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How do urban trees vary across the USA: It depends on where and how you look

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Abstract:	Urban forests provide ecosystem services important for climate regulation, wildlife, and human well-being. However, they vary in composition and physiological traits due to their unique biophysical and social contexts. This variation complicates assessment of urban forests important to biodiversity conservation and climate adaptation. We conducted sampling of tree species composition and externally-sourced traits (i.e., drought tolerance and water use capacity), in residential yards, unmanaged areas, and natural reference ecosystems in six cities across the continental U.S to compare the characteristics of the 'urban forest'. Compared to natural and unmanaged forests, residential yards had markedly higher tree 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.

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Title: How do urban trees vary across the USA: It depends on where and how you look.

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Abstract

Urban forests provide ecosystem services important for climate regulation, wildlife, and human well-being. However, they vary in composition and physiological traits due to their unique biophysical and social contexts. This variation complicates assessment of urban forests important to biodiversity conservation and climate adaptation. We conducted sampling of tree species composition and externally-sourced traits (i.e., drought tolerance and water use capacity), in residential yards, unmanaged areas, and natural reference ecosystems in six cities across the continental U.S to compare the characteristics of the 'urban forest'. Compared to natural and unmanaged forests, residential yards had markedly higher tree 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.

Keywords: Urban forests, ecosystem services, tree species composition, physiological traits, climate adaptation, residential yards

Introduction

Urban forests are significant ecological features of the urban environment that provide many ecosystem services (e.g., climate regulation, wildlife habitat, and recreation). There is a wide variety of natural, managed and cultivated green spaces in cities containing trees; from street trees and other planted trees to large tracts of relict forests, and 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.

Many assessments of urban forests vary in scale and focus, making it difficult to compare across land-uses and cities. 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 exotic tree species in highly heterogeneous urban forests. For example, Pregitzer *et al*. (2019) compared assessments of urban forest within New York City and found that the type of sampling (coarse-scale vs. fine-scale), provided different results of native urban tree canopy (42.8% vs. 83.9%). Therefore, disparities among assessments of urban trees leads to different conclusions about urban forests and the services they provide (McHale *et al*. 2017; Pregitzer *et al*. 2019). Fine-scale sampling (e.g., patch level) vs. coarse-scale (e.g., landscape 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. Here, human preferences for particular species act as an environmental filter (Pearse *et al*. 2018). Human

choices are a key driver of the introduction, transportation, and cultivation of species, some of which may become invasive, with the potential to spread at continental (Padullés Cubino *et al*. 2019a), and global scales (Aronson *et al*. 2014; Avolio *et al*. 2021). Human preferences and management have also been shown to 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 each other 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 (e.g., droughts).

In this study, we conducted a comparative analysis of urban forest (trees and shrub) species composition within three different land uses (natural reference areas, interstitial sites, residential yards) across six different cities located in different climatic regimes in the continental US. We also analyzed drought tolerance and water use capacity information for every species from external databases to compare physiological traits important to climate adaptation between land-use type. Our goal was to identify the composition of the 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 U.S? 2) How do tree species vary among different areas of the cities? 3) What are the implications of urban trees for native biodiversity and climate adaptation capacity in different components of urban forests across the U.S.?

Methods

Our analysis encompassed six major U.S. Metropolitan Statistical Areas (cities): Boston, MA (BOS), Baltimore, MD (BAL), Los Angeles, CA (LAX), Miami, FL (MIA), Minneapolis-St. Paul, MN (MSP) and Phoenix, AZ (PHX) that represent six different ecological biomes and/or major climatic regions across the U.S. (Trammell *et al*. 2016).

For each city, we focused on three distinctive land-use types: natural areas (reference), relatively unmanaged areas (interstitial), and residential sites. We selected four to six reference sites representative of the natural ecological biomes where 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; pine flatwoods (MIA), oak savannah; tallgrass prairie; bluff prairie; maple-basswood forest (MSP), and Sonoran Desert (PHX).We selected four to six interstitial sites on public lands within the cities that represented relatively unmanaged systems with vegetation that had developed spontaneously. Due to their proximity to managed areas, these sites were more likely to have species that may have dispersed from residential areas than the reference 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 Padullés Cubino *et al*. (2020).

