower and fruit data were grouped together (values of 0–2 for showy flowers and 0–1 for showy fruit), and anything over a 2 in showiness was identified as a species with showy reproductive parts.

**Analysis**

We used a suite of complementary approaches to analyse tree community and trait distributions. Individually based rarefaction curves and randomized and smoothed species accumulation curves were constructed for each city to compare overall taxonomic biodiversity (Gotelli & Colwell, 2001; Colwell et al., 2004). Differences in tree density, sampling intensity (number of samples) and plot size all influenced the number of individuals identified and thus the need for rarefaction-based comparisons. For such comparisons we used a standardized metric of the second-order jack-knife richness estimator based on 500 individuals. Results from analyses with both lower (132) and higher (1000) numbers of individuals were all consistent. Diversity indices and rarefaction analyses were calculated using ESTIMATES 9.0 (http://viceroy.eeb.uconn.edu/Estimates).

Similarity between cities was assessed with the Jaccard similarity metric, which varies from 1 (complete similarity) to 0 (complete turnover). Non-metric multidimensional scaling (NMDS) ordination of the tree communities, created from the species presence–absence matrix (ESTIMATES 9.0), was used to evaluate variation among city tree community assemblages. This nonlinear ordination technique creates a representation that maximizes distance based on rank-order agreement with species dissimilarities (Austin, 2005). After projecting the ordination (mid-scale function in Matlab, The Mathworks, http://www.mathworks.com/) the distance between cities in ordination space reflects the dissimilarity in species composition.

To compare tree community patterns with local climate, we obtained 1981–2010 climate normals for winter minimum temperature, summer maximum temperature and annual precipitation for each city from the NOAA National Climatic Data Center and Environment Canada. We used two metrics to quantify climate variation among cities. For evaluating climate differences between cities we calculated the Euclidean dissipimilarities between cities based on both temperature and precipitation following a z-score transformation. To evaluate the role of a climate-based environmental filter we compared distributions of NMDS ordination axes, richness, origins and aesthetic traits with each of the climate variables independently through regression analysis. To evaluate potential influences of social sources of variation we also evaluated for correlations with population size and percentage of adults with 4-year college education (variables obtained from the government census surveys conducted in 2010 for the USA and 2011 for Canada). Education is strongly related with other socioeconomic variables, including income (Krieger et al., 1997), and is a consistent variable across countries.

**RESULTS**

Urban tree communities in our cross-section of cities were highly variable in magnitudes of diversity, community composition, origins and trait distribution. Rarefaction from each survey showed large differences in the accumulation of biodiversity among cities (Fig. 2). In total, the surveys identified 25,874 individual trees from 416 unique species. Many of the individual city accumulation curves were either at or approaching saturation, although in the high-diversity warm cities diversity continued to increase throughout sampling.
Within the individual cities the total number of tree species recorded varied from 22 (Kelowna) to 147 (Los Angeles, CA) species and the number of individuals sampled varied from 131 (Riverside) to 4000 (Tampa).

The fully pairwise tree community similarity comparisons reinforced the pattern of widespread urban variation (Fig. 3). While similar tree communities (high similarity) between cities in similar local climate conditions were observed, as climate differences between cities increased the tree communities showed consistently low similarities. Twenty-three percent of city pairs had tree community similarity scores of less than 0.05, where a similarity score of 0.0 represents communities with no overlapping species. Consistent with the community similarity patterns, NMDS ordination of the tree presence and abundance distributions suggested a broad diversity of community compositions (Fig. 4a). Grouping cities based on minimum winter temperatures either above or below 0.0°C, led to distinct clusters ($P < 0.0001$; permutation ANOVA, R-vegan function adonis). Consistent with this, the first NMDS axis was related to minimum winter temperature (Fig. 4b) and the second NMDS axis was related to annual precipitation (Fig. 4c). Mean summer high temperature, population and percentage of the population with a college education were not significantly related to either NMDS axis (Table S2).

