RESEARCH PAPER

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.

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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.

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.

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
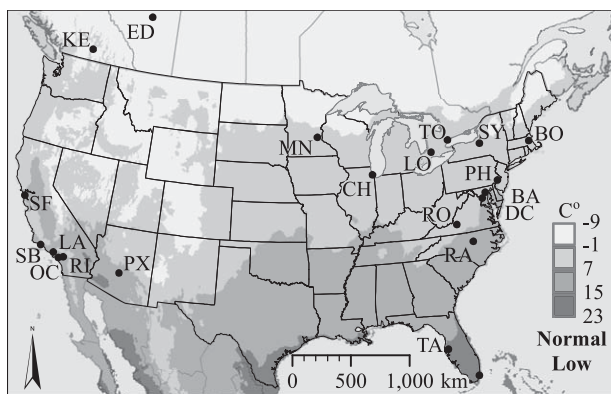
biome and included a tropical biome the species was coded as having a tropical origin. For Australia and the USA, GRIN also provided the states where the species were native and allowed refined biome classification. Otherwise, if the country of origin included multiple biomes a more refined range distribution 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 inconspicuous 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 (midscale 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 dissimilarities 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.
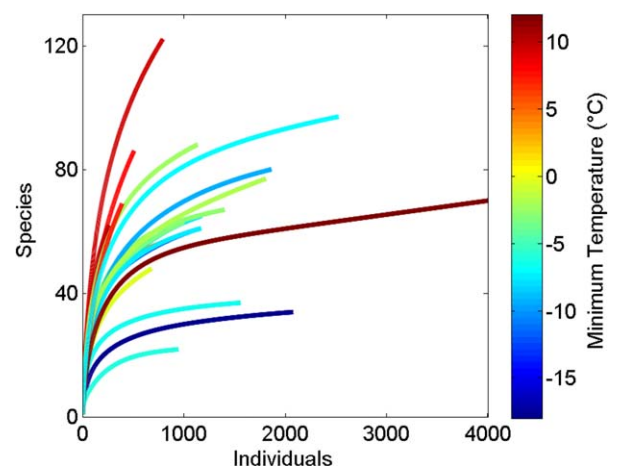

Figure 2 Individual-based rarefaction from tree community surveys conducted within each city. Each rarefaction curve is colour coded based on the mean minimum temperature for the city.
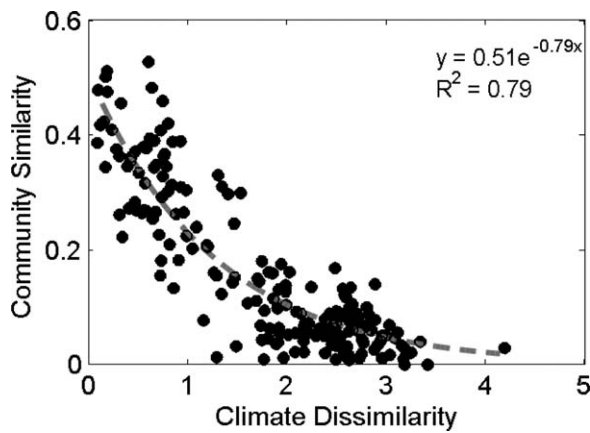
Figure 3 Pairwise urban tree community similarity and climate. Each point represents the Jaccard similarity between two cities and associated climate dissimilarity, which were related through a negative exponential model ($P < 0.001$).
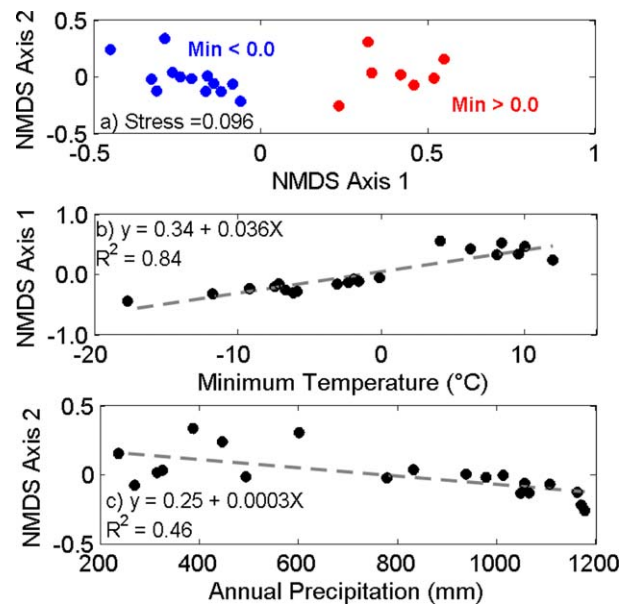