Within reference and interstitial sites, eight, 8-m radius plots 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 the plant presence/absence data is stored at the Environmental Data Initiative (EDI) portal, and can be found by searching the reference number edi.309.1, or by the following https://doi.org/10.6073/pasta/8b29dc7fd536f4649f8cf6a536421fc9. Each plant species was classified as native or introduced using the USDA PLANTS (https://plants.usda.gov) and the Encyclopedia of Life (http://www.eol.org) databases. According to the USDA PLANTS database, native species are those which are naturally occurring within a state (in the U.S.), while introduced species are classified 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." Two ordinal traits important to climate adaptation were recorded for species available in USDA PLANTS: drought tolerance (none, low, medium, high), and water use capacity (low, medium, high), and only one categorical value is possible for each species. Drought tolerance is based on relative tolerance of the plant to drought conditions relative to other species with similar growth habits, while water use capacity is based on a species' physiological ability to acquire water from the soil relative to other species in the same (or similar) soil moisture availability in the region (USDA, 2023).

All data analysis was conducted in R Version 2022.12.0+353 (R Core). Differences in number of trees/shrubs (cacti in Phoenix) species (i.e., species richness), drought tolerance, and water use capacity among land-use type 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 and reference sites and residential yards (WebFigure 1).

Results

Residential yards contained significantly higher numbers of species than reference and interstitial sites (Fig.1a; $x^2 = 11.62$, $p < 0.001$) across cities. The percentage of native species (Fig. 1b) was the lowest in residential yards in all cities. The highest percentage of native species was observed in the reference and interstitial sites in the driest cities (Los Angeles and Phoenix; Fig. 1b; $x^2 = 9.12$, $p = 0.01$).

The driest cities (Los Angeles and Phoenix) had significantly ($x^2 = 14.94$, $p < 0.001$) higher percentages of species with high drought tolerance in reference and interstitial sites than the more humid cities (Fig. 2). Species with high drought tolerance were less common in the residential yards in these dry cities, for example, all tree species found in the natural and interstitial sites in Phoenix were native and had high drought tolerance. Similarly, in Los Angeles and Miami the percent of species with high drought tolerance was higher in natural and interstitial sites compared to residential yards. In Minneapolis-St. Paul, the percent of species with high drought tolerance was higher in natural sites than in residential yards.

The percent of species with a high water use capacity was lower across cities and land-use type, than species with lower water use capacity, but these species were particularly rare in the driest cities (Fig. 3). Differences between land use were statistically significant, ($x^2 = 19.61$, $p < 0.001$). Species with high drought tolerance and low water use capacity were common in cities with hot climates (Los Angeles, Miami, and Phoenix) within reference sites. Most species identified across cities had medium water use capacity.

Discussion

Urban forests are part of the heterogeneous urban ecosystem, which makes them diverse in composition. Our dominant finding is that residential yards support dramatically larger numbers of woody species (150) than natural reference (29) or interstitial (30) areas across the

U.S. A major question is if this increase in species numbers creates resilience or vulnerability to 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 native reference, interstitial, and residential yard sites suggest that different sampling strategies for characterizing urban forests that include different land use types to different degrees may produce different 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 (Padullés Cubino *et al*. 2019b, Pearse et al. 2018), have shown that human preferences and management of vegetation play a strong role 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 in other cities found that biotic homogenization plays a strong role at subcontinental scales (Jenerette *et al*. 2016; McHale *et al.* 2017). Here, our focus is on the comparison of tree species in residential yards versus interstitial areas (areas with intact soil profiles where vegetation develops spontaneously) and native reference areas, 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.

Given human preference for certain species traits common to introduced species, such as showy flowers (Avolio et al. 2015; Pataki et al. 2013), there is great uncertainty about the effect of these preferences on the ability of urban ecosystems to support native biodiversity (e.g., plants and wildlife; Aronson *et al*. 2014; Narango *et al*. 2017) and to be resilient to environmental change (e.g., species adaptation to disturbances), posing a challenge in urban conservation (Gaetner *et al*. 2017).

