How do urban trees vary across the US? It depends on where and how you look

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Urban forests provide ecosystem services important for regulating climate, conserving biodiversity, and maintaining human well-being. However, these forests vary in composition and physiological traits due to their unique biophysical and social contexts. This variation complicates assessing the functions and services of different urban forests. To compare the characteristics of the urban forest, we sampled the species composition and two externally sourced traits (drought tolerance and water-use capacity) of tree and shrub species in residential yards, unmanaged areas, and natural reference ecosystems within six cities across the contiguous US. As compared to natural and unmanaged forests, residential yards had markedly higher tree and shrub species richness, were composed primarily of introduced species, and had more species with low drought tolerance. The divergence between natural and human-managed areas was most dramatic in arid climates. Our findings suggest that the answer to the question of "what is an urban forest" strongly depends on where you look within and between cities.

Front Ecol Environ 2024; 22(7): e2777, doi:10.1002/fee.2777

Urban forests are major ecological features of the urban environment that provide many ecosystem services (eg climate regulation, wildlife habitat, recreation). Within cities, a wide variety of natural, managed, and cultivated green spaces contain trees, ranging from street trees and other planted trees to large tracts of relict forests, as well as cultivated and spontaneous trees in yards (Pregitzer *et al.* 2019; Trammell *et al.* 2020). This variation greatly complicates assessment of the functions and services of urban forests, their relevance to diverse stakeholder groups, and their resilience in the face of multiple, interacting environmental and social changes.

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Many assessments of urban forests vary in scale and focus, making comparisons across different land-use types and cities challenging. One focus of urban forest assessments is finer scale assessments of specific components of urban forests. Large parks or other tracts of native vegetation provide important services related to native biodiversity (Pregitzer *et al.* 2019; Templeton *et al.* 2019). However, the scale of urban forest assessments may impact inferences on the characteristics of urban forests, such as the proportions of native and introduced tree species in highly heterogeneous urban forests. For example, Pregitzer *et al.* (2019) compared assessments of urban forests within New York City and found that the type of sampling (coarse-scale versus fine-scale) generated different results for native urban tree canopy cover (42.8% versus 83.9%). Therefore, disparities among assessments of urban trees can lead to different conclusions about urban forests and the services they provide (McHale *et al.* 2017; Pregitzer *et al.* 2019). As compared to coarse-scale (eg landscape-level) sampling, fine-scale (eg patch-level) sampling also facilitates mechanistic assessments of forest response to environmental change and urban resilience (McHale *et al.* 2017; Zhou *et al.* 2017).

A second focus of urban forest assessments has been on residential parcels. In this case, human preferences for particular species act as an environmental filter (Pearse *et al.* 2018). Human choices are a key driver of the introduction, transport, and cultivation of species, some of which may become invasive, with the potential to spread at continental (Padullés Cubino *et al.* 2019a) and global (Aronson *et al.* 2014; Avolio *et al.* 2021) scales. Human preferences and management also have a homogenizing effect on the structure and composition of cultivated and spontaneous plant communities in residential systems across cities (Groffman

et al. 2017; Padullés Cubino *et al.* 2020), whereby tree communities in cities are more similar to one another than to the native ecosystems that they replaced (Pearse *et al.* 2018). The effect of this homogenization on urban forest resilience to environmental change is a growing concern in an urbanizing world (Jenerette *et al.* 2016). Plant species origin and biological traits influence the fitness of tree species for the urban environment (Kendal *et al.* 2012; Pataki *et al.* 2013; Avolio *et al.* 2015) and may help to predict their performance under altered future physical, chemical, and biological conditions (eg droughts).

In this study, we conducted a comparative analysis of urban forest (tree and shrub) species composition under three different land uses (natural areas [reference sites], interstitial sites, and residential yards) in six cities located in different climatic regimes across the contiguous US. We also analyzed drought tolerance and water-use capacity information for every tree and shrub species using data from external sources to compare physiological traits vital to climate adaptation between land-use types. Our goal was to identify the general composition of US urban forests on continental and municipal scales and investigate implications for native biodiversity and climate adaptation capacity. Our study sought to answer three questions: (1) What tree species are found in urban forests across diverse regions of the US?, (2) How do tree species vary among different areas of the cities?, and (3) What are the implications of urban trees for native biodiversity and climate adaptation capacity in different components of urban forests across the US?