Minimum winter temperature, a key environmental restriction filter variable, was an important correlate with plant diversity, origins and an aesthetic ecosystem service trait compared with other climate and social predictors (Table S3). Estimates of richness across all cities standardized to a consistent number of individuals showed a positive relationship with minimum winter temperature ($P = 0.001$; $R^2 = 0.34$; Fig. 5a). The relatively low predictive skill for richness with minimum temperature suggests that other important factors remain unexplored. The regionally native trees within each city varied between 7% (Orange County) and 95% (Raleigh, NC) of the total community composition and this proportion was negatively related to minimum winter temperature ($P = 0.0001$; $R^2 = 0.61$; Fig. 5b). The native biome of origin for tree communities varied from 100% of trees originating from temperate environments to communities with predominantly tropical or dryland species. Trees from tropical origins, a biome outside the local conditions of any of our cities, were absent from cities in climates with low minimum winter temperatures but consistently increased up to 64% (Tampa) of the tree community with increasing minimum winter temperatures ($P < 0.0001$; $R^2 = 0.79$; Fig. 5c). The proportion of trees with showy reproductive parts, our metric of an aesthetic ecosystem service, showed a positive correlation with minimum winter temperature ($P = 0.0001$; $R^2 = 0.80$; Fig. 5d). Kelowna was a notable outlier, exceeding the minimum temperature model prediction for the proportion of showy reproductive traits by 30%. Consistent with the coordinated effects of mean minimum temperature, each of these tree community composition indicators were themselves correlated, with frequency of showy reproductive parts positively correlated with tropical tree abundance and negatively correlated with native tree abundance (Table S4). A second climate variable, annual precipitation, was negatively related to the proportion of regionally native trees ($P = 0.0006$; $R^2 = 0.49$; Fig. 6). Combined in a multiple regression analysis, both minimum winter temperature and annual precipitation were significant predictors that explained 85% of the variation in the proportion of regionally native trees among cities.

**Figure 3** Pairwise urban tree community similarity and climate. Each point represents the Jaccard similarity between two cities and associated climate dissimilarity, which were related through a negative exponential model ($P < 0.001$).

**Figure 4** Tree community ordination and relationships with climate. (a) Non-metric multidimensional scaling (NMDS) plot with cities grouped as either below or above a mean minimum freezing temperature. (b) Relationships between the first NMDS axis with mean minimum winter temperature. (c) Relationships between the second NMDS axis with annual precipitation. Dashed lines represent significant regression models ($P < 0.001$).
DISCUSSION

We found that urban tree diversity, community composition, origins and an aesthetic ecosystem service varied widely among cities and that patterns in this variation were consistent with predictions from CT-TC mechanisms. A weak environmental filter, including no freezing temperatures and active management through irrigation, poses little or no restrictions on the ability of a tree species to survive, and coupled with the global commercial distribution of urban plants allowed urban residents choose more variety – more species from more biomes and more biogeographical provinces. However, when local climate tolerance filtering is strong, urban tree composition becomes less diverse and more restricted to regionally native species or those from the same biome. Thus, climatologically similar cities share a similar tree community composition. However, cities at opposite ends of the climate gradient were composed of an almost completely distinct tree community with origins more divergent than corresponding native communities through the importation of trees from other biomes and biogeographical provinces. An outcome of the flexibility provided by a weak climate tolerance filter was the increase in trees with showy reproductive parts, a broadly valued aesthetic ecosystem service. Across all cities, we found climate tolerance filtering was closely related to minimum winter temperature. In contrast, the effects of high temperature were not observed, precipitation had only limited influence and social differences between cities were not observed. The combination of cold tolerance, trait choices and urban assisted dispersal within the CT-TC hypothesis provides a valuable lens for understanding the macroecological patterns of urban trees.