Figure 4 Tree community ordination and relationships with climate. (a) Non-metric multidimensional scaling (NMDS) plot with cities grouped as either below or above a mean minimum freezing temperature. (b) Relationships between the first NMDS axis with mean minimum winter temperature. (c) Relationships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

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 per cent 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, varied between 4% (Edmonton, AB) and 64% (Tampa) and was also positively correlated with minimum winter temperature ($P < 0.001$; $R^2 = 0.80$; 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.
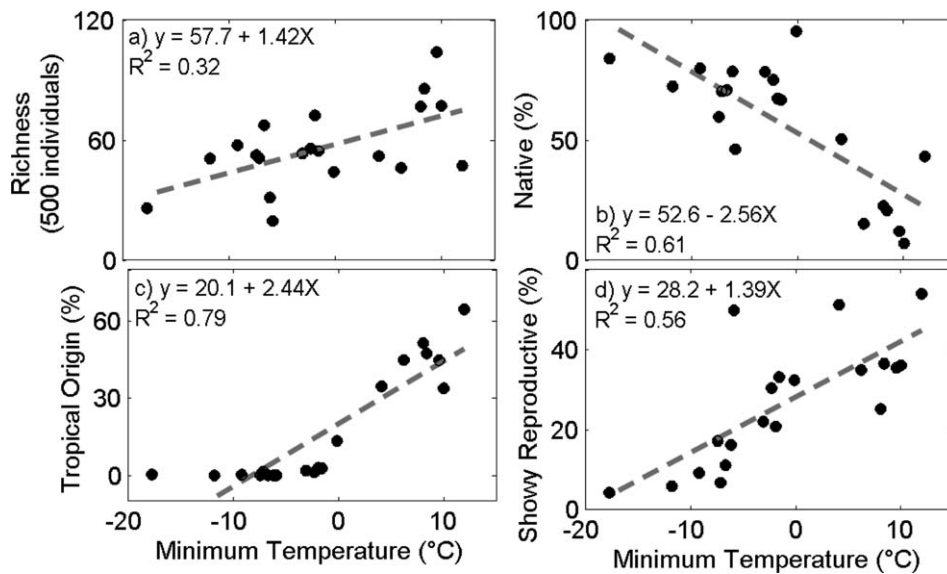
Figure 5 Relationships between January mean minimum temperature, and tree community richness (a), percentage of trees that are regionally native (b), percentage of trees with a tropical origin (c), and percentage of trees with showy reproductive parts (d). Dashed lines represent significant regression models ($P < 0.001$).

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
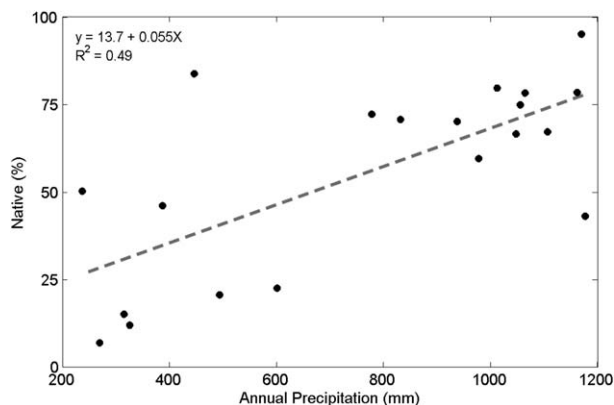

Figure 6 Relationship between mean annual precipitation of the proportion of regionally native tree species ($P < 0.001$).

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 limited by the coarse-scale analysis of species native ranges, improved range delineation will allow a more complete evaluation 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 previous 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 evaluation 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 naturalized 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 community macroecological distributions are structured by general ecological principles.