Methods

Our analysis encompassed six major US Metropolitan Statistical Areas (cities): Boston, Massachusetts (BOS); Baltimore, Maryland (BAL); Los Angeles, California (LAX); Miami, Florida (MIA); Minneapolis-St Paul, Minnesota (MSP); and Phoenix, Arizona (PHX). These cities represent six different ecological biomes and/or major climatic regions across the contiguous US (Trammell *et al.* 2016).

For each city, we focused on three distinctive land-use types: natural areas (reference sites), relatively unmanaged areas (interstitial sites), and residential yards. We selected four to six reference sites representative of the natural ecological biomes in which the cities were located (Padullés Cubino *et al.* 2020). Natural biomes sampled included oak and tulip poplar forests (BAL); northern hardwood forests and pastures (BOS); southern California coastal sage scrub (LAX); pine rockland, subtropical hardwood hammock, coastal hammock, and pine flatwoods (MIA); oak savanna tallgrass prairie, bluff prairie, and maple-basswood forests (MSP); and Sonoran Desert (PHX). We selected four to six interstitial sites on public lands within the cities that represented relatively unmanaged systems with relatively intact soil profiles where vegetation developed spontaneously. Given their proximity to managed areas, these sites were more likely to contain species that may have dispersed from residential areas rather than from the natural areas. Finally, we sampled four types of residential yards (12–16 per city) in each city: high fertilizer-input, low fertilizer-input, wildlife-certified, and water-wise (xeriscaping in Phoenix and Los Angeles, rain gardens in other cities). Site selection and characterization are described in greater detail in Padullés Cubino *et al.* (2020).

Within reference and interstitial sites, eight plots, each with a radius of 8 m, were established randomly to assess tree and shrub (and cacti in Phoenix) species presence, with a total of 64 plots in each city. In the residential sites, all tree species that occurred in yards (cultivated and spontaneous) were identified. All plant presence/absence data are stored at the Environmental Data Initiative (EDI) repository and can be accessed by searching the reference number edi.309.1, or by the navigating to doi.org/10.6073/pasta/8b29dc7fd536f4649f8cf6a536421fc9 (Padullés Cubino and Narango 2019). Each plant species was classified as native or introduced based on data obtained from the USDA PLANTS (https://plants.usda.gov) and Encyclopedia of Life (www.eol.org) databases. According to the USDA PLANTS database, native species are those that occur naturally within a state (in the US), whereas introduced species are defined as "(1) non-native (or alien) to the ecosystem under consideration and (2) a species whose introduction causes or is likely to cause economic harm, environmental harm, or harm to human health". The USDA PLANTS database also clarifies that the term "introduced" is used because "it is [more] widely known…than the similar term naturalized". For species available in the USDA PLANTS database, two ordinal traits important to climate adaptation were recorded: drought tolerance (none, low, medium, high) and water-use capacity (low, medium, high); each trait was recorded for each species, but only one categorical value was possible for each trait. Drought tolerance is based on a given plant's tolerance to drought conditions relative to other species with similar growth habits, whereas water-use capacity is based on a species' physiological ability to acquire water from the soil relative to other species growing under the same (or similar) soil moisture availability conditions in the region.

All data analyses were conducted in R (v2022.12.0+353; R Core Team 2021). Differences in the number of tree/shrub (cactus in Phoenix) species (ie species richness), drought tolerance, and water-use capacity among land-use types in each city were assessed with the Kruskal-Wallis rank sum test followed by a post-hoc pairwise comparison test. Rarefaction was conducted using the *iNEXT* package in R (Hsieh *et al.* 2016) to account for sampling differences between interstitial/reference sites and residential yards (Appendix S1: Figure S1).