Our findings help resolve inconsistencies arising from predictions of both biome matching and urban homogenization hypotheses. At subcontinental scales both biome matching and homogenization mechanisms operate to influence urban biodiversity. However, at continental scales neither mechanism is sufficient to explain the changes in urban tree communities. In cities with frequent freezing temperatures, biome matching mechanisms dominate community assembly and the potential for global dispersal associated with urbanization has limited effects on tree communities. This finding is consistent with studies conducted primarily within temperate forest biomes of eastern North America or northern Europe, showing the importance of climate matching (Ricotta et al., 2009; McBride & Douhovnikoff, 2012; Nock et al., 2013). However, in moderate climates characterized by infrequent freezing and where irrigation can reduce water limitation (e.g. the south-western United States), we found minimal restrictions posed by a climate tolerance filter. The lack of a similar climate tolerance filter associated with high temperature (Chown & Duffy, 2015) or a high vapour pressure deficit (Litvak et al., 2011) likely occurs through moderating effects of irrigation. The absence of climate restrictions coupled with urban assisted dispersal allows the importation of species from a global species pool. The importation of

**Figure 5** Relationships between January mean minimum temperature, and tree community richness (a), percentage of trees that are regionally native (b), percentage of trees with a tropical origin (c), and percentage of trees with showy reproductive parts (d). Dashed lines represent significant regression models ($P < 0.001$).

**Figure 6** Relationship between mean annual precipitation of the proportion of regionally native tree species ($P < 0.001$).
species from other biomes and biogeographical provinces in
some cities is in contrast to hypotheses of homogenization
(Yang et al., 2015) but is consistent with other warm dryland
cities in Australia (Kirkpatrick et al., 2011) and subtropical
Hong Kong (Jim & Zhang, 2015). As our assessment is lim-
ited by the coarse-scale analysis of species native ranges,
improved range delineation will allow a more complete eval-
uation of plant origins. The variation in the origins of plant
species among cities, spanning biome matching to biome
importation, reflects a changing climate tolerance filter across
continental scales.

The use of field surveys that included both naturalized and
cultivated species leads to different conclusions from previ-
ous comparisons of urban naturalized floras (Aronson et al.,
2014; La Sorte et al., 2014): our findings suggest that urban
plant communities can be composed primarily of non-native
species. Some of this discrepancy may result from our evalu-
ation of trees compared with complete plant communities;
however, studies of the primarily annual plant communities
in gardens also suggest the potential for a high frequency of
non-natives (Clarke & Jenerette, 2015). Including both natu-
ralized and cultivated species in many cities is critical, as the
cultivated trees may have large influences on many other
community, ecosystem and service characteristics. Further,
as we show here, the combined cultivated and naturalized com-

munity macroecological distributions are structured by gen-

eral ecological principles.

Variation in the urban climate tolerance filter was associ-
ated with the presence of an ecosystem service trait, namely
the presence of showy reproductive parts. Tree species with
this trait are generally found in tropical and subtropical cli-
mates and are geographically restricted by a low freezing tol-
erance. The increasing proportion of showy reproductive
parts with the relaxation of the climate tolerance filter reflects
the general desire for aesthetic ecosystem services shown in
surveys of urban residents and their local landscapes (Loram
et al., 2008; Avolio et al., 2015b) that cannot be met in colder
environments. Variation among cities in the distributions of
other ecosystem service traits, such as shading, will likely
depend on the environmental filtering constraints of the
plants providing the specific service. The interactive role of
desires and the environment shown here is consistent with
regional patterns of urban ecosystem service distributions
(Avolio et al., 2015b). The realization of the desire for showi-

ness, an ecosystem service trait driven by human choice, is
contingent on the suitability of climate, a geographically
determined environmental restriction.

Unlike at intra-city scales, where the importance of social
variation on urban biodiversity has been shown, we did not
observe correlations between urban tree community variation
and either human population or a socioeconomic status indi-
cator. Even with urban population size in our study spanning
88,000 (Santa Barbara, CA) to 3 million residents (Los
Angeles), this variable had no detectable influence on urban
tree communities. Similarly, a socioeconomic source of urban
variation, the percentage of adults with college education,
ranging from 13.5% (Kelowna) to 66% (Orange County),
was also unrelated to tree community composition.