Here, we found that the effect of human preferences on increased the numbers of introduced woody species is most obvious in residential yards, and in warmer climates such as Los Angeles, Miami and Phoenix. For example, in Baltimore, Boston, and Minneapolis-St. Paul, approximately 50% of tree species in residential yards were native, while less than 25% were native in Los Angeles, Miami and Phoenix. Our results build on those presented by Padullés Cubino *et al*. (2019a) from the same residential yards studied here, which found that introduced species (including woody and herbaceous species) were ubiquitous in Los Angeles and Phoenix residential yards. In these warm 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, e.g., watering restrictions that may accompany drought or real estate disruptions (Ripplinger *et al*. 2017).

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

In contrast to Los Angeles and Phoenix, Miami had the highest percentage of introduced species in interstitial areas. These results suggest that hot and wet cities may be most vulnerable to declines in ecosystem services associated with native biodiversity (e.g., plants and wildlife) in

the face of increases in urbanization and other components of environmental change. For example, decreasing native biodiversity and similarities in species composition in cities can also cause cascading effects on wildlife that depend on a diverse native urban forest (Aronson *et al*. 2014; Narango *et al*. 2017). On the other hand, these cities may have increased resilience of services provided by general greening (shading, carbon sequestration, latent heat flux) regardless of continental origin as many introduced species have been able to spontaneously colonize and grow in these cities. Introduced species were also a significant component of natural 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 at the same time increasing the resilience of 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 shown by the differences between unmanaged and human-managed spaces in our study. There is particular concern about how the continued and projected rise in temperatures in the coming years will impact urban forests (Esperon-Rodriguez *et al*. 2022), which are already exposed to increased temperatures through 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 study showed that physiological traits, such as drought tolerance and water use capacity are useful metrics understanding climate adaptability, which have shown to predict 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 suggest that human management (e.g., selection of certain species and irrigation) might reduce urban forest adaptability to a changing climate with implications for their resilience and ecosystem services. The percent of species with high or medium drought tolerance was lower in residential yards and interstitial areas than in reference areas in most cities, due to numerous introduced species that were not drought tolerant. In the driest cities, differences between urban and natural areas were particularly marked, such as in Los Angeles interstitial sites, where none of the species were introduced or had low drought tolerance or high water use. On the one hand, in all studied cities, the number of species with high drought tolerance was higher in residential yards compared to interstitial and natural areas. This suggests that human management, via the introduction of multiple drought-tolerant species, might increase urban forest adaptability to a changing climate.

However, the effects of urbanization in hot and dry environments on tree physiological responses are neither linear nor easily predictable from trends observed in natural environments (Pataki *et al*. 2011). For example, California sycamore (*Platanus racemosa*), a tree 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. However, an *in-situ* empirical study of transpiration of multiple southern California trees in natural and urban environments revealed that California sycamores tend to use extremely high amounts of water in urban settings (~100 kg tree-1 day-1 on average), which were up to an order of magnitude larger than many non-native species (Pataki *et al*. 2011). Another study, based in Los Angeles Arboretum, observed higher transpiration rates in arid horticultural plants native to the region, compared to non-native

284 plants from temperate environments (Goedhart and Pataki 2012). Therefore, it possible that some
285 species in our study have different physiological responses based on land-use, but this was
286 beyond the scope of our study. Overall, high species diversity (Avolio *et al*. 2015), large percent
287 of drought-sensitive non-native species, and water use patterns (e.g., irrigation) make the
288 adaptability of urban forests in dry cities to changing climate highly uncertain.
289
290 **Conclusion**

291 Our analysis suggests that the species composition, proportions of native to introduced
292 species, and the distribution of drought-tolerant and water-conserving species largely depends on
293 where (i.e., the land-use type) you look within and between cities. Our detailed sampling of
294 natural (reference) and interstitial areas show domination of urban tree communities by native
295 species across diverse climate zones of the U.S. However, surveys of residential yards show
296 dramatically higher numbers of species, and a higher proportion of introduced species. The
297 divergence between relatively natural and human-managed areas is most dramatic in arid
298 climates, where human preferences for introduced species have likely increased vulnerability to
299 reductions in natural or anthropogenic water supply. In cooler and wetter cities, the presence on
300 introduced species is likely decreasing ecosystem services that derive from native biodiversity
301 but may be increasing the resilience of services deriving from general greenness.