Variation in the urban climate tolerance filter was associated 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 climates and are geographically restricted by a low freezing tolerance. 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 showiness, 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 indicator. 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.*, 2015a) 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 variables to influence macroecological patterns of urban tree biodiversity, they do suggest that if any such relationships exist, their influences are complex. For example, the unexpectedly high frequency of trees with showy reproductive parts in Kelowna results primarily from the widespread occurrence of a single species, *Malus domesticus* (apple), which is extensively grown regionally and reflects opportunities 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 temperature tolerances (e.g. Chown & Duffy, 2015) may be particularly 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, variation in economic, cultural, and historical factors can influence dispersal opportunities, values and management practices (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 Canada 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 influencing 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 exploring 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 influence trajectories of urban biodiversity change. These factors may have differing and interactive effects on plant communities 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.

ACKNOWLEDGEMENTS

REFERENCES

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H. *et al.* (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133330.

Austin, M.P. (2005) Vegetation and environment: discontinuities and continuities. *Vegetation ecology* (ed. by E. Van Der Maarel), pp. 52–84. Blackwell, Oxford.

Avolio, M., Pataki, D.E., Gillespie, T., Jenerette, G.D., McCarthy, H.R., Pincetl, S. & Weller-Clarke, L. (2015a) Tree diversity in southern California's urban forest: the interacting roles of social and environmental variables. *Frontiers in Ecology and Evolution*, **3**, doi: 10.3389/fevo.2015.00073.

Avolio, M.L., Pataki, D.E., Pincetl, S., Gillespie, T., Jenerette, G.D. & McCarthy, H.R. (2015b) Understanding preferences for tree attributes: the relative effects of socio-economic and local environmental factors. *Urban Ecosystems*, **18**, 73–86.

Boone, C.G., Cadenasso, M.L., Grove, J.M., Schwarz, K. & Buckley, G.L. (2010) Landscape, vegetation characteristics, and group identity in an urban and suburban watershed: why the 60s matter. *Urban Ecosystems*, **13**, 255–271.

Chown, S.L. & Duffy, G.A. (2015) Thermal physiology and urbanization: perspectives on exit, entry and transformation rules. *Functional Ecology*, **29**, 902–912.

Clarke, L.W. & Jenerette, G.D. (2015) Biodiversity and direct ecosystem service regulation in the community gardens of Los Angeles, CA. *Landscape Ecology*, **30**, 637–653.

Clarke, L.W., Jenerette, G.D. & Davila, A. (2013) The luxury of vegetation and the legacy of tree biodiversity in Los Angeles, CA. *Landscape and Urban Planning*, **116**, 48–59.

Colwell, R.K., Mao, C.X. & Chang, J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717–2727.

Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature*, **329**, 326–327.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

Duncan, R.P., Clemants, S.E., Corlett, R.T., Hahs, A.K., McCarthy, M.A., McDonnell, M.J., Schwartz, M.W., Thompson, K., Vesk, P.A. & Williams, N.S.G. (2011) Plant traits and extinction in urban areas: a meta-analysis of 11 cities. *Global Ecology and Biogeography*, **20**, 509–519.

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hulber, K., Jarosik, V., Kleinbauer, I., Krausmann, F., Kuhn, I., Nentwig, W., Vila, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.L., Roques, A. & Pysek, P. (2011) Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences USA*, **108**, 203–207.

Faeth, S.H., Warren, P.S., Shochat, E. & Marussich, W.A. (2005) Trophic dynamics in urban communities. *Bioscience*, **55**, 399–407.

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness–climate relationship for angiosperms. *The American Naturalist*, **161**, 523–536.

Funk, J.L., Cleland, E.E., Suding, K.N. & Zavaleta, E.S. (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution*, **23**, 695–703.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Groffman, P.M., Cavender-Bares, J., Bettez, N.D., Grove, J.M., Hall, S.J., Heffernan, J.B., Hobbie, S.E., Larson, K.L., Morse, J.L., Neill, C., Nelson, K., O'neil-Dunne, J., Ogden, L., Pataki, D.E., Polsky, C., Chowdhury, R.R. & Steele, M.K. (2014) Ecological homogenization of urban USA. *Frontiers in Ecology and the Environment*, **12**, 74–81.

Hahs, A.K., McDonnell, M.J., McCarthy, M.A., Vesk, P.A., Corlett, R.T., Norton, B.A., Clemants, S.E., Duncan, R.P., Thompson, K., Schwartz, M.W. & Williams, N.S.G. (2009) A global synthesis of plant extinction rates in urban areas. *Ecology Letters*, **12**, 1165–1173.