Socioeconomic status has repeatedly been shown to influence
urban vegetation diversity (Hope et al., 2003; Avolio et al.,
2015) and in particular the selection of aesthetic traits (Wu,
2013; Clarke & Jenerette, 2015). While our findings don’t
remove the potential for other socioeconomic or cultural vari-
ables to influence macroecological patterns of urban tree
biodiversity, they do suggest that if any such relationships
exist, their influences are complex. For example, the unex-
pectedly high frequency of trees with showy reproductive
parts in Kelowna results primarily from the widespread
occurrence of a single species, Malus domestica (apple),
which is extensively grown regionally and reflects opportuni-
ties for human decisions to counter general trends. Still, the
apparent contrasting responses of urban vegetation to social
drivers at intra- and inter-urban scales suggests important
hierarchical effects that should be considered together in
structuring plant distributions.

Key directions for extending a macroecological theory of
urban vegetation distributions include looking toward more
globally distributed cities, including other plant communities
and expanding to multiple scales of analysis. Linking plant
distributions with an ecophysiological understanding of tem-
perature tolerances (e.g. Chown & Duffy, 2015) may be par-
cularly useful for identifying mechanistic underpinnings of
continental variation in urban plant communities. At global
scales we expect the effects of the climate tolerance filter are
broadly consistent with those observed here. However, vari-
ation in economic, cultural, and historical factors can influ-
ence dispersal opportunities, values and management prac-
tices (Kinzig et al., 2005; Boone et al., 2010; Essl et al.,
2011). These differences can influence trait choices and also
lead to changes in habitat suitability, such as those resulting
from irrigation. Comparisons of cities in Asia, Africa and
Latin America with much greater social and environmental
diversity than our in surveys may differ substantially from
CT-TC predictions derived from cities in the USA and Can-
ada alone. Other functional groups of plants, including
annuals, are important directions for future research as
annuals may avoid extreme hot or cold climate periods and
thereby circumvent limitations posed by climate tolerances.

Finally, the scale of analysis may have a strong influence on
factors important for urban vegetation; resolution at scales of
individual parcels could increasingly emphasize factors influ-

encing individual land managers’ choices. The usefulness of
the CT-TC framework for trees suggests that applications to
other plants is warranted and provides a direction for explor-
ing determinants of urban plant communities in response to
social and biophysical factors acting across multiple scales.

The dynamics of urban tree biodiversity implied by CT-TC
suggest that multiple social and biophysical factors related to
dispersal, desires and environmental conditions may influ-
ence trajectories of urban biodiversity change. These factors
may have differing and interactive effects on plant commun-
ities depending on the direction of change and the local
environmental conditions. Increases in the availability of urban tree biodiversity over the past century (Pincetl et al., 2013), corresponding with increased globalization and expanding dispersal opportunities, likely have effects on increasing diversity that may not be realized for decades (Essl et al., 2011). In the context of a changing climate, we expect that a relaxation of the cold-dependent climate filter would tend to increase opportunities for diversity; however, associated increasing droughts may pose new irrigation limitations and therefore restrict diversity. With a projected increase of 2.5 billion more urban residents by 2050 (United Nations Department of Economic and Social Affairs Population Division, 2014), urban plant communities will rapidly expand. A CT-TC approach provides a useful foundation for understanding the dynamics of broad-scale distributions of urban plant diversity that links variation in biophysical constraints and residential choices among cities.

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**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web-site:

**Table S1** Description of sampling characteristics and survey measurements for each city.

**Table S2** P-values between predictors and non-metric multidimensional scaling axes 1 and 2.

**Table S3** P-values from all regression models and dependent shown in Figure 5 & 6.

**Table S4** Pearson correlations between indicators of urban tree community variation. Only significant (P < 0.05) correlations are shown.

**BIOSKETCH**

Our research team is dedicated to improving the understanding and management of urban ecosystems. Individually our work emphasizes place-based studies of specific urban regions. Together our network is exploring macroecological patterns of urban systems and working toward standardized urban ecological methods for improved comparisons.

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