302 The clear differences that we observed between sampling in residential yards, natural
303 reference, and interstitial sites suggests that there is a clear need for more systematic approaches
304 to characterization of urban forests that account for these differences (McHale *et al*. 2017;
305 Pregitzer *et al*. 2019; Song *et al*. 2019). As global expansion of urban areas increases, systematic
306 and detailed characterization of urban forests is important to understanding climate adaptability
307 of species and native vegetation preservation in cities (Aronson *et al*. 2014). There is a need to

consider assessments that capture the heterogeneity of urban forests, given the myriad of factors (e.g., land-use and human preferences) that create diverse patterns of tree species distribution across the urban environment (Cadenasso *et al*. 2007), to make relevant and useful comparisons within and across cities (Davies *et al*. 2013; Raciti *et al*. 2021). 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 that benefit humans, such as 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).

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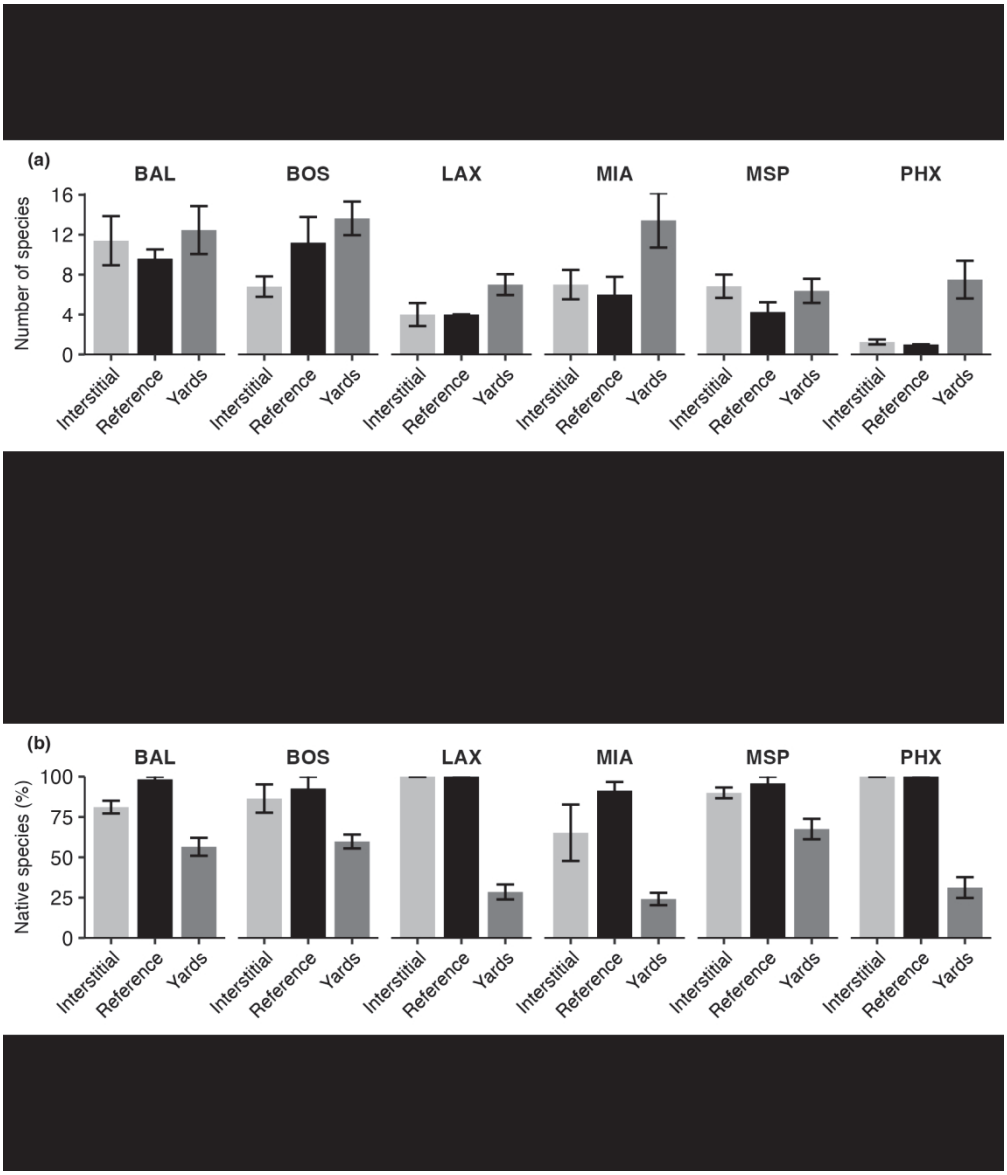
Figures Legend

Figure 1. Panels a) total number of tree species b) percent native species determined in interstitial areas, native reference sites, and residential yards, in cities (n = 6) across the continental U.S. BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St. Paul, PHX = Phoenix. Comparisons over all cities showed significant differences in the total number of species and percent of native species between yards and interstitial areas, and yards and reference areas ($p < 0.001$, $p = 0.01$, respectively).