Results

Residential yards contained significantly higher numbers of species than reference and interstitial sites ($\chi^2 = 11.62$, $P < 0.001$; Figure 1a) across cities. The percentage of native species

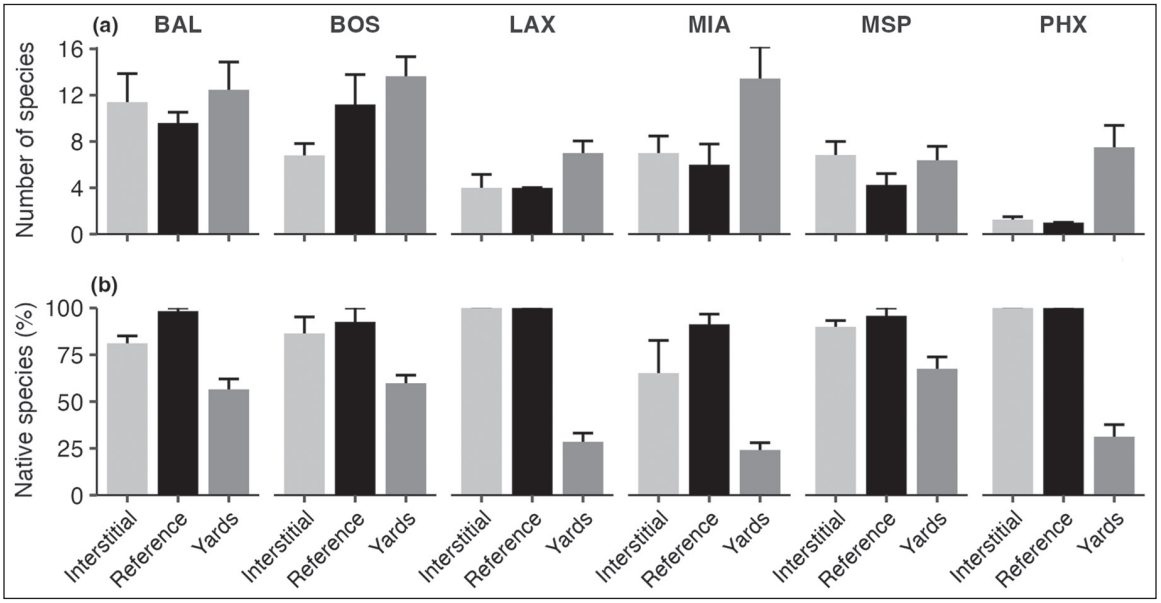

Figure 1. Total number of tree and shrub species (a) and percent of native tree and shrub species (b) in interstitial sites, (natural) reference sites, and residential yards in six cities across the contiguous US (BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St Paul, PHX = Phoenix). In both (a) and (b), comparisons across all cities revealed significant differences between residential yards and interstitial sites ($P < 0.001$) and between yards and (natural) reference sites ($P = 0.01$). Error bars represent standard error (upper limit shown).

(Figure 1b) was lowest in residential yards in all cities. The highest percentage of native species was observed in reference and interstitial sites in the driest cities (Los Angeles and Phoenix, $\chi^2 = 9.12$, $P = 0.01$; Figure 1b).

The driest cities (Los Angeles and Phoenix) had significantly ($\chi^2 = 14.94$, $P < 0.001$) higher percentages of species with high drought tolerance in reference and interstitial sites than the more humid cities (Figure 2). Species with high drought tolerance were less common in residential yards in the driest cities. Notably, all tree species found in natural and interstitial sites in Phoenix were native and had high drought tolerance. Similarly, in Los Angeles and Miami, the percentage of species with high drought tolerance was higher in natural and interstitial sites than in residential yards. In Minneapolis-St Paul, the percentage of species with high drought tolerance was higher in natural sites than in residential yards.

Across cities and land-use types, species with high water-use capacity were proportionally lower than species with medium or low water-use capacity; however, species with high water-use capacity were particularly rare in the driest cities (Figure 3). Differences between land-use types were statistically significant ($\chi^2 = 19.61$, $P < 0.001$). Species with high drought tolerance and low water-use capacity were common in reference sites in cities with hot climates (Los Angeles, Miami, and Phoenix). Most species identified across the six cities had medium water-use capacity.

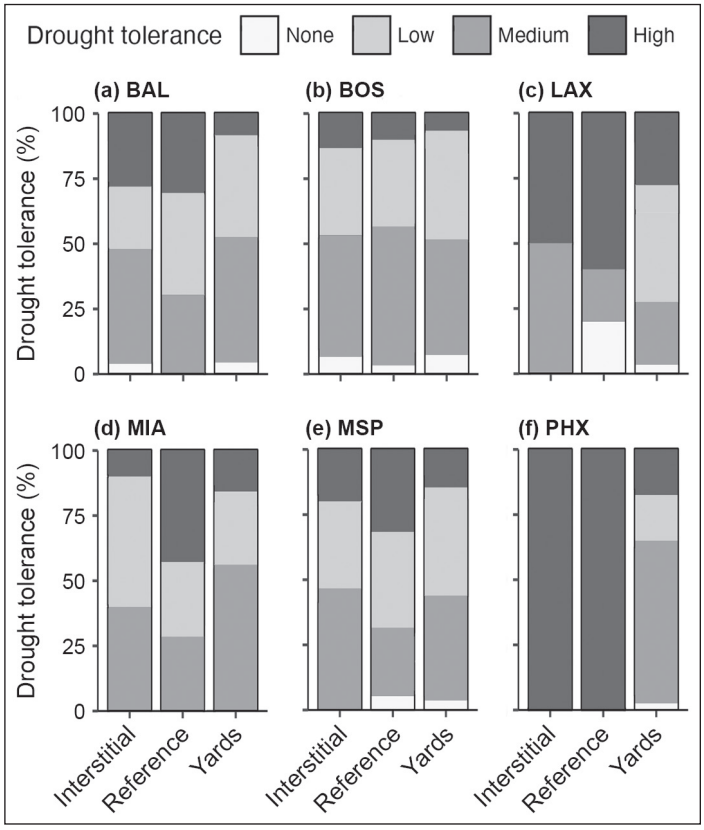

Figure 2. Percent of total species in different drought tolerance classes found in interstitial sites, (natural) reference sites, and residential yards in six cities across the contiguous US (BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St Paul, PHX = Phoenix). Comparisons across all cities revealed significant differences in species drought tolerance between residential yards and interstitial sites ($P < 0.001$) and between yards and (natural) reference sites ($P < 0.001$).

Discussion

Urban forests are part of the heterogeneous urban ecosystem, which makes them diverse in composition. Our primary

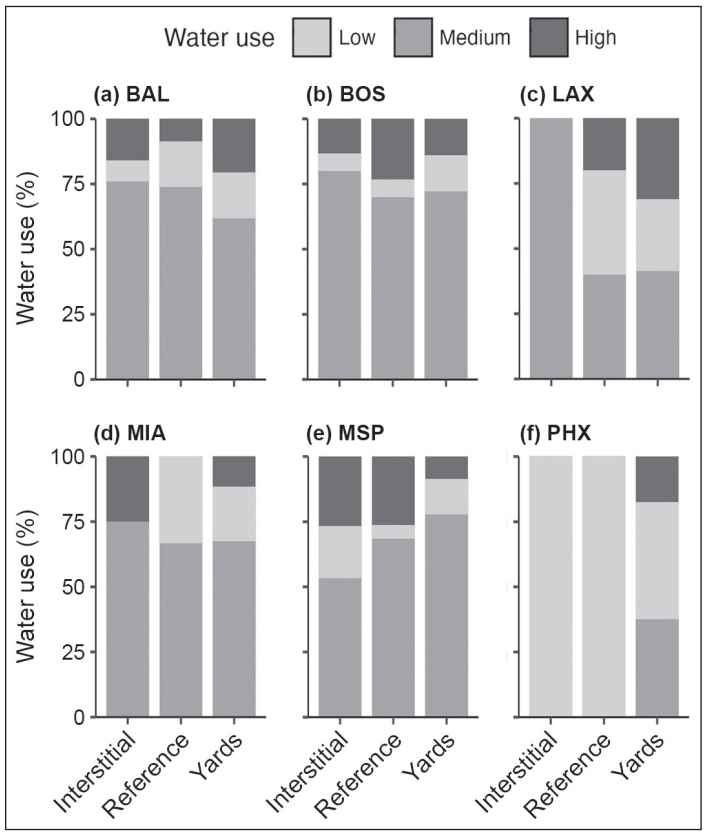

Figure 3. Percent of total species in different water-use capacity classes for tree species determined in interstitial sites, (natural) reference sites, and residential yards in six cities across the contiguous US (BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St Paul, PHX = Phoenix). Comparisons across all cities revealed significant differences in species water-use capacity between residential yards and interstitial sites ($P < 0.001$) and between yards and (natural) reference sites ($P < 0.001$).

finding was that—across the US—residential yards support dramatically larger (mean) numbers of woody species (150) than do reference (29) or interstitial (30) sites. A major question is whether this increase in species numbers increases the resilience or vulnerability of ecosystem services related to general urban greening and/or native biodiversity (Keeler *et al.* 2019). The marked differences in species number, composition, and traits between reference sites, interstitial sites, and residential yards suggest that different sampling strategies for characterizing urban forests that include different forms of land use may produce divergent assessments of native biodiversity and the capacity of urban forests to adapt to a changing climate.

Previous analyses of data from our six study cities (Pearse *et al.* 2018; Padullés Cubino *et al.* 2019b) have shown that human preferences for and management of vegetation play strong roles in influencing the species composition of urban ecosystems, leading to an ecological homogenization at multiple scales, including for both spontaneous and cultivated species pools. Studies conducted in other cities have found that biotic homogenization plays a strong role at subcontinental scales (Jenerette *et al.* 2016; McHale *et al.* 2017). Here, our focus was on the comparison of tree and shrub species in residential yards versus interstitial sites and in residential yards versus reference sites, to highlight the challenges of assessing biodiversity and response to environmental change in urban ecosystems given the huge number of species in residential yards—many of which are introduced. In light of the human preference for certain traits common to introduced species, such as showy flowers (Pataki *et al.* 2013; Avolio *et al.* 2015), there is great uncertainty about the effect of these preferences on the ability of urban ecosystems to support native biodiversity (eg plants and wildlife; Aronson *et al.* 2014; Narango *et al.* 2018) and to be resilient to environmental change (eg species adaptation to disturbances), posing a challenge in urban conservation (Gaertner *et al.* 2017).

Here, we found that the effect of human preferences—as manifested by high numbers of introduced woody species—is most obvious in residential yards and in cities with warmer climates, such as Los Angeles, Miami, and Phoenix. For example, in the northern cities of Baltimore, Boston, and Minneapolis-St Paul, approximately 50% of tree species in residential yards were native, whereas in the southern cities of Los Angeles, Miami, and Phoenix, less than 25% of tree species in residential yards were native. Our results build on those reported by Padullés Cubino *et al.* (2019a) from the same residential yards analyzed here; in that earlier study, the authors found that introduced species (including woody and herbaceous species) were ubiquitous in residential yards in Los Angeles and Phoenix. In these warmer cities, the availability of irrigation water and fertilizer allows for the expression of human preferences but may create vulnerabilities to potential reductions in water and nutrient supply (eg watering restrictions that may accompany drought or reductions in supplemental watering during disruptions to the residential housing market; Ripplinger *et al.* 2017).

Data from the interstitial sites shed light on which species, both native and introduced, are capable of thriving under urban conditions. These unmanaged areas, surrounded by highly managed areas, contain species with the ability to colonize and grow spontaneously under these conditions (Pearse *et al.* 2018; Padullés Cubino *et al.* 2019b). A major finding of our study was that introduced species were absent from interstitial and reference sites in cities with arid climates (Los Angeles and Phoenix). While this result indicates that introduced species in Los Angeles and Phoenix are not generally invasive, it also amplifies concern about the vulnerability of vegetation in residential yards to reductions in water availability in hot and dry cities.

In contrast to Los Angeles and Phoenix, Miami had the highest percentage of introduced species in interstitial sites. These results suggest that hot and wet cities may be especially vulnerable to declines in ecosystem services associated with native biodiversity (eg plants and wildlife) in response to increasing urbanization and other components of

environmental change. For example, within cities like these, decreases in native biodiversity and similarities in species composition can also have cascading effects on wildlife that depend on a diverse native urban forest (Aronson *et al.* 2014; Narango *et al.* 2018). On the other hand, such cities may exhibit increased resilience in services derived from general greening (shading, carbon sequestration, latent heat flux) regardless of plant origin, given that many introduced species have spontaneously colonized and become established in these cities. Introduced species were also an important component of reference and interstitial sites in cool, wet cities (Boston, Baltimore, Minneapolis-St Paul) and are likely contributing to declines in ecosystem services provided by native biodiversity while simultaneously increasing resilience in services derived from general greening (Keeler *et al.* 2019).

The effects of environmental change on urban tree communities may depend on the traits of the species in these communities, as reflected in the differences between unmanaged and human-managed spaces revealed in our study. There is particular concern about how the continuing and projected rise in temperatures in the coming years will impact urban forests (Esperón-Rodríguez *et al.* 2022), which are already exposed to elevated temperatures driven by the urban heat island effect (Ziter *et al.* 2019). The long-term studies that have shown marked differences in species composition between understory and canopy layers have raised questions about the adaptability of native species to a changing climate (Pregitzer *et al.* 2019; Trammell *et al.* 2020). Our results demonstrated that physiological traits, such as drought tolerance and water-use capacity, are useful metrics for assessing climate adaptability and predicting the capacity of trees to tolerate rising temperatures and weather extremes (Niinemets and Valladares 2006; Pataki *et al.* 2013; Jenerette *et al.* 2016). In addition, these traits affect key ecosystem processes, such as evapotranspiration (Grimmond and Oke 1999; Pataki *et al.* 2011; Goedhart and Pataki 2012), which mitigates the urban heat island effect (Arnfield 2003; Ziter *et al.* 2019).

Our results also suggest that human management (eg selection of certain species and irrigation) might reduce the ability of urban forests to adapt to a changing climate, with implications for their resilience and the ecosystem services they provide. In most cities, the proportion of species with high or medium drought tolerance was lower in both residential yards and interstitial sites than in reference sites, due to the presence of numerous introduced drought-intolerant species. In the driest cities, differences between urban and natural areas were particularly marked; for example, in Los Angeles interstitial sites, all observed species were native and none were associated with low drought tolerance or high water use. In all of the cities included in our study, greater numbers of species that were more drought-tolerant occurred in residential yards than in both interstitial and reference sites. This suggests that human management, via the planting of multiple drought-tolerant species, might improve urban forest adaptability to a changing climate.

However, the effects of urbanization on tree physiological responses in hot and dry environments are neither linear nor easily predictable from trends observed in natural environments (Pataki *et al.* 2011). For example, California sycamore (*Platanus racemosa*), a species that naturally grows along rivers and canyons in southern California, is also a popular urban tree in the region because of its perceived low water consumption. Yet an in situ empirical study of transpiration rates in multiple southern California trees in natural and urban environments revealed that California sycamores actually consume extremely high amounts of water in urban settings (~100 kg of water per tree per day, on average), as much as an order of magnitude greater than many non-native species (Pataki *et al.* 2011). Another California-based study, this one based at the Los Angeles Arboretum, observed higher transpiration rates in arid horticultural plants native to the region as compared to non-native plants from temperate environments (Goedhart and Pataki 2012). Therefore, it is possible that some species included in our study have different physiological responses depending on land-use type, although this was beyond the scope of our study. Overall, factors such as high species diversity (Avolio *et al.* 2015), a large proportion of drought-sensitive non-native species, and water-use patterns (eg irrigation) make the climate adaptation capacity of urban forests in dry cities highly uncertain.

Conclusion

Our analysis suggests that species composition, the relative proportions of native and introduced species, and the distribution of drought-tolerant and water-conserving species largely depend on where (ie the land-use type) one looks within and between cities. Our detailed sampling of natural areas (reference sites), relatively unmanaged areas (interstitial sites), and residential yards revealed that, while urban tree communities are dominated by native species across diverse climate zones of the US, residential yards contain dramatically higher numbers of species and a higher proportion of introduced species. The divergence between relatively natural and human-managed areas is most apparent in arid climates, where human preferences for introduced species have likely increased vulnerability to reductions in natural or anthropogenic water supplies. In cooler and wetter cities, it is likely that introduced species are not only displacing native biota and hence negatively impacting their associated ecosystem services but also increasing the resilience of ecosystem services derived from general greening.

A more systematic and detailed characterization of urban forests will be required to account for the differences that we observed between sample locations (reference sites, interstitial sites, and residential yards) (McHale *et al.* 2017; Pregitzer *et al.* 2019; Song *et al.* 2020). As urban areas continue to

expand globally, such a characterization of urban forests is important not only to improve the understanding of species capacities to adapt to climate change but also to preserve native vegetation in cities (Aronson *et al.* 2014). Given the myriad factors (eg land-use types and human preferences) that create diverse patterns of tree species distributions across urban environments (Cadenasso *et al.* 2007), there is a need to consider assessments that capture the heterogeneity of urban forests to make relevant and useful comparisons within and across cities (Davies *et al.* 2013; Raciti *et al.* 2012). Human preferences are interwoven into the biophysical fabric of urban forests. Thus, future management of urban forests must include adopting strategies for sustaining urban forests in a changing climate and meeting other essential ecosystem services, such as ensuring equitable access to public urban forests and designing residential yards to simultaneously reflect yard manager values and characteristics that contribute to environmental resiliency and equity (Gerrish and Watkins 2018; Watkins and Gerrish 2018; Locke *et al.* 2021; McDonald *et al.* 2021).

Acknowledgements

This research was supported by the Macrosystems Biology program of the Biological Sciences Directorate at the US National Science Foundation (NSF) through collaborative awards DEB-1638648 (Baltimore), DEB-1638606 (Los Angeles), DEB-1638560 (Boston), DEB-1638725 (Phoenix), DEB-1638657 (Miami), DEB-1638519 (Minneapolis-St Paul), DEB-1638690, DEB-1836034, and DEB-1638676. The authors are appreciative of all the field coordinators and assistants who helped collect the data that made this project possible. In Baltimore, the authors thank L Templeton for coordinating the field campaign and data management; B Glass-Seigel, D Dillon, J Botero, K Ralston, and A Wellman Houde for S Nelson, S Ruiz for fieldwork; and Baltimore City, Baltimore County, and the State of Maryland for providing permission to work in natural areas and interstitial sites. In Boston, the authors thank the Massachusetts Department of Conservation and Recreation and Mass Audubon for permission to work in natural and interstitial sites. In Los Angeles, the authors thank University of California, Los Angeles/La Kretz Center for California Conservation Science; National Park Service; Los Angeles City Department of Recreation and Parks; the Audubon Center; Mountains Recreation and Conservation Authority; and Palos Verdes Peninsula Conservancy for providing permission to work in natural and interstitial sites. In Miami, the authors thank M Zapata, S Nelson, and S Ruiz for fieldwork and Miami-Dade County Parks, Florida State Parks, and the Pine Ridge Sanctuary for providing permission to work in natural areas and interstitial sites. In Minneapolis-St Paul, the authors thank C Buyarski for coordinating fieldwork and data management, and the Minnesota Department of Natural Resources, The Nature Conservancy, Three Rivers Park District, the cities of Brooklyn Park, Eden Prairie, Arden Hills, and Ramsey County Parks and Recreation for providing permission to work in interstitial and natural sites. In Phoenix, the authors thank L Steger for coordinating the field campaign and data management; A Flores, J Talarico, and B Strobel for fieldwork; and Maricopa County Parks and Recreation Department, City of Scottsdale, and City of Phoenix for providing permission to work in natural and interstitial sites. The findings and conclusions in this paper are those of the author(s) and should not be construed to represent any official USDA or US Government determination or policy.

Data Availability Statement

Data are already published and publicly available, with those publications cited herein. All plant presence/absence data are stored at the Environmental Data Initiative portal (package ID edi.309.1), which can be accessed via the following link (https://portal.edirepository.org/nis/mapbrowse?packageid=edi.309.1) or DOI (doi.org/10.6073/pasta/8b29dc7fd536f4649f8cf6a536421fc9).

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Supporting Information

Additional material can be found online at http://onlinelibrary.wiley.com/doi/10.1002/fee.2777/suppinfo