Hall, S.J., Learned, J., Ruddell, B. *et al.* (2016) Convergence of microclimate in residential landscapes across diverse cities in the United States. *Landscape Ecology*, **31**, 101–117.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo,

A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Hope, D., Gries, C., Zhu, W.X., Fagan, W.F., Redman, C.L., Grimm, N.B., Nelson, A.L., Martin, C. & Kinzig, A. (2003) Socioeconomics drive urban plant diversity. *Proceedings of the National Academy of Sciences USA*, **100**, 8788–8792.

Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**, 10–18.

Jenerette, G.D. & Potere, D. (2010) Global analysis and simulation of land-use change associated with urbanization. *Landscape Ecology*, **25**, 657–670.

Jenerette, G.D., Harlan, S.L., Buyantuev, A., Stefanov, W.L., Declet-Barreto, J., Ruddell, B.L., Myint, S.W., Kaplan, S. & Li, X.X. (2016) Micro-scale urban surface temperatures are related to land-cover features and residential heat related health impacts in Phoenix, AZ, USA. *Landscape Ecology*, **31**, 745–760.

Jim, C.Y. & Zhang, H. (2015) Effect of habitat traits on tree structure and growth in private gardens. *Landscape Ecology*, **30**, 1207–1223.

Kaye, J.P., Burke, I.C., Mosier, A.R. & Guerschman, J.P. (2004) Methane and nitrous oxide fluxes from urban soils to the atmosphere. *Ecological Applications*, **14**, 975–981.

Kendal, D., Williams, N.S.G. & Williams, K.J.H. (2012a) A cultivated environment: exploring the global distribution of plants in gardens, parks and streetscapes. *Urban Ecosystems*, **15**, 637–652.

Kendal, D., Williams, K.J.H. & Williams, N.S.G. (2012b) Plant traits link people's plant preferences to the composition of their gardens. *Landscape and Urban Planning*, **105**, 34–42.

Kinzig, A.P., Warren, P., Martin, C., Hope, D. & Katti, M. (2005) The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. *Ecology and Society*, **10**(1): 23. URL: http://www.ecologyandsociety.org/vol10/iss1/art23/

Kirkpatrick, J.B., Daniels, G.D. & Davison, A. (2011) Temporal and spatial variation in garden and street trees in six eastern Australian cities. *Landscape and Urban Planning*, **101**, 244–252.

Kleidon, A. & Mooney, H.A. (2000) A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biology*, **6**, 507–523.

Knapp, S., Dinsmore, L., Fissore, C., Hobbie, S.E., Jakobsdottir, I., Kattge, J., King, J.Y., Klotz, S., McFadden, J.P. & Cavender-Bares, J. (2012) Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient. *Ecology*, **93**, S83–S98.

Krieger, N., Williams, D.R. & Moss, N.E. (1997) Measuring social class in US public health research: concepts, methodologies, and guidelines. *Annual Review of Public Health*, **18**, 341–378.

La Sorte, F.A., Aronson, M.F.J., Williams, N.S.G., Celesti-Grapow, L., Cilliers, S., Clarkson, B.D., Dolan, R.W., Hipp, A., Klotz, S., Kuhn, I., Pysek, P., Siebert, S. & Winter, M. (2014) Beta diversity of urban floras among European and non-European cities. *Global Ecology and Biogeography*, **23**, 769–779.

Lasky, J.R., Sun, I.F., Su, S.H., Chen, Z.S. & Keitt, T.H. (2013) Trait-mediated effects of environmental filtering on tree community dynamics. *Journal of Ecology*, **101**, 722–733.

Lebrija-Trejos, E., Perez-Garcia, E.A., Meave, J.A., Bongers, F. & Poorter, L. (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, **91**, 386–398.

Litvak, E., McCarthy, H.R. & Pataki, D.E. (2011) Water relations of coast redwood planted in the semi-arid climate of southern California. *Plant Cell and Environment*, **34**, 1384–1400.

Loram, A., Thompson, K., Warren, P.H. & Gaston, K.J. (2008) Urban domestic gardens (XII): the richness and composition of the flora in five UK cities. *Journal of Vegetation Science*, **19**, 321. U67.