Figure 2. Percent of total species in different drought tolerance classes found in interstitial areas, native reference sites, and residential yards in cities (n = 6) across the continental U.S. BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St. Paul, PHX = Phoenix. Comparisons over all cities showed significant differences in species drought tolerance between yards and interstitial areas, and yards and reference areas ($p < 0.001$).

Figure 3. Percent of total species in different water use capacity classes for tree species determined in interstitial areas, native reference sites, and residential yards in cities (n = 6) across the continental U.S. BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St. Paul, PHX = Phoenix. Comparisons over all cities showed significant differences in species water use capacity between yards and interstitial areas, and yards and reference areas ($p < 0.001$).



Panels a) total number of tree species b) percent native species determined in interstitial areas, native reference sites, and residential yards, in cities (n = 6) across the continental U.S. BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St. Paul, PHX = Phoenix. Comparisons over all cities showed significant differences in the total number of species and percent of native species between yards and interstitial areas, and yards and reference areas ($p < 0.001$, $p = 0.01$, respectively).

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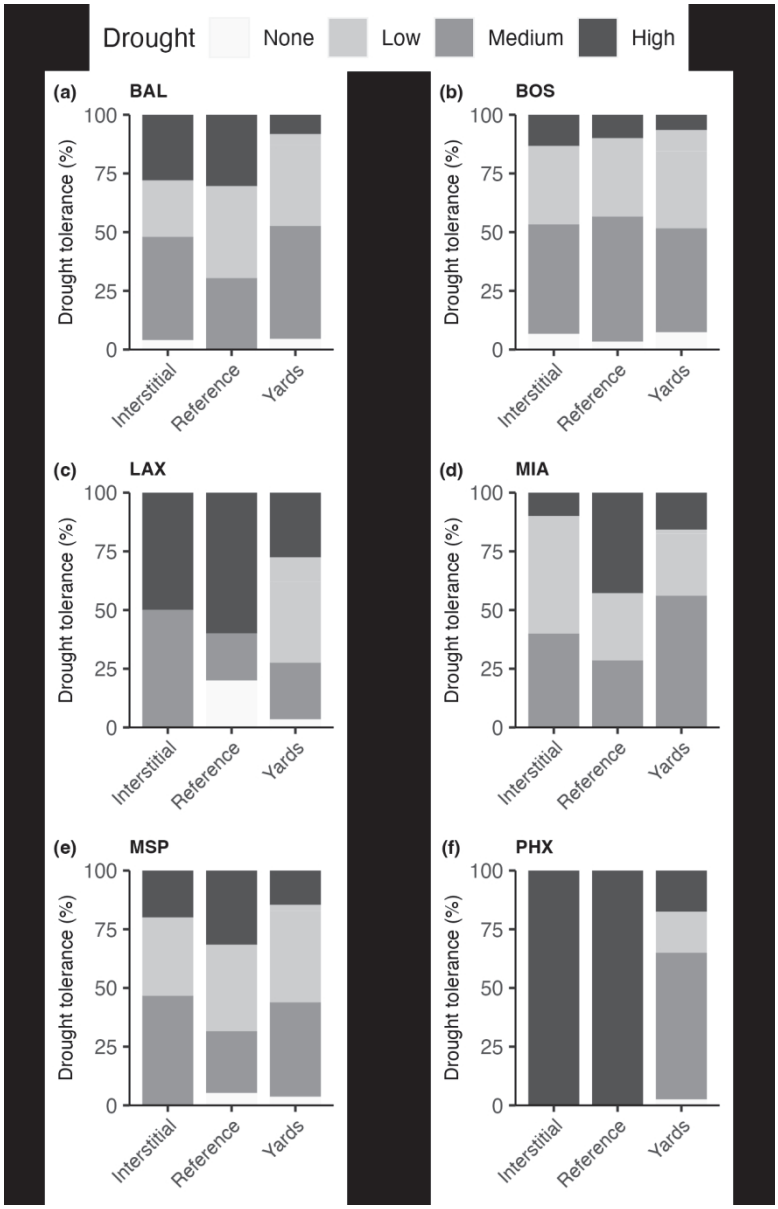
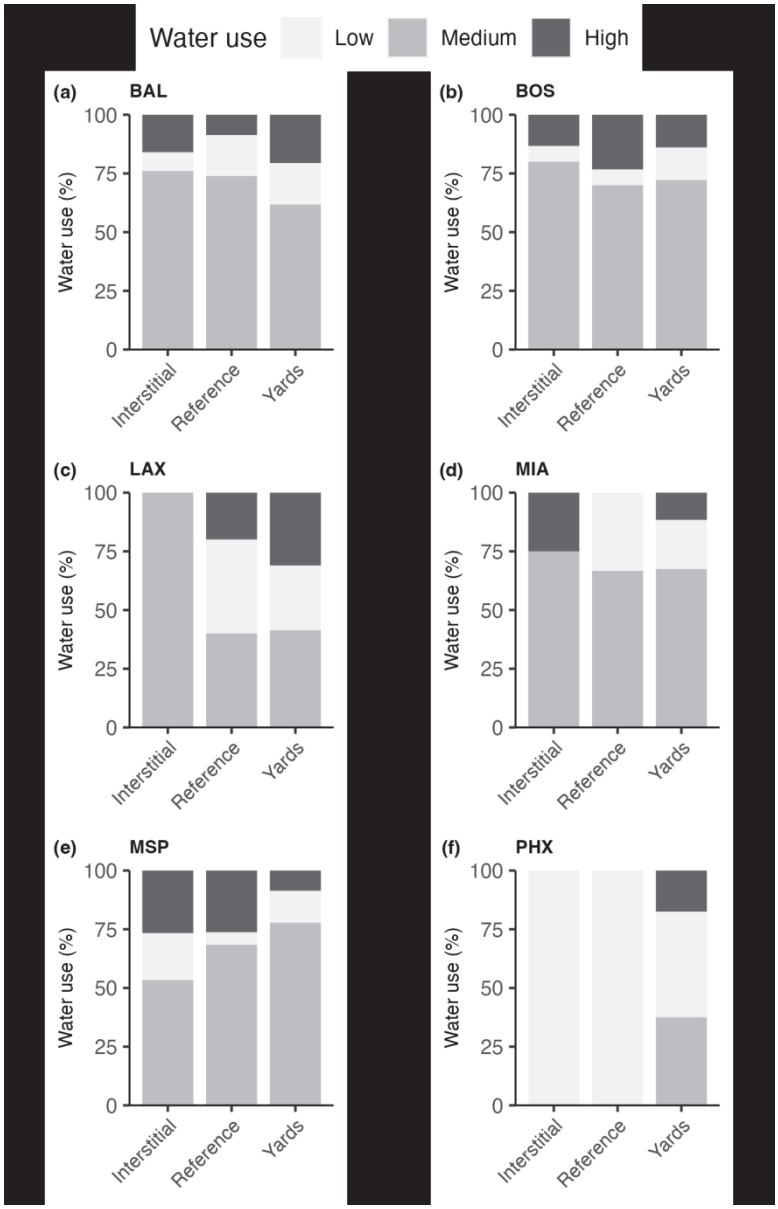


Percent of total species in different drought tolerance classes found in interstitial areas, native reference sites, and residential yards in cities (n = 6) across the continental U.S. BAL = Baltimore, BOS = Boston, LAX = Los Angeles, MIA = Miami, MSP = Minneapolis-St. Paul, PHX = Phoenix. Comparisons over all cities showed significant differences in species drought tolerance between yards and interstitial areas, and yards and reference areas ($p < 0.001$).

114x177mm (300 x 300 DPI)



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Mejía *et al.* – Supporting Information

WebFigure 1. Species diversity interstitial, reference, and yards calculated using rarefraction analysis showing sampling distribution in relation to species.