Lovell, S.T. & Taylor, J.R. (2013) Supplying urban ecosystem services through multifunctional green infrastructure in the United States. *Landscape Ecology*, **28**, 1447–1463.

McBride, J.R. & Douhovnikoff, V. (2012) Characteristics of the urban forests in arctic and near-arctic cities. *Urban Forestry and Urban Greening*, **11**, 113–119.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.

Nock, C.A., Paquette, A., Follett, M., Nowak, D.J. & Messier, C. (2013) Effects of urbanization on tree species functional diversity in eastern North America. *Ecosystems*, **16**, 1487–1497.

Nowak, D.J., Crane, D.E., Stevens, J.C. & Hoehn, R.E. (2003) The urban forest effects (UFORE) model: field data collection manual. USDA Forest Service, Northeastern Research Station, Syracuse, NY.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the worlds: a new map of life on Earth. *Bioscience*, **51**, 933–938.

Pataki, D.E., McCarthy, H.R., Gillespie, T., Jenerette, G.D. & Pincetl, S. (2013) A trait-based ecology of the Los Angeles urban forest. *Ecosphere*, **4**, 1–20

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.C. & Costanza, R. (2001) Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review of Ecology and Systematics*, **32**, 127–157.

Pincetl, S., Prabhu, S.S., Gillespie, T.W., Jenerette, G.D. & Pataki, D.E. (2013) The evolution of tree nursery offerings in Los Angeles County over the last 110 years. *Landscape and Urban Planning*, **118**, 10–17.

Pouyat, R.V., Belt, K.T., Pataki, D.E., Groffman, P.M., Hom, J. & Band, L.E. (2007) Urban land-use change effects on biogeochemical cycles. *Terrestrial ecosystems in a changing world* (ed. by P. Canadell, D. Pataki and L. Pitelka). pp. 45–58. Springer-Verlag, Berlin.

Qiao, X.J., Jabot, F., Tang, Z.Y., Jiang, M.X. & Fang, J.Y. (2015) A latitudinal gradient in tree community assembly processes evidenced in Chinese forests. *Global Ecology and Biogeography*, **24**, 314–323.

Raciti, S.M., Hutyra, L.R., Rao, P. & Finzi, A.C. (2012) Inconsistent definitions of 'urban' result in different conclusions about the size of urban carbon and nitrogen stocks. *Ecological Applications*, **22**, 1015–1035.

Ramage, B.S., Roman, L.A. & Dukes, J.S. (2013) Relationships between urban tree communities and the biomes in which they reside. *Applied Vegetation Science*, **16**, 8–20.

Ricotta, C., La Sorte, F.A., Pysek, P., Rapson, G.L., Celesti-Grapow, L. & Thompson, K. (2009) Phyloecology of urban alien floras. *Journal of Ecology*, **97**, 1243–1251.

Savard, J.P.L., Clergeau, P. & Mennechez, G. (2000) Biodiversity concepts and urban ecosystems. *Landscape and Urban Planning*, **48**, 131–142.

Smith, R.M., Thompson, K., Hodgson, J.G., Warren, P.H. & Gaston, K.J. (2006) Urban domestic gardens (IX): composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation*, **129**, 312–322.

United Nations Department of Economic and Social Affairs Population Division (2014) *World urbanization prospects: the 2014 revision, highlights* (ST/ESA/SER.A/352).

Wang, Z.H., Fang, J.Y., Tang, Z.Y. & Lin, X. (2011) Patterns, determinants and models of woody plant diversity in China. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2122–2132.

Williams, N.S.G., Schwartz, M.W., Vesk, P.A., McCarthy, M.A., Hahs, A.K., Clemants, S.E., Corlett, R.T., Duncan, R.P.,

Norton, B.A., Thompson, K. & McDonnell, M.J. (2009) A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology*, **97**, 4–9.

Wu, J. (2013) Landscape sustainability science: ecosystem services and human well-being in changing landscapes. *Landscape Ecology* **28**, 999–1023.

Yang, J., La Sorte, F.A., Pysek, P., Yan, P.B., Nowak, D. & McBride, J. (2015) The compositional similarity of urban forests among the world's cities is scale dependent. *Global Ecology and Biogeography*, **24**, 1413–1423.

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 ecosystems and working toward standardized urban ecological methods for improved comparisons.

Editor: Karl